Moose and Predator Numerical Responses

to Anthropogenic Features in the Alberta Oil Sands Region

A Final Report to the Petroleum Technology Alliance of Canada

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Contents

EXECUTIVE SUMMARY

Landscape disturbance is typically synonymous with habitat loss and fragmentation, and subsequent biodiversity loss. However, the effects of landscape disturbance vary among species and disturbance types; multiple disturbances also act synergistically, resulting in cumulative effects of different resource sectors on species. In Canada's oil sands, petroleum extraction interacts with logging and road-building to create an extensively disturbed landscape. This anthropogenic disturbance is implicated in woodland caribou declines, mediated by predators and apparent competitors; however, the specific responses of different species to the changing landscape are poorly known. We investigated the numerical response of moose, wolves, bears, and other species, to natural and anthropogenic features within Alberta's northeast boreal forest. We used three years of camera data collected using a systematic stratified design in *ca.* 3000 km^2 study area near Winefred and Christina Lakes, Alberta. We modelled the number of months of species occurrence as an index of abundance, against natural and anthropogenic features using an information-theoretic approach. For every species, anthropogenic features were a key component of the best-supported model, indicating their importance in shaping species distribution. Some species were positively, and others negatively, associated with landscape disturbance, and anthropogenic and natural features had similar effect sizes on species abundance. Increasing landscape fragmentation and permeability are likely changing wildlife community dynamics in the oil sands, favoring generalist predators and browsers, and possibly altering ecosystem processes. A reclamation program that targets only seismic lines but ignores the effects of forest harvesting, road infrastructure, and other petroleum extraction features is unlikely to be effective at mediating those mechanisms of woodland caribou declines that involve moose, deer, and predators. We therefore recommend a more integrated approach to mitigating the impacts of anthropogenic disturbance on wildlife in Alberta's oil sands.

INTRODUCTION

Boreal woodland caribou (*Rangifer tarandus*) populations are declining across Canada. Consequently, the Government of Canada listed boreal woodland caribou as 'Threatened' under the Species at Risk Act, requiring the provinces to develop range plans for conserving local boreal caribou herds. The proximate cause of caribou population decline is predation, and wolves (*Canis lupus*) are thought to be the primary predator of caribou in the oil sands region of northeast Alberta (McLoughlin et al. 2003, Latham et al. 2011b). However, through apparent competition (Holt 1977, Holt and Kotler

1987) other ungulates likely play a major role. Increasing white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) populations bolster wolf numbers, thus increasing predation rates on caribou (Latham et al. 2011c, Latham et al. 2013), with consequences for caribou persistence (DeCesare et al. 2009). Moreover, other predators such as black bears (*Ursus americanus*) may predate caribou neonates and thus play a large role in caribou persistence (Latham et al. 2011a).

These complex interspecific interactions occur against a backdrop of an equally complex landscape. The boreal forest is a highly heterogeneous patchwork of upland deciduous and lowland conifer, with wetlands, mixedwoods, and bogs interspersed. Overlaying the forest is a meshwork of extensive landscape disturbance – defined here as anthropogenic changes to the quantity, structure, and distribution of native vegetation communities. Landscape disturbance is typically synonymous with habitat loss and fragmentation, which have well-known impacts on biodiversity (Fahrig 1997, 2003). However, emerging research illustrates that landscape disturbance complexly affects species population size, distribution, and persistence, and that these effects vary among disturbance types and species (Tscharntke et al. 2012). Differential response to disturbance allows some species to increase (or invade) whereas others decrease, creating "winners and losers" in human-dominated ecosystems (McKinney and Lockwood 1999, O'Brien and Leichenko 2003).

Extensive landscape disturbance has contributed to collapsing ranges and altered trophic dynamics within North America's mammalian communities (Terborgh and Estes 2010). Modern distributions of many mammals reflect patterns of human land use in the US and southern Canada (Laliberte and Ripple 2004), and rates of industrial disturbance are expanding rapidly in Canada's northern boreal forests (Hansen et al. 2010). Anthropogenic activities leading to ecological disturbance are often economically important (Czech et al. 2000) and politically popular. Moreover, disturbance is usually attributable to multiple landscape development activities, creating cumulative effects on ecological processes and biotic communities (Spaling et al. 2000, Schneider et al. 2003). Reconciling conservation goals with the realities of lingering historical impacts and humanity's growing resource consumption is one of the most controversial topics in ecology today (Kareiva et al. 2011, Doak et al. 2014). Petroleum extraction is one of the prime catalysts of this debate (Parmesan and Yohe 2003, Kelly et al. 2009, Souther et al. 2014), and the oil sands region (OSR) in Alberta, Canada, sits at its epicenter.

In Alberta's boreal forest, oil and gas industry, timber harvesting, and increasing road density all contribute to expanding spatially extensive landscape disturbance (Spaling et al. 2000). Petroleum extraction in particular creates "profoundly novel" landscapes completely different from historical

systems (Pickell et al. 2015). These novel and cumulative disturbances have been implicated in woodland caribou (*Rangifer tarandus*) declines through a convolution of direct and indirect effects (Wasser et al. 2011, Boutin et al. 2012). Abundant linear features – seismic lines, pipelines, roads, and trails – facilitate wolf (*Canis lupus*) movement, increasing predation rates on caribou (Whittington et al. 2011, McKenzie et al. 2012). Moreover, wolf populations are apparently increasing in Alberta's boreal forest, due in part to expanding populations of white-tailed deer (*Odocoileus virginianus*) (Latham et al. 2011c), and perhaps beavers (*Castor canadensis*) (Latham et al. 2013). Moose (*Alces alces*) are also expected to increase in this landscape, where conversion of mature forest into early seral vegetation provide abundant ungulate forage (Fisher and Wilkinson 2005).

Whereas wildlife management in the OSR is primarily focused on woodland caribou, little is known about the effects of extensive landscape disturbance on other boreal mammals. We expect the shifting vegetation structure and spatial configuration of this industrializing landscape (Pickell et al. 2015) to have widespread effects across the entire mammalian community (Figure 1).
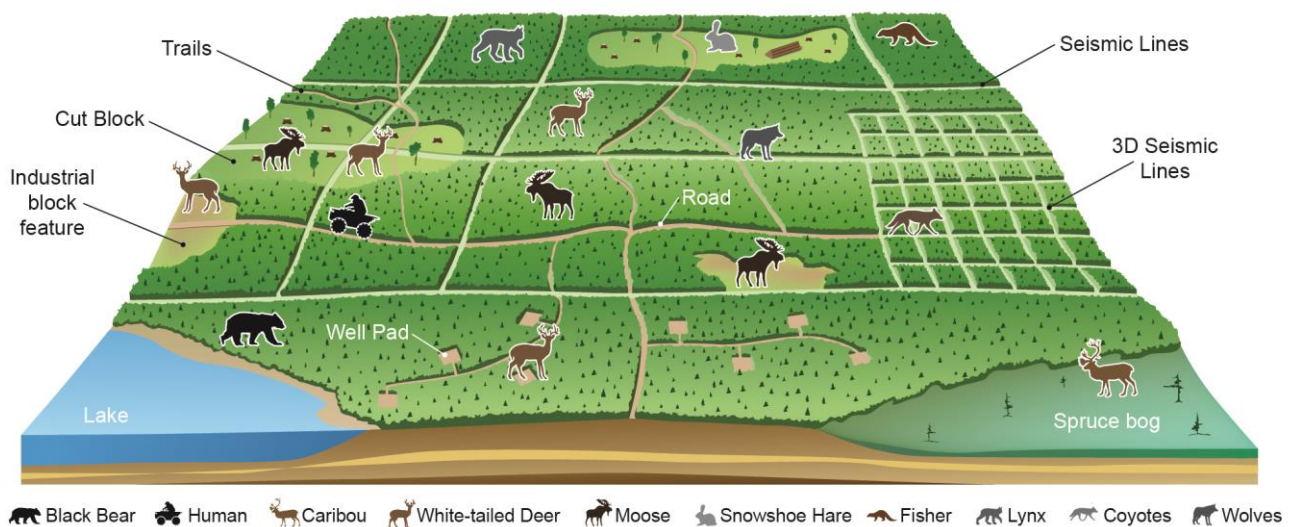
Figure 1. Anthropogenic features are expected to affect the suite of mammal species in the northeast boreal forest, based on known habitat associations. Large and small herbivores are known to benefit from early seral vegetation in cutblocks, and perhaps also in industrial block features and well sites. Predators are known to use linear features such as seismic lines for travel, but may avoid active road networks due to mortality risk. These hypothesized relationships overlay habitat associations with natural landscape features: upland and lowland forest, water, and bogs. Illustration by Jeff Dixon, based on research by Fisher and Wilkinson (2005) and Fisher et al. (2011).

We used camera trapping—a powerful, noninvasive survey method (O'Connell et al. 2011, Burton et al. 2015) —and species distribution models (Guisan and Thuiller 2005) to assess the influence of anthropogenic features on the distribution of species implicated in caribou declines in northeast Alberta boreal forest: black bear (*Ursus americanus*), wolf, white-tailed deer, and moose. However, we did not expect the effects of landscape development to be restricted to these species. A meta-analysis of past research showed that the introduction of early seral vegetation and removal of mature forest has effects on the entire mammal community of the boreal forest (Fisher and Wilkinson 2005). Recent research on Alberta's East Slopes showed that anthropogenic features can also affect mid-size carnivores (Heim 2015). We therefore also assessed the effects of anthropogenic landscape features on coyote (*Canis latrans*), Canada lynx (*Lynx canadensis*), fisher (*Pekania pennanti*), red fox (*Vulpes vulpes*), snowshoe hare (*Lepus americanus*), and red squirrels (*Tamiasciurus hudsonicus*). Our objectives were: (1) Determine the relative effects of natural and anthropogenic landscape features in explaining spatial variation in the relative abundance of mammal species in the northeast boreal forest around Winefred and Christina Lakes. (2) Identify which feature types have the greatest effect size on moose and predator relative abundance and distribution, to inform ongoing planning for feature reclamation or mitigation. We hypothesized that different natural and anthropogenic landscape features have consistent and predictable effects on moose and predator relative abundance and distribution.

METHODS

Study Area

Our research was conducted in the boreal forest northeast of Lac La Biche, Alberta, Canada (Figure 2). The study area is approximately 3000 km^2 and encompasses the area around Christina Lake and Winefred Lakes, north of the Cold Lake Air Weapons Range. This landscape is a boreal mosaic of white (*Picea glauca*) and black spruce (*Picea mariana*), aspen (*Populus tremulodies*), jack pine (*Pinus banksiana*), and *Ledum groenlandicum*-dominated muskeg. There is extensive forestry, roads (major and minor), petroleum extraction and other development dispersed throughout the study area (Figure 2).

Mammal Relative Abundance

We sampled mammal occurrence at sites deployed across a 3000 km^2 area in a stratified random design based on digital forest inventory data in a geographic information system (GIS). We deployed one Reconyx PC900 Hyperfire^{TM} infra-red remote digital camera (Holmen, WI, USA) at each of 61

sampling sites for three years: October 2011 - October 2014. Species were identified from 141,140 images. See Fisher et al. (2016) for more information.
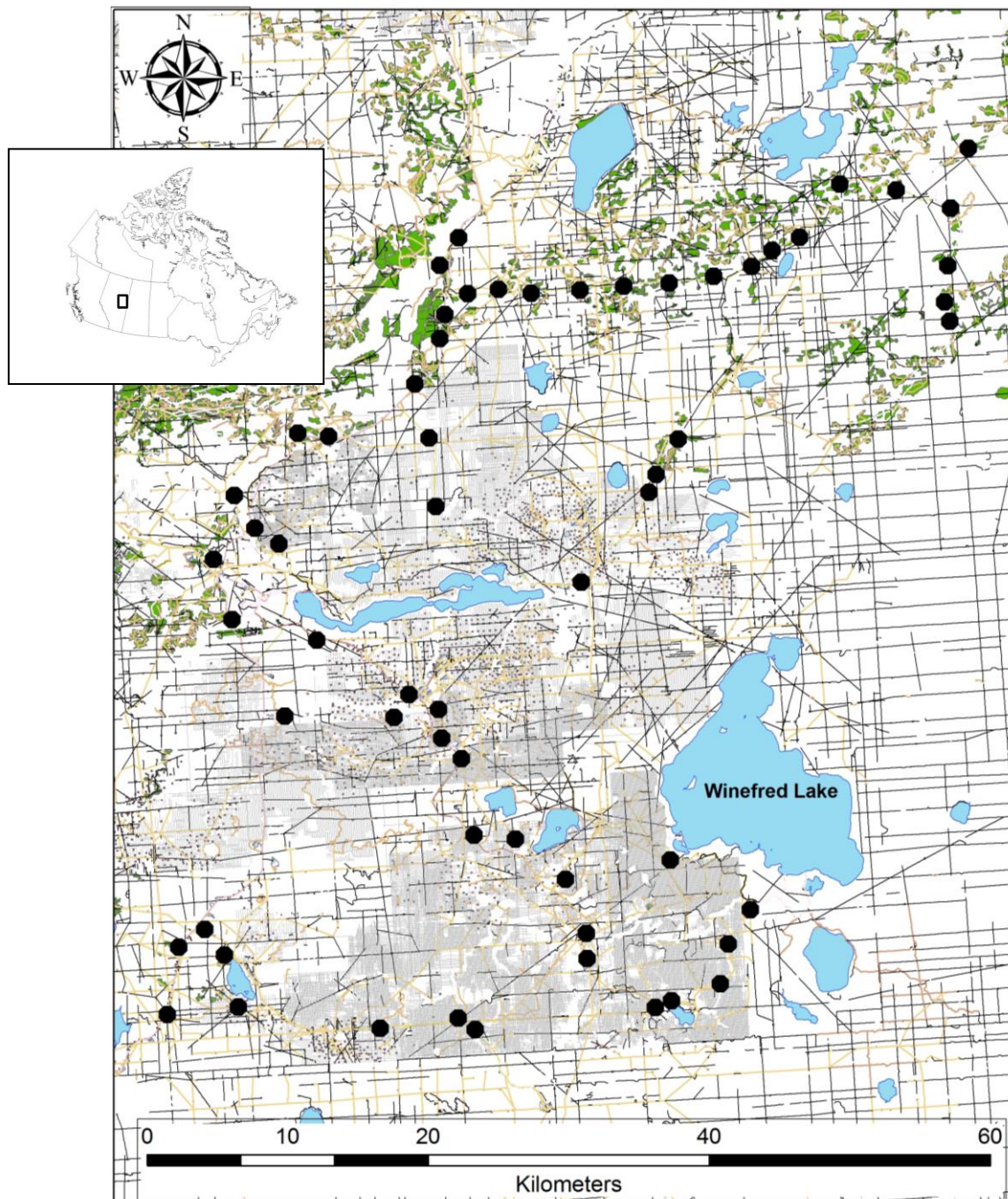
Figure 2. Mammal occurrence was surveyed October 2011 – 2014 in the northeast boreal forest near Winefred Lake, Alberta, Canada, at camera-trap sites (black dots). The landscape is superimposed by 3D seismic lines (grey), traditional seismic lines (black), well sites (red and orange), forest cutblocks (green), block features (grey dots) and roads and trails (light green).

Tracking numerical responses of mammals to natural and anthropogenic landscape features requires converting numbers of camera trap images into an index of abundance. There are multiple possible ways that this is done, most without any statistical basis (Burton et al. 2015). We could use raw numbers of images, but doing so introduces a design confound: a single animal can appear multiple times on a camera, inflating the abundance estimate. The most rigorous way is to estimate density using new methods applicable to camera trapping that account for imperfect detection, multiple re-sites, and varying sizes of home ranges (Chandler and Royle 2013, Sollmann et al. 2013). We are doing this for white-tailed deer (Fisher et al. 2015), but to do so for the suite of mammals in the boreal forest is computationally extensive and beyond the scope of this project. We opted for a very conservative measure of numerical response: the repeated occurrence of a species across a series of one-month survey periods. This measure assumes that a species is more likely to consistently use a site over subsequent months when the population size is such that the species persists at that site for an extended period of time. We therefore recorded the occurrence of each species at each site within month-long survey periods, yielding a response variable of 0-36 months for each species at each site, which we treated as relative abundance. As we are comparing one site to another, the absolute value of this metric does not matter; it is how this metric compares among sites that we are measuring.

Quantifying Landscape Structure

We quantified the landscape from three spatial digital resource inventories. First, we quantified natural landscape composition based on the Alberta Vegetation Inventory (AVI), a digital forest inventory dataset provided by Alberta Environment and Parks. We categorized tree species as coniferous [black spruce (Sb), jack pine (Pj), white spruce (Sw), and balsam fir (Fb)] or deciduous [paper birch (Bw), aspen (Aw), balsam poplar (Pb), and tamarack (Lt)]. We determined the area of each polygon within each grid cell represented by each canopy species, and multiplied that by the percentage of the canopy in that polygon. We designated each polygon as lowland if the moisture regime was designated aquatic or wet, or upland if not. For each polygon, the canopy cover designations and moisture regime information were combined to create thirteen land cover categories (Table 1). We calculated the percent area of each habitat category around each camera site.

Second, we used the Alberta Biodiversity Monitoring Institute (ABMI) 2010 Human Footprint Map Ver 1.1 (ambi.ca) to calculate the percent of area of several anthropogenic features (Table 1) around

each camera site. Third, as this map did not provide contemporary information about linear features, which is changing rapidly in this landscape, we used an ABMI & University of Alberta linear features layer updated to 2012 to calculate the area of linear features (buffered to create polygons from polylines) around each camera site.

Table 1. Landscape reclassification for camera-based species distribution model analyses. GIS data from multiple sources were reclassified and combined to create 20 different landscape feature categories. We calculated the percent area of each category around each camera site, to create 20 independent variables.

#	Habitat Class	Source[1]	Description[2]
1	Upland deciduous	AVI	(Aw, Pb, Bw >=70% canopy), moisture = d or m
2	Lowland deciduous	AVI	(Aw, Pb, Bw >=70% canopy), moisture = w or a
3	Upland mixedwood	AVI	(40% -60%) canopy, moisture = d or m
4	Lowland mixedwood	AVI	(40% -60%) canopy, moisture = w or a
5	Upland spruce	AVI	(Sb, Sw, Fb >=70% canopy), moisture = d or m
6	Lowland spruce	AVI	(Sb,Sw,Fb >=70% canopy), moisture = w or a
7	Pine[o]	AVI	All Pj (>=70%)
8	Tamarack	AVI	All Lt (>=70%)
9	Open wetland	AVI	<6% crown closure; moisture = w or a
10	Upland shrubs	AVI	>25% shrub cover; <6% tree cover; moisture = d or m
11	Water	AVI	Standing or flowing water
12	Cutblocks	ABMI	Forest harvested cutblocks of any age
13	Nonforest[o]	AVI	Areas with < 6% canopy
14	Block features	ABMI	Combination variable including mining borrow pits, dugouts, sumps, industrial sites, and sites categorized as "other disturbed vegetation". No mature trees; usually reclaimed or surrounded by grass or shrubs.
15	Well sites	ABMI	Petroleum extraction sites including a well and surrounding area, usually grassy vegetation
16	3D seismic lines	UALF	3D seismic petroleum exploration lines, deployed in a high-density hashmark pattern.
17	Cutlines	UALF	Traditional, single petroleum exploration lines, less dense than 3D seismic lines.
18	Roads	UALF	Combination variable of one and two lane roads, gravel and paved, and unimproved roads.
19	Pipelines	UALF	Petroleum pipelines and their rights of way, usually wide and grass-covered.
20	Trails	UALF	Combination of trails (navigable by off road vehicle, horses, and people) and truck trails (navigable by trucks but without gravel).

[1]AVI – Alberta Vegetation Index; UALF = University of Alberta Linear Features Map Updated 2012; ABMI = Alberta Biodiversity Monitoring Institute Human Footprint Map Updated 2010.
[2]Aw = aspen, Pb = poplar, Bw = white birch, Sb = black spruce Sw = white spruce, Fb = balsam fir, Pj = jack pine, Lt = tamarack/larch; d = dry, m = mesic, w = wet, a = aquatic
[3]Linear features were buffered for areal calculations as follows: 'Two Lane Undivided Paved Road': 9m; 'One Lane Undivided Paved Road': 6m; 'Rail Line': 5.5m; 'Rail Line- spur': 5.5m; 'Two Lane Gravel Road': 7m; 'One Lane Gravel Road': 5m; 'Driveway': 2m; 'Unimproved Road': 6m; 'Trail': 6m; 'Truck Trail': 6m; 'Electrical Transmission Line': 17m; 'Pipeline': 12m; '3D': 2m; 'Cutline': 2m.
[o]Omitted from analysis to prevent collinearity with other variables.

We omitted correlated variables (r > 0.7) from multiple-variable models (Zuur et al. 2010) to prevent multicollinearity (Faraway 2004). We combined variables only sparsely represented in the data (< 1-2% of area) into a single, combination variable (Table 1). We rescaled each variable (subtract mean, divide by standard deviation) using the *scale* function in program R, to allow comparison of effect sizes.

The Spatial Scale of Analysis

The species distribution models we use assume that relative abundance is related to the landscape within some defined area around that site (Morrison et al. 2006). Defining the appropriate scale of this area is difficult, because different processes operate at different spatial scales (Fisher et al. 2011). The area affecting a species' occurrence at a camera site may be smaller than a home range, reflecting the influence of small-scale, local patch choices by individuals; or larger than a home-range, reflecting processes such as predation, or competition (Kotliar and Wiens 1990, Fisher et al. 2011). As we don't know the size of the landscape that might affect a species' occurrence – and getting the size wrong can lead to incorrect conclusions – a rigorous approach is to test several different landscape sizes and determine which best predicts that occurrence (Fisher et al. 2011). We quantified the landscape within buffers of different sizes, or *spatial scales* (Figure 3). These spatial scales ranged from a 250-m radius circle to a 5000-m radius circle, in 250-m increments, around each camera site. This yielded 20 different spatial scales we could compare to test which scale best explained species' relative abundance. At each scale, we modelled each species' relative abundance (0-36, over three years) against all landscape variables using generalized linear models (Binomial errors, logit link) in *R* ver. 3.2.2 (R Foundation for Statistical Computing 2014). A reliable predictive model is one that best explains the variance in response data (*e.g.* mammal relative abundance) by using the least number of independent variables possible (Burnham and Anderson 2002). We generated these models using the minimum adequate model approach (Crawley 2012), which starts with a global model containing all independent variables, sequentially drops least-significant variables, and tests them for explanatory power.

For each scale, we created a global generalized linear model (binomial errors, default link) in R that included additive effects for all non-correlated predictor variables. We reduced the global model with the step-AIC function in R package MASS (Ripley et al. 2011). This stepwise routine ranks models' explanatory power and simplicity based on Akaike's Information Criterion (AIC) scores (Burnham and Anderson 2002), which is a function of the number of variables in the model, and the log-likelihood of the model – a function of the amount of variance in species relative abundance that the model can

explain. A model with a low AIC score indicates that this model better explains species relative abundance than a model with a high AIC score. We normalised AIC scores of the best-fit 20 "scale models" as AIC weights (Anderson 2008); AIC weights of a set of models sum to 1.0, and are analogous to the probability that a model is the best one of the set. For example, if the best-fit model has an AIC weight of only 0.2, there is only a 20% chance that it is really best of the lot. If the best model has an AIC weight of 0.9, there is a 90% chance it is the really the best.
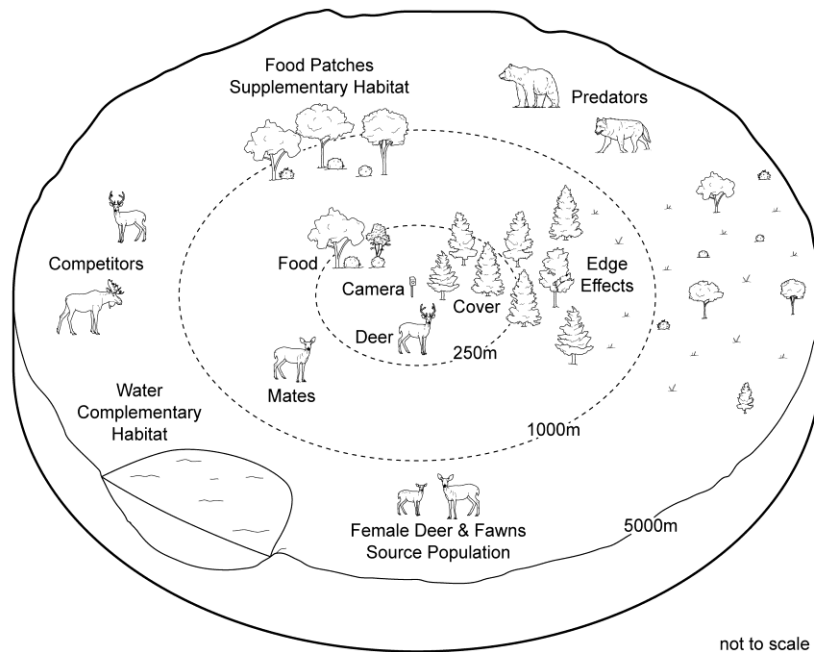
Figure 3. Different ecological processes occur at different spatial scales, each involving different landscape features. At small scales – the immediate area around a camera site – food and cover be important. At intermediate scales, the presence of potential mates or other conspecifics may be important. Patch edge effects may play a role, as well as complementary or supplementary food sources. At even larger scales, the presence of predators in the landscape, and a source population of conspecifics, may be important. As landscape variables proxy these different processes, the degree to which landscape variables explain deer occurrence is expected to change across scales. Illustration by Jeff Dixon, from Fisher et al. (2015).

Models at each scale were ranked against one another using the same approach, allowing us to identify (1) the best spatial scale for each species, and (2) the best-supported model for each species, containing those landscape variables that best explained relative abundance. We tested each best model

for overdispersion (Zuur et al. 2007, Zuur et al. 2010). We assessed the fit of the best supported models with 10-fold cross validation using the *boot* package in software R (Zhang 1993) and calculated the deviance explained by each model. We used the program ggplot2 in R software (Wickham 2009) to illustrate the relationships between a species and a landscape variable. We used univariate plots and Poisson regressions as approximations of the binomial multivariate regressions, to generate plots that are only approximations, but illustrate the range of observed data and the general relationship.

RESULTS

In our three-year survey we detected wolves (2508 images), black bears (2657), moose (500), white-tailed deer (112648), coyote (2290), lynx (1940), red fox (197), fisher (326), snowshoe hare (10652), and red squirrels (491). We also detected caribou (273), but due to the sparse data caribou models performed poorly, so we did not include them in these results.

Spatial Scale of Analysis

Each species was best predicted by landscape features measured at different spatial scales. As a side bar, we modelled this best-fit spatial scale against species' average body mass, as we expected body mass to predict habitat selection scale, as per Fisher et al. (2011). Interestingly, we did find a significant, quadratic relationship between body mass and habitat selection scale ($p_{\text{log mass}} = 0.04$; $p_{\text{logmass}^2} = 0.03$; residual deviance = 3.2, 7 D.O.F.) (Figure 4). We used variables measured at these best-fit scales for each species, to identify those variables that best predict relative abundance.

Numerical Responses of Species to Anthropogenic Features

The influence of anthropogenic disturbance was pervasive across the mammal community. Variables describing anthropogenic landscape features were retained in best-supported models for all ten species studied, though some relationships were positive, and others were negative (Figure 5). For example, relative abundances for 8 of 10 species were best explained by the percent of 3D seismic disturbance in the landscape surrounding camera sites – more than any other natural or anthropogenic landcover. Seven species were predicted by industrial block features, and trails; 6 species by well sites, and 5 species by cutlines, pipelines, and roads. The relationships between relative abundance and cutlines, pipelines, and well sites were mostly negative. Cutblocks affected the fewest species – 4 of our 10 mammals, and these relationships were mostly positive (i.e. relative abundances higher at sites with greater percentages of cutblock area in surrounding landscape).
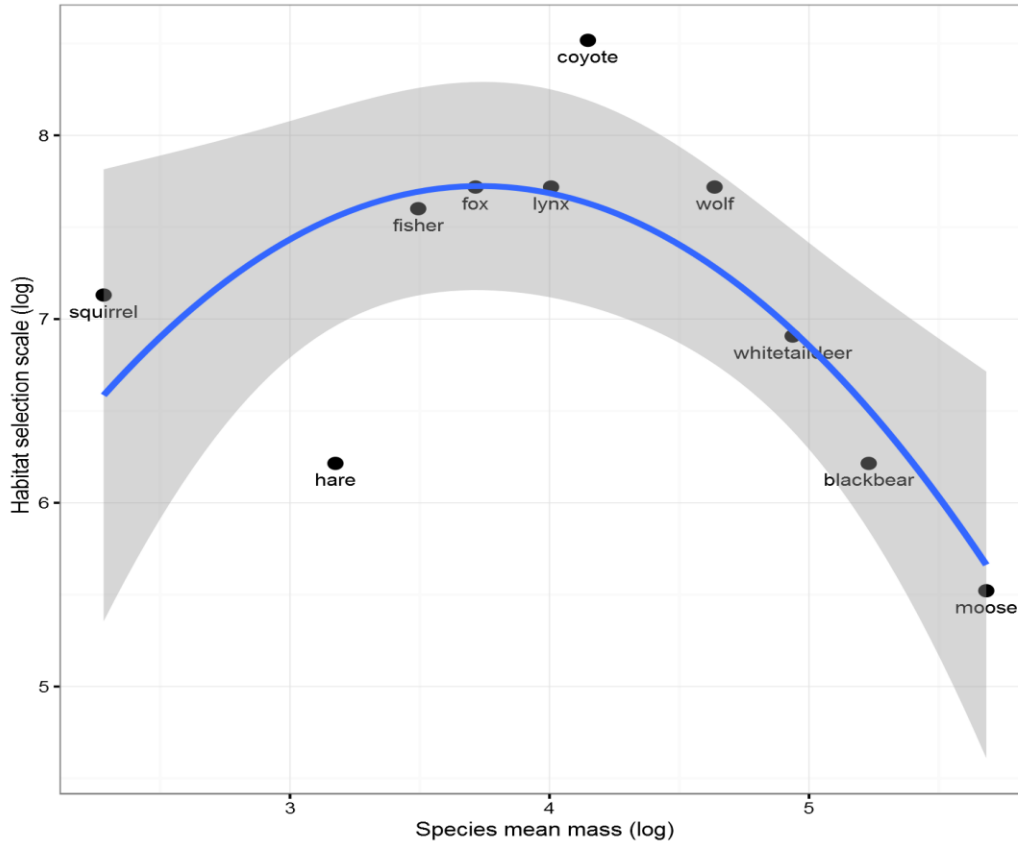
Figure 4. The spatial scale (radius around the camera site) at which landscape features best predicted mammal species' relative abundance varied with body mass in a quadratic log-log relationship.

In addition to the pervasiveness of anthropogenic features in the best-fit models, the mean effect sizes – conceptually, the strength of the relationship between abundance and a feature – of most anthropogenic variables were as great as the effect sizes of natural land cover variables (Figure 6). The proportion of area covered by block features (disturbed industrial sites) had the greatest positive effect on mammals' relative abundance; the next greatest was upland deciduous forest, which dominates the landscape. The percent of 3D seismic lines had the greatest negative effect on species, eclipsed only by lowland mixedwood, which appeared in one model (red fox). The percent of cutlines and well sites also had comparatively large negative effects on species' relative abundance.

Figure 6. Mean effect sizes (slope of the relationship between abundance and landscape) varied among natural and anthropogenic features. Some relationships were positive (green bars) and some were negative (red bars). Note the negative y axis has been truncated.

Species-specific Relationships: Moose

Moose relative abundance was strongly positively related to lowland and upland spruce forests, cutblocks, and 3D seismic lines (Table 2). Moose relative abundance markedly decreased in relation to cutlines (traditional seismic lines), well sites, trails, and pipelines. K-fold cross validation suggested prediction error was 2.5%. The model explained 49.38% of the deviance in moose relative abundance.

Table 2. Standardized parameter estimates from the best supported model of *moose relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-1.49	0.06	-24.11	< 2e-16
Lowland spruce	0.49	0.07	7.32	0.00
Upland spruce	0.24	0.05	4.41	0.00
Cutblocks	0.16	0.07	2.26	0.02
3D seismic lines	0.16	0.07	2.21	0.03
Upland mixedwood	0.14	0.09	1.64	0.10
Lowland mixedwood	0.14	0.07	1.96	0.05
Open wetland	0.12	0.06	1.96	0.05
Block features	0.11	0.06	1.70	0.09
Lowland deciduous	0.10	0.06	1.77	0.08
Pipelines	-0.14	0.08	-1.82	0.07
Trails	-0.15	0.07	-2.05	0.04
Well sites	-0.19	0.07	-2.66	0.01
Cutlines	-0.35	0.08	-4.36	0.00
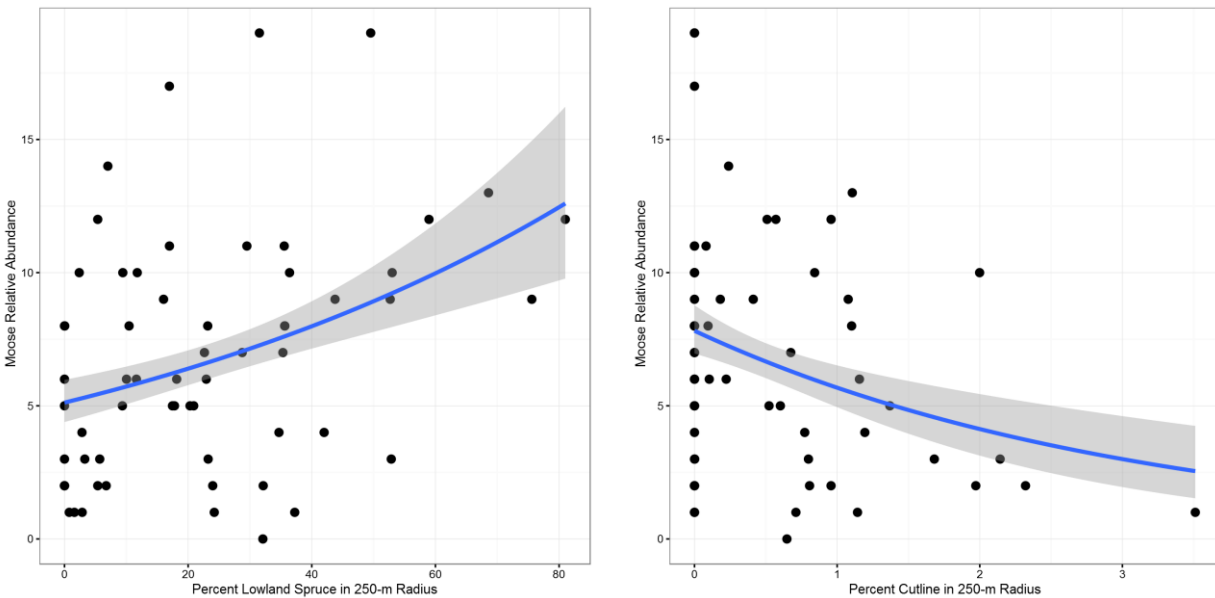
Figure 7. Relationships between moose relative abundance and lowland spruce (left) and cutlines (right), the landscape features with the strongest positive and negative effects on abundance, respectively. Black dots are observed data; the shaded area represents 95% confidence intervals.
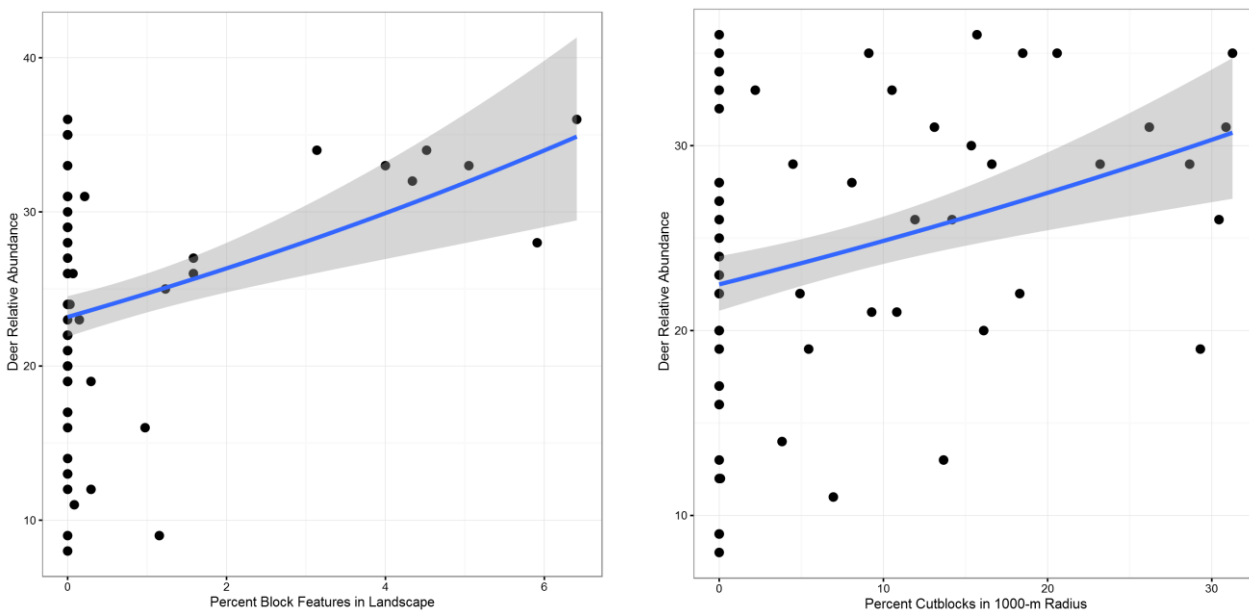
White-tailed Deer

White-tailed deer relative abundance was most strongly positively related to cutblocks, industrial block features, upland deciduous forest, and upland shrubs (Table 3). Deer relative abundance decreased in relation to trails, lowland deciduous, and cutlines (traditional seismic lines). K-fold cross validation suggested prediction error was 2.0%. The model explained 69.6% of the deviance in deer relative abundance.

Table 3. Parameter estimates from the best supported model of *white-tailed deer relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	1.25	0.06	19.53	< 2e-16
Cutblocks	0.78	0.10	7.87	0.00
Block features	0.67	0.09	7.19	0.00
Upland deciduous forest	0.64	0.08	8.47	< 2e-16
Upland shrubs	0.43	0.11	3.98	0.00
Well sites	0.37	0.07	5.39	0.00
Lowland spruce	0.32	0.07	4.63	0.00
Lowland mixedwood	0.22	0.06	3.56	0.00
Water	0.19	0.09	2.17	0.03
Upland mixedwood	0.15	0.06	2.55	0.01
Tamarack forest	0.09	0.06	1.52	0.13
Cutlines	-0.14	0.06	-2.26	0.02
Lowland deciduous	-0.17	0.07	-2.47	0.01
Trails	-0.43	0.08	-5.55	0.00

Figure 8. Relationships between white-tailed deer relative abundance and block features (left) and cutblocks (right), the landscape features with the strongest effects on abundance.

Black Bear

Black bear relative abundance was positively related to water bodies only (Table 4). Black bear relative abundance decreased most significantly in relation to 3D seismic lines and industrial block features. K-fold cross validation suggested prediction error was 1.5%. The model explained 34.5% of the deviance in black bear relative abundance.

Table 4. Parameter estimates from the best supported model of *black bear relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-1.18	0.07	-17.35	< 2e-16
Water	0.15	0.07	2.12	0.03
Upland shrubs	-0.11	0.07	-1.48	0.14
Roads	-0.11	0.08	-1.48	0.14
Lowland deciduous forest	-0.14	0.07	-2.04	0.04
Block features	-0.24	0.09	-2.62	0.01
3D Seismic lines	-0.44	0.08	-5.52	0.00
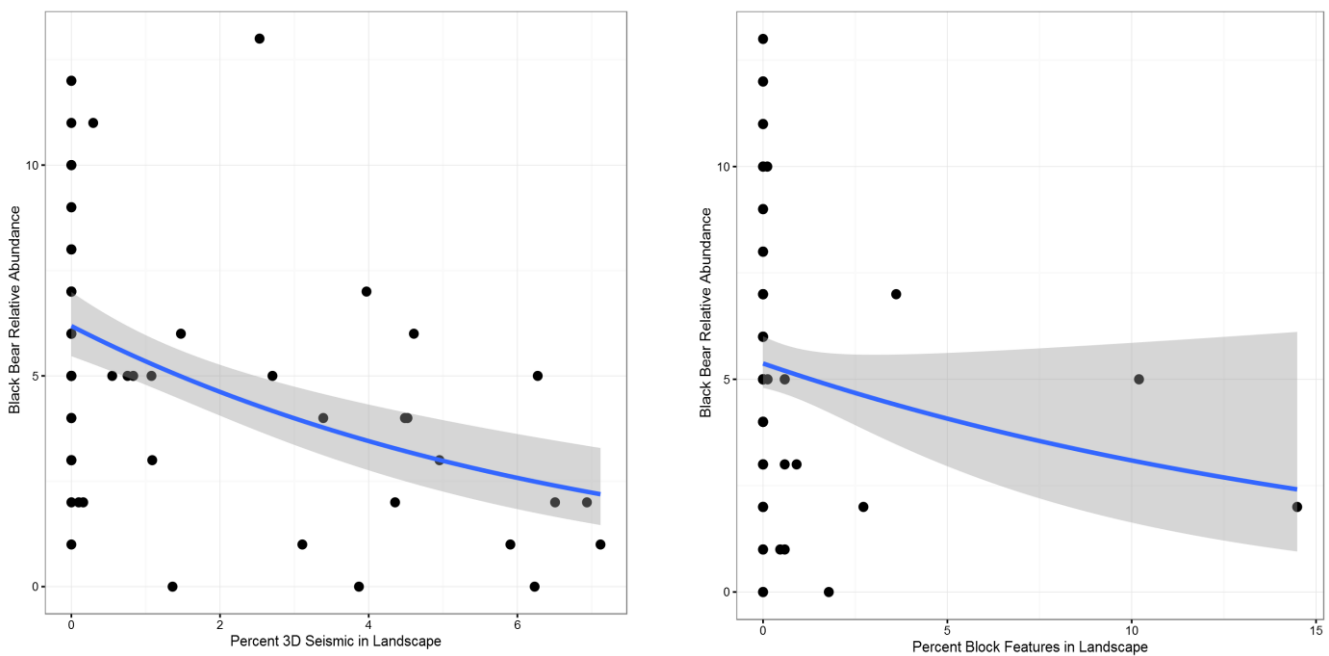
Figure 9. Relationships between black bear relative abundance and 3D seismic lines (left) and industrial block features (right), the landscape features with the strongest effects on abundance. Black dots are observed data; the shaded area represents 95% confidence intervals.

Wolf

Wolf relative abundance was most strongly positively related to industrial block features and trails (Table 5). Wolf relative abundance decreased in landscapes with extensive road networks. K-fold cross validation suggested prediction error was 0.6%. The model explained 52.9% of the deviance in wolf relative abundance.

Table 5. Parameter estimates from the best supported model of *wolf relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

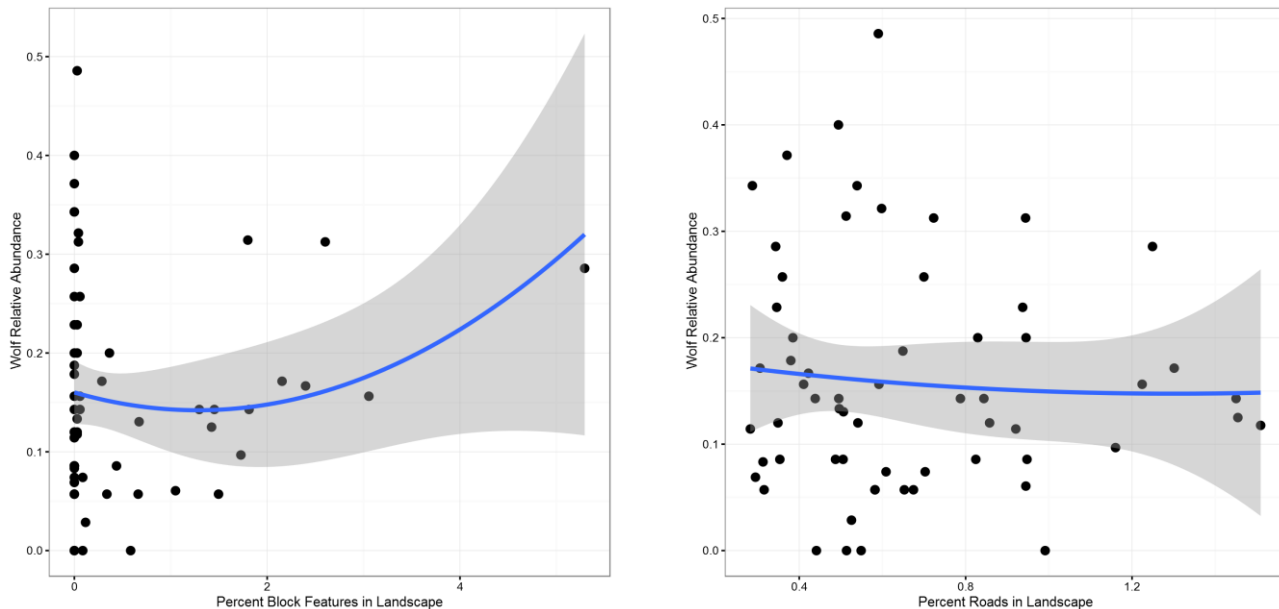| Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-1.75	0.07	-26.22	< 2e-16
Block features	0.36	0.08	4.63	0.00
Trails	0.35	0.08	4.30	0.00
Upland spruce	0.18	0.08	2.32	0.02
Upland deciduous	0.17	0.07	2.42	0.02
Water	0.14	0.07	2.00	0.05
Open wetland	0.12	0.07	1.71	0.09
Lowland deciduous	0.12	0.07	1.77	0.08
Roads	-0.26	0.09	-3.01	0.00

Figure 10. Relationships between wolf relative abundance, industrial block features (left), and roads (right) the landscape features with the strongest positive and negative effects on relative abundance. Black dots are observed data; the shaded area represents 95% confidence intervals.

Coyote

Coyote relative abundance was strongly and positively related to roads, 3D seismic lines, upland mixedwood, traditional seismic lines, and tamarack stands (Table 6). Coyote relative abundance decreased most markedly in relation to industrial block features, upland deciduous forest, and pipelines. K-fold cross validation suggested prediction error was 2.4%. The model explained 50.8% of the deviance in coyote relative abundance.

Table 6. Parameter estimates from the best supported model of *coyote relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-1.33	0.06	-22.87	< 2e-16
Roads	0.88	0.10	8.81	< 2e-16
3D Seismic lines	0.45	0.10	4.43	0.00
Upland mixedwood forest	0.42	0.08	5.26	0.00
Cutlines	0.32	0.09	3.50	0.00
Tamarack	0.32	0.08	4.04	0.00
Upland shrubs	0.16	0.09	1.77	0.08
Upland spruce	0.15	0.09	1.60	0.11
Water	-0.19	0.07	-2.52	0.01
Lowland mixedwood	-0.24	0.08	-3.18	0.00
Pipelines	-0.29	0.08	-3.40	0.00
Upland deciduous	-0.33	0.11	-2.88	0.00
Block features	-0.41	0.11	-3.75	0.00
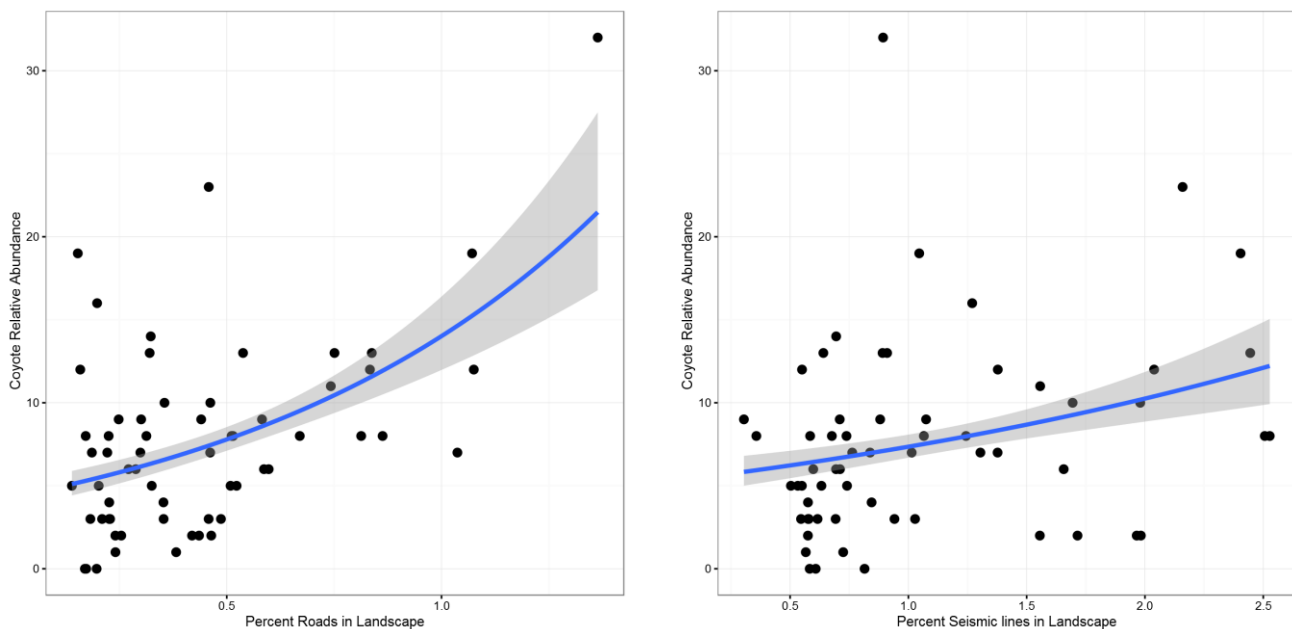
Figure 11. Relationships between coyote relative abundance, roads (left), and seismic lines (right) the landscape features with the strongest effects on relative abundance. Black dots are observed data; the shaded area represents 95% confidence intervals.

Lynx

Lynx relative abundance was strongly positively related to trails, lowland deciduous forest, 3D seismic lines, and cutblocks (Table 7). Lynx relative abundance decreased most markedly in relation to upland deciduous forest, open wetland, pipelines, upland spruce, and well sites. Prediction error (from K-fold cross validation) was 2.0%. The model explained 48.0% of the deviance in lynx relative abundance.

Table 7. Parameter estimates from the best supported model of *lynx relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-1.42	0.06	-23.40	< 2e-16
Trails	0.41	0.09	4.60	0.00
Lowland deciduous	0.35	0.07	4.97	0.00
3D Seismic lines	0.29	0.08	3.90	0.00
Cutblocks	0.28	0.10	2.84	0.00
Roads	0.18	0.07	2.63	0.01
Lowland mixedwood	0.14	0.07	2.17	0.03
Water	0.10	0.06	1.62	0.10
Upland mixedwood	-0.11	0.07	-1.66	0.10
Well sites	-0.21	0.08	-2.54	0.01
Upland spruce	-0.23	0.09	-2.69	0.01
Pipelines	-0.23	0.07	-3.25	0.00
Open wetland	-0.28	0.07	-3.75	0.00
Upland deciduous	-0.60	0.08	-7.83	0.00

Red Fox

Red fox relative abundance was strongly positively related to industrial black features, lowland spruce, and open wetland (Table 8). Red fox relative abundance decreased most markedly in relation to lowland mixedwood forest, 3D seismic lines, traditional seismic lines, upland shrubs, and well sites. Prediction error (from K-fold cross validation) was 0.26%. The model explained 79.6% of the deviance in red fox relative abundance.

Table 8. Parameter estimates from the best supported model of *red fox relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-9.03	1.34	-6.76	0.00
Block features	2.64	0.58	4.53	0.00
Lowland spruce	1.70	0.69	2.47	0.01
Open wetland	1.58	0.57	2.75	0.01
Tamarack	1.49	0.54	2.77	0.01
Upland deciduous forest	1.48	0.58	2.53	0.01
Upland spruce forest	1.30	0.48	2.71	0.01
Water	0.49	0.33	1.49	0.14
Wellsites	-0.98	0.35	-2.83	0.00
Upland shrubs	-1.12	0.89	-1.26	0.21
Cutlines	-1.28	0.47	-2.72	0.01
3D Seismic lines	-1.48	0.56	-2.65	0.01
Lowland mixedwood	-6.64	1.75	-3.80	0.00

Fisher

Fisher relative abundance was strongly positively related to open wetland (Table 9). Fisher relative abundance decreased most markedly in relation to 3D seismic lines and upland shrubs. Prediction error (from K-fold cross validation) was 0.3%, but the model explained only 28.8% of the deviance in fisher relative abundance.

Table 9. Parameter estimates from the best supported model of *fisher relative abundance* modelled against landscape features. Variables are listed from strongest selection to strongest avoidance.

Variables	Estimate	Std. Error	z value	P-value
(Intercept)	-2.74	0.10	-27.31	< 2e-16
Open wetland	0.31	0.12	2.72	0.01
Lowland spruce	0.19	0.12	1.49	0.14
Pipelines	0.13	0.09	1.44	0.15
Trails	-0.18	0.10	-1.72	0.08
Upland shrubs	-0.37	0.19	-1.94	0.05
3D seismic lines	-0.40	0.11	-3.45	0.00

DISCUSSION

Extensive landscape disturbance is not a new phenomenon, as much of eastern North America has been converted to agriculture, urban centers, or other land uses, with concomitant effects on large and mid-size mammals (Laliberte and Ripple 2004). Unique to Alberta's boreal forest is the rapid pace of development (Global Forest Watch Canada 2014), the marked extent of development (Pickell et al. 2016), and the geometry of the novel landscapes produced (Pickell et al. 2015). Rates of Alberta forest loss in the last decade outpace global averages, even exceeding rates from deforestation hotspots like the Brazilian Amazon (Global Forest Watch Canada 2014). Development is expected to increase further as it is spurred by the economic advantages of petroleum extraction (Bayoumi and Mhleisen 2006).

The spatial configuration of anthropogenic disturbances in Alberta's oil sands is unique: whereas agriculture and timber harvest remove polygonal patches of habitat, the extensive network of linear features imposed upon this boreal landscape does not have many analogs elsewhere on the globe. The effects of removing large swatches of mature boreal forest and replacing it with regenerating early seral vegetation have been well researched (reviewed in (Fisher and Wilkinson 2005)). Likewise, the effects of fragmenting forested habitats with large linear barriers such as paved roads have received considerable attention (Fahrig and Rytwinski 2009). However, the permeation of forests by a web of seismic lines, pipelines and minor roads remains has been studied for only wolves (Latham et al. 2011b, McKenzie et al. 2012), caribou (Dyer et al. 2002), and a few other species (Bayne et al. 2005, Tigner et al. 2014). While roads are often barriers to connectivity, linear networks may facilitate connectivity for some species, creating new movement corridors in disturbed habitats. Recent research has documented the role of linear features in facilitating wolf predation of caribou (McKenzie et al. 2012), but it is unlikely that wolves are the only predators to exploit this feature. Moreover, there has been no explicit study of the combined effects forage subsidy, mature forest loss, and general effects of "linearizing" a landscape. Synergy among multiple forms of disturbance ("cumulative effects") is a hot and immediate topic in ecology (Brook et al. 2008, Darling and Côté 2008, Côté et al. 2016). Generalizations about the importance of cumulative effects of disturbance on ecological systems have thus far proved elusive. Illustrating this point, our research in Alberta's boreal forest results suggest mammals show both positive and negative responses to anthropogenic features. In fact, responses to anthropogenic disturbances varied considerably across species, and even across disturbance types within species. A few key species directly implicated in woodland caribou declines are worth highlighting.

Moose and White-tailed deer

Moose make use of both deciduous and conifer stands, as each provide different forage types as well as life-history requirements (Telfer 1970, Krefting et al. 1974, Osko et al. 2004, Dussault et al. 2005). Within our study area in northeastern Alberta, moose were more abundant at sites with greater areas of upland and lowland spruce and mixedwood. Confirmation of these previously documented habitat associations lend confidence in our model results, and in the other observed relationships with anthropogenic features. Like other ungulates, moose make extensive use of early successional forest stands for foraging (Fisher and Wilkinson 2005). In the presence of fire suppression, forest harvesting has become the most significant disturbance regime that maintains favoured moose forage (Krefting et al. 1974). Moose make extensive use of young clearcuts (Cederlund and Okarma 1988, Crête et al. 1995, Rempel et al. 1997), though the juxtaposition of mature forest for cover and cutblocks for foraging is likely important (Forbes and Theberge 1993, Månsson et al. 2007, Herfindal et al. 2009). Our results suggest industrial block features and 3D seismic lines may likewise provide abundant browse, as moose were more abundant in landscapes with more of these features. In contrast, there were fewer moose in landscapes with cutlines (traditional seismic lines), well sites, trails, and pipelines. We contend that wolves' known use of these features (Latham et al. 2011b, Whittington et al. 2011, McKenzie et al. 2012) increase predation risk and either render these features less suitable – the "risky places" hypothesis (Creel et al. 2008, Basille et al. 2015) – or increase mortality and decrease relative abundance, or a combination of the two. Telemetry data are needed to discern the fine-scale mechanisms generating this response for moose. Finally, the net result of the two contrasting forms of disturbance – forage subsidy in cutblocks and block features, and increased predation or risk at linear features – is currently unknown. An examination of moose density across this study area, and adjacent areas with varying degrees of forage subsidy and linear features, is needed to arrive at a final conclusion.

Upland deciduous forest is well-established as an important habitat for white-tailed deer (Hewitt 2011, Stewart et al. 2011). Abundant forage is critical to deer persistence; white-tailed deer diet is dominated by the leaves and stems of woody plants, and conifer needles offer comparatively low nutritional value (Moen 1978, Hewitt 2011). Likewise, the early seral vegetation in regenerating cutblocks is often selected by deer (St-Louis et al. 2000, Fisher and Wilkinson 2005, Fisher et al. 2015) and likely bolsters deer abundance. Our results suggest that other anthropogenic features such as block features and well sites lead to increased deer relative abundance, likely because they provide early-seral forage subsidies. The cumulative effects of multiple resource sectors collectively increase the amount of

the landscape covered by early seral vegetation, augmenting natural deciduous landcover, providing abundant deer browse. In contrast, landscapes with linear features – cutlines and trails – had fewer white-tailed deer. Trails are cleared linear features accessible by foot and off-road vehicle, and provide human access into forested areas that is not easy or possible in intact areas. Moreover, as linear features increase predation rates of wolves on woodland caribou (Whittington et al. 2011, McKenzie et al. 2012), it is reasonable to assume that wolves using cutlines may likewise pose a predation risk (Creel and Christianson 2008, Creel et al. 2008, Basille et al. 2015) and / or direct mortality to white-tailed deer. In our analysis of telemetry data, Fisher et al. (2016) showed that satellite-collared female deer do strongly avoid trails and roads, suggesting a behavioural response, but our results here also suggest a numerical response to these features.

Two commonalities appear in moose and deer numerical responses to anthropogenic features. First, polygonal anthropogenic features that replace mature forest with regenerating trees and shrubs lead to an increase in ungulate relative abundance. Second, linear features lead to decreases in ungulate relative abundance, likely due to predation risk and direct mortality. The net result of the two contrasting forms of disturbance – forage subsidy in cutblocks and block features, and increased predation or risk at linear features – is currently unknown. In the best-case scenario for management, they cancel each other out; however expanding white-tailed deer populations in the region (Fisher et al. 2015, Fisher et al. 2016) suggests that forage subsidies may supersede any negative effects. We highly recommend further research and monitoring to track community changes over time in relation to ongoing landscape changes, and to assess the efficacy of management actions.

Wolves and Black bears

Wolves are generalist predators adept at exploiting different landscapes, habitats, and prey types (Latham et al. 2011c, Wasser et al. 2011, Lesmerises et al. 2012, Llaneza et al. 2012, McKenzie et al. 2012). Likewise, black bears are omnivores with an even greater degree of forage, prey, and habitat flexibility (Tietje and Ruff 1983, Brodeur et al. 2008, Mosnier et al. 2008, Latham et al. 2011a, Tigner et al. 2014). The relative abundance of each species decreased with increasing road density in the landscape. This is perhaps surprising given that wolves are known to use linear features to hunt ungulates. However, roads provide human access that may contribute to wolf mortality or predation risk, with a net effect of decreasing local abundance. Roads are a primary source of mortality for grizzly bears (Benn and Herrero 2002, Nielsen et al. 2004) and the same may be true of black bears in the

northeast boreal forest. Black bear abundance also decreases with 3D seismic lines and industrial block features, though we do not have a hypothesis to explain why.

Interestingly, black bears relative abundance was not positively related to any anthropogenic feature. This is not to say that individual bears do not select these features; telemetry data will provide that conclusion. However, we have no evidence for an abundance response to any resource sector in the northeast boreal forest. In contrast, wolf relative abundance increases in landscapes with greater areas in industrial black features and trails. As moose and deer are abundant in industrial block features, it follows that wolf abundance is likewise high. Trails – lightly traveled by humans – are very likely functioning the same as seismic lines in facilitating wolf movement (Latham et al. 2011b, Whittington et al. 2011, McKenzie et al. 2012) and thereby increasing wolf relative abundance. Again, we do not know the net effect of these contrasting positive and negative relationships, but the apparently expanding wolf populations in northeast Alberta suggest a positive net effect for wolves, and an unknown net effect for black bears.

CONCLUSIONS

We suggest that the ubiquity of effects of extensive landscape disturbance on mammals in the oil sands region indicate a large-scale restructuring of spatial ecological processes in Alberta's boreal forests. The widespread conversion of mature forest to early seral vegetation by both forest harvesting and petroleum extraction provides preferred ungulate habitat that increases local ungulate abundances. The linear features imposed by petroleum extraction and road infrastructure have a mixed effect on multiple species' relative abundances: predators decrease in conjunction with linear features with human use (roads) but increase in areas with linear features with less human use (trails). Perhaps consequently, ungulates decrease in local landscapes with those linear features. This is consistent with predator-prey relationships mediated by linear features and human access elsewhere in Alberta (Muhly et al. 2011, Rogala et al. 2011). The implications for management are profound: seismic lines are not the only linear feature type affecting predator-prey relative abundance in the northeast boreal forest. Three sectors are heavily implicated: forest harvesting, petroleum extraction, and road infrastructure. If reclamation is to be an effective tool in stemming woodland caribou declines, then it should target multiple feature types and engage multiple sectors, rather than relying solely on seismic line reclamation.

The term "novel ecosystem" is currently an ecological buzzword as ecologists come to terms with the fact that anthropogenic disturbance profoundly changes how landscape function (Seastedt et al.

2008, Hobbs et al. 2009). We contend it is likely that the cumulative effects of multiple resource sectors are changing ecological processes within the northeast boreal landscape. We have taken the first examination of large-scale patterns across the mammal community, as a basis for forming hypotheses about mechanisms. The potential for complex, indirect effects is high, as predator-prey and competitive interactions will undoubtedly continue to be altered by differential responses across species and space. For instance, increased early-seral vegetation fosters further expansion of white-tailed deer (Dawe et al. 2014, Fisher et al. 2015), which affects forest structure (Côté et al. 2004) and maybe songbird abundance, as has been shown in other systems (Martin et al. 2011, Cardinal et al. 2012). The increase in deer is likely contributing to caribou declines in an apparent competition process mediated by top carnivores (DeCesare et al. 2009). Spatially mediated competition (Amarasekare 2003) among other species may change with landscape disturbance, altering interspecific interactions within herbivore and carnivore guilds. For example, adaptable "winners" like coyotes may be released where disturbances deter larger predators, and gain a competitive edge over other species that "lose" in a developed landscape (*e.g.* lynx, fisher) (Ripple et al. 2011). Such dynamics within the predator guild will interact with those among herbivore "winners and losers" causing cascading effects to other parts of the ecosystem. These hypotheses are based in sound theory (Prugh et al. 2009, Ritchie and Johnson 2009) (Terborgh and Estes 2010) but remain untested, and as such there is a great need for further ecological research and monitoring of wildlife responses to extensive landscape disturbance in Alberta's oil sands (Burton et al. 2014). Our modelling results provide important empirical evidence of species-landscape relationships. However, there remains considerable uncertainty in these relationships. Rather than over-interpreting model results as final conclusions, we suggest that they represent important working hypotheses about these changing relationships. Continued research and monitoring is critical to testing and refining these hypotheses and improving our understanding of anthropogenic impacts on wildlife communities in the boreal forest. As world leaders contemplate continental-scale pipelines and international climate change agreements (Swart and Weaver 2012), the regional-scale impacts of oil sands development take on global significance. The OSR's spatial footprint is manifested across the boreal forest mammal community, and the future trajectory of these species may hinge on global decisions.

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