OIL SANDS MONITORING: MAMMALS

2024-2025 TECHNICAL REPORT

DR. JASON T FISHER

TERRESTRIAL BIOLOGICAL MONITORING TEAM

DR. ANDREW BARNAS
DR. MARISSA DYCK
EMERALD ARTHURS
MEGAN BRAUN
AIDAN BRUSHETT
JAMIE CLARKE
SHAY MARKS

ACME
Applied Conservation
Macro Ecology Lab

UNIVERSITY OF VICTORIA

With data and input from
DR. DAVID ROBERTS, DR. MELANIE DICKIE, MARCUS BECKER
ALBERTA BIODIVERSITY MONITORING INSTITUTE

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OIL SANDS
MONITORING
PROGRAM

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1. MAIN MESSAGES FOR OIL SANDS MONITORING

The ACME Lab's Oil Sands Monitoring (OSM) Mammal Monitoring Program was funded as requested for 2024-2025. We delivered on field monitoring for four Landscape Units under the BADR design. Here we report the summary statistics from that program. We also use OSM-BADR data to answer core questions of the OSM program, as well as questions posed last year by the Terrestrial Biological Monitoring's (TBM) Technical Advisory Committee (TAC) and Science and Indigenous Knowledge Integration Committee (SIKIC), highlighted in the 2024-2025 TBM Workplan.

Core Questions

1. *Has the abundance of wildlife species changed?* The answer is yes, as evidenced by all of the papers reviewed in Roberts et al. (2022) and the papers on boreal mammal communities(Fisher and Burton 2018, Burgar et al. 2019, Tattersall et al. 2020a, b, Beirne et al. 2021a, Fisher et al. 2021a, Fisher et al. 2021c, Wittische et al. 2021b, Fisher and Ladle 2022b, Sun et al. 2022, Boczulak et al. 2023, Barnas et al. 2024c) we have published in the past years of the program.. The outcomes of this year's analyses (below) continue to corroborate these conclusions: the abundance of wildlife species has changed, and OS activities are a driver of that change. In the 2024-5 report, we dive into three key mammal species identified by scientists and Indigenous communities as important indicators of boreal communities: white-tailed deer, black bears, and coyotes.

2. *To what extent is that change driven by oil sands activities?* That same research shows that the effect sizes (the strength of a stressor-response relationship) of some OS features can be greater than roads or forest harvesting, depending on the species examined, and the ecological context considered (Fisher et al. 2021c, Wittische et al. 2021b, Aubertin-Young 2022, Darlington et al. 2022, Fisher and Ladle 2022b, Roberts et al. 2022, Boczulak et al. 2023, Fuller et al. 2023, Barnas et al. 2024c). Seismic lines are important but so are other linear and polygonal features. The 2024-2025 analysis examines the spatial scales at which features have the greatest impact on different species, and what *zone of influence* each of these features has on boreal mammal species. This work is covered in Chapter 4, with a separate complementary analysis in the ABMI-UVIC joint deliverable.

3. *What are the cumulative effects of oil sands pressures on wildlife?* We have shown that anthropogenic features affect mammal species (Fisher et al. 2020, Fisher et al. 2021c, Wittische et al. 2021b, Boucher et al. 2022, Darlington et al. 2022, Fisher and Ladle 2022b, Fuller et al. 2022) – OS features play a demonstrable role, but are not alone in this. Multiple forms of disturbance, including forest harvest and transportation, alter boreal mammal communities. Parsing apart the relative contributions of various features to causing boreal mammal community change is the goal of ongoing analyses and is addressed in all chapters.

2024-2025 Questions

In the 2024 Workplan, we outlined these knowledge gaps:

1. *How do mammal responses to OS activities change over time?*

The answer to this question is the key target of the BADR's 3-year rotation design. The first series of data were collected in 2021 and in the 2024 year we started to collect the first re-samples of the original Landscape Units.

2. *How do mammals' response to OS activities change with context across the OSR; that is, do species respond negatively to OS activities under some conditions and positively under others? How do mammal densities change in response to OS activities, within an LU and between LUs?*

In this year we built toward answering this question by sampling the last four remaining Landscape Units identified in the BADR design. These data were collected in fall 2024, image-analyzed in winter 2024, and data-analyzed in spring 2025. This analysis a multi-stage process that will push into the 2025-2026 year. The first step in this analysis is to determine the spatial scale at which OS and other industrial features affect each boreal mammal species. Understanding this scale dependence is key to further analysis and to informing landscape planning and restoration. This question is addressed in the several chapters herein.

3. *Which OS features most strongly affect indicator species' relative abundance and distribution?*

To bridge this gap, we utilise structural equation modelling to identify which OS stressors significantly contribute to changes in mammal distribution, and how these compare to cumulative effects stressors. We examine linkages identified in the TBM conceptual model and estimate the effect sizes for these different linkages, to show which features (and modelled species-feature processes) have the greatest effect on a key species indicator: white-tailed deer (Chapter 7). We outline an approach that we are planning to pursue in 2025-2026 that we suspect will yield new insights into the relative effects of different OS features on mammal species.

2. 2024-2025 MAMMAL MONITORING: LANDSCAPE UNIT CAMERA DEPLOYMENT

Overview

Mammal monitoring at the scale of landscape units (LUs) followed the OSM Terrestrial Biological Monitoring (TBM)'s Before-After Dose-Response (BADR) design (Bayne et al. 2021b). In 2024-2025 we sampled four LU's identified using the BADR design (Figure 1): LU 09, 14, 16 and 22. We also deployed resampling of the first LU's first sampled in 2021 – LUs 02 and 03 – as well as deployed new sampling for LUs 04 and 08, which had not been supported in the funding decision of 2021 (Figure 1).

Sampling Design

In addition to the JEM sites selected by the TBM team and embedded in each LU, 40-50 cameras were deployed across each LU in a stratified random design to minimise correlation among environmental covariates and spread sampling effort across the range of natural heterogeneity. The landscape was stratified into dominant (> 50%) forest classes: conifer forest, deciduous forest, and mixedwood forest, using similar criteria as for JEM sites. The intent is to distribute the cameras somewhat evenly among these strata, to "control" for natural variability while examining the role of industrial features on mammal communities.

In ArcGIS the landscape was overlain by a hexagonal grid of 2-km^2 cells. This cell size allows us to space cameras sufficiently far apart to allow some degree of independence (Diniz-Filho et al. 2003, Hawkins et al. 2007, Gilbert et al. 2020) for species-habitat models, typically conducted in a linear regression framework (Fisher and Burton 2018, 2020, Fisher et al. 2020). It also meets the requirements of density estimation models, which require at least 2-3 cameras be deployed within an individual's home range size, such that it could be detected on multiple cameras (Royle et al. 2014, Sun et al. 2014, Burgar et al. 2018, Burgar et al. 2019).

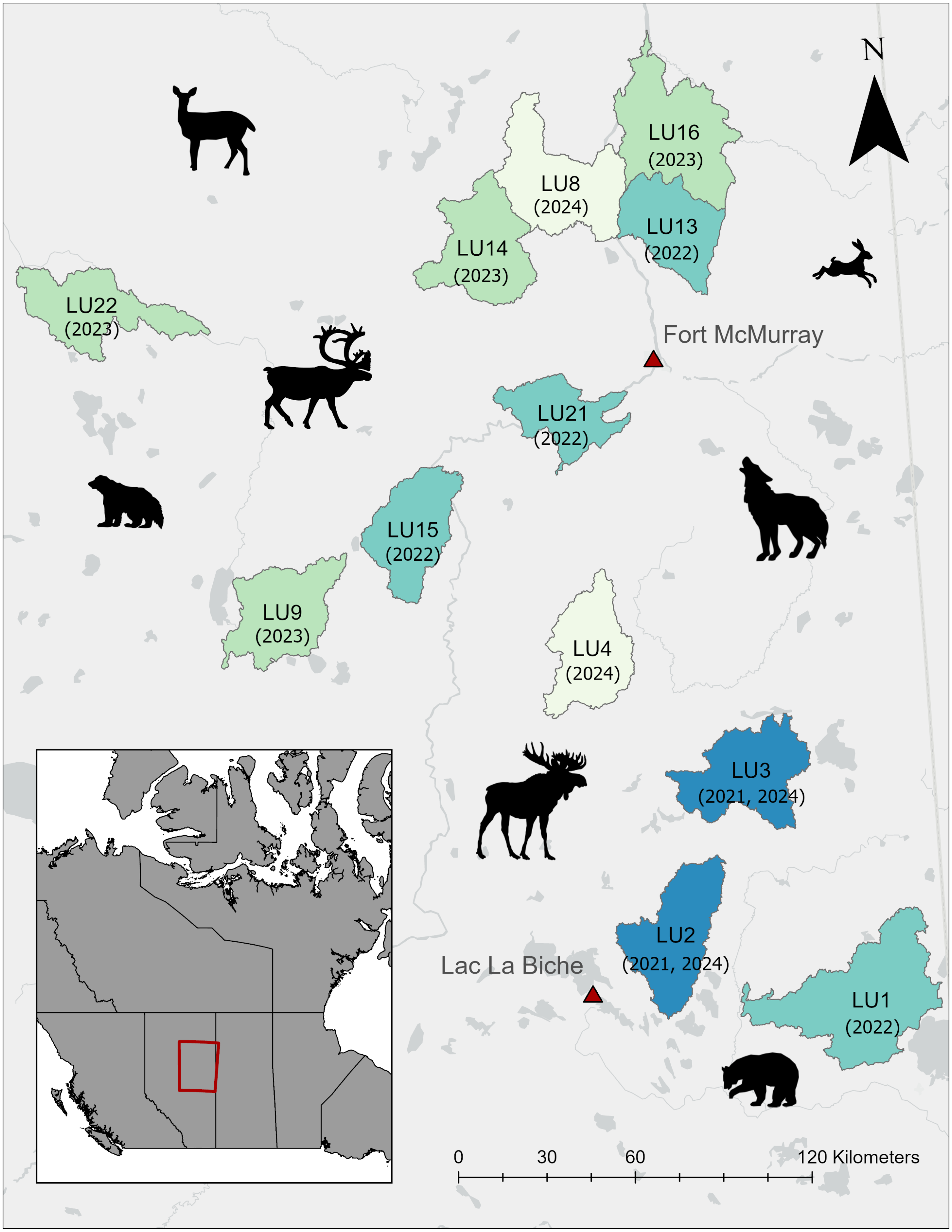


Figure 1. The OSM TBM's BADR design showing the 12 LUs selected for sampling, and the years sampled.

Using data from a review of mammal home ranges sizes (Holling 1992) and analyses of caribou (Dalerum et al. 2007) and white-tailed deer (Fisher et al. 2016) from the region, we determined the smallest home-range size was for white-tailed deer and that a 2-km^2 cell size would accommodate model requirements.

Where possible we constrained the resulting hexagonal grid to cells within 100-m of a vehicle-accessible road or trail, as determined by ABMI human footprint inventory. This logistical necessity reduced expensive helicopter time, although in the low-disturbance landscape helicopter access was required for access to all sites. We then randomly selected 30 cells from each of the three strata. When we could not find 30 cells within each stratum, we relaxed the definition of “upland” or “lowland” from > 50% of the cell to > 25% of the cell, and then randomly selected sites to yield a complete set of candidate sites.

In the field, the deployment team visited each accessible cell and identified active wildlife trails suitable for deployment within that cell (ensuring that cameras within adjacent cells were the minimum 1-km apart); this increases probability of detection given animal presence within the cell (MacKenzie et al. 2002, MacKenzie and Royle 2005, MacKenzie et al. 2017a), as data density is important to make statistical models function (Burgar et al. 2019). No bias is expected(Stewart et al. 2019a) as game trails represent where wildlife use these complex landscapes; in fact not using game trails biases estimates downward, because one is sampling places that animals do not use, or use very rarely. One Reconyx PC900 or Hyperfire II camera (Holmen, WI, USA) was deployed within the hex cell and secured to a tree using a Reconyx lock box and a python cable lock. The statistical unit is thus the cell, not the site itself, and the cell is the basis for modelling and inference. At a subset of sites, ABMI deployed an additional camera directly at the cell centroid to represent a random paired site which will allow for improved inter-operability of datasets for different density estimation methods(Nakashima et al. 2018, Nakashima et al. 2020). This design was fully integrated with the JEM-site scale sampling. That is, where a JEM site falls within a cell, the JEM site was used – there is no double-sampling. This integrated approach is not only more cost-effective, but it also allows us to conduct cross-scale comparisons key to the hierarchical BADR design. The final deployment spanned major gradients of interest across the LUs (Figure 1).

Sampling began in 2021 where funding for two LU’s was approved, switching to four LU’s per year as described in the full BADR implementation. The LU mammal monitoring data now available are summarised in Figure 2.

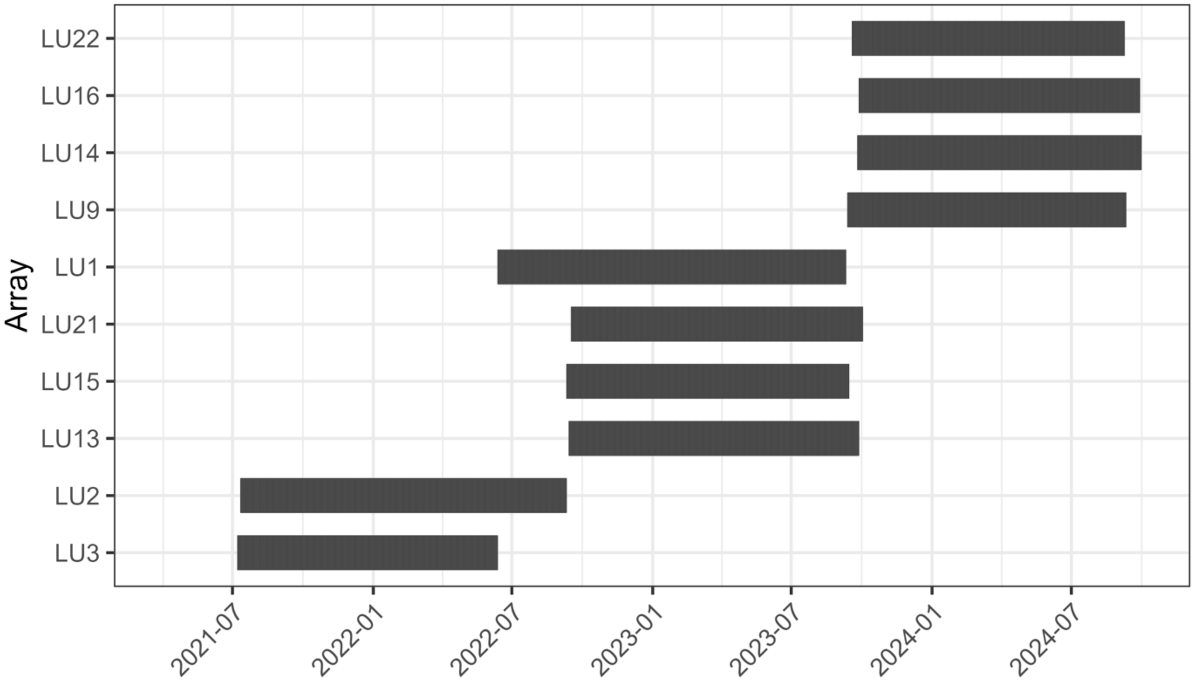


Figure 2. The timeline of camera deployments for the OSM TBM’s mammal monitoring. To date 10 LU’s have been fully sampled, two are being re-sampled, and two are being sampled for the first time due to being declined for monitoring in 2021.

3. 2024-2025 MAMMAL MONITORING: LANDSCAPE UNIT DATASET SUMMARY

Monitoring Results to Date

Workplan approvals for this fiscal year were provided April 11, 2024. The AEP research agreement with UVIC was signed July 2024. Camera collection and deployment occurred September – October 2024. A one-year sample is required for most effective LU-scale mammal monitoring, consistent with all our past camera-trapping research in the boreal forest(Fisher and Burton 2018, Burgar et al. 2019, Fisher and Burton 2020, Fisher et al. 2020, Tattersall et al. 2020b, a, Fisher et al. 2021a, Fisher et al. 2021c, Wittische et al. 2021b, Fisher and Ladle 2022b, Frey et al. 2022, Sun et al. 2022). We made the decision to collect cameras deployed in 2024 in *September 2025*, so image classification of those cameras will occur at that time. Herein, we provide an update of data collected Fall 2024 (deployed 2023).

LU09 Array (In-situ)

Coyote and white-tailed deer are two of the most abundant and widespread species in LU09. Coyote occupied 94% of sampling sites, and white-tailed deer 92%. Snowshoe hare (70%) and red squirrel (92%) were also abundant and widespread, as were black bears (80%). Furbearers' marten and fisher were unusually widespread (56% each) although with very low relative abundance. Moose, a key indicator for Indigenous communities, was almost absent from this landscape (9 detections, 16% occupancy).

LU14 array (Low development)

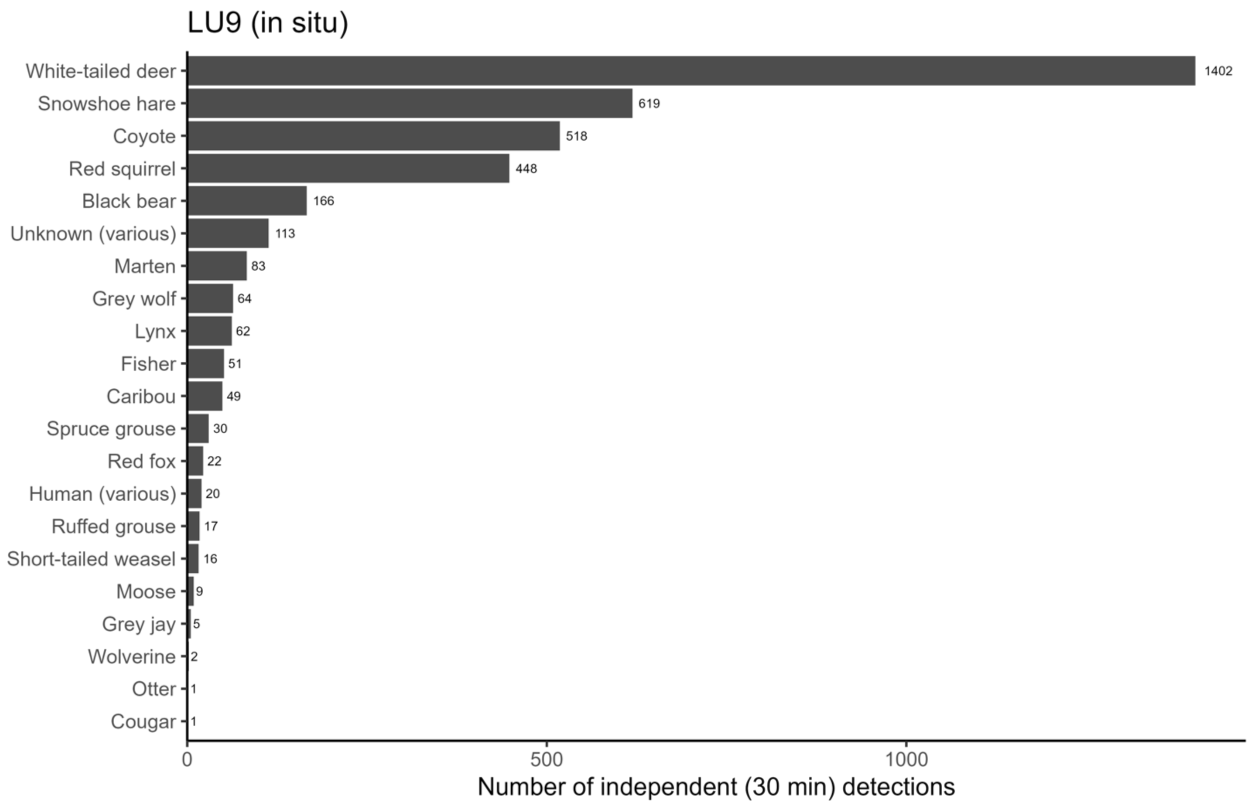
Red squirrel (92%), black bear (82%), and snowshoe hare (73%) are the 3 most abundant and widespread species in this LU. Unlike the in-situ array, moose are widespread (69%) and abundant here. Lynx, fisher, wolves, and marten have intermediate occupancy and abundance. Invasive white-tailed deer are not abundant (68 detections) nor as widespread as in the in-situ LU (45%). Likewise, coyotes are not abundant (32) and not widespread (29% occupancy).

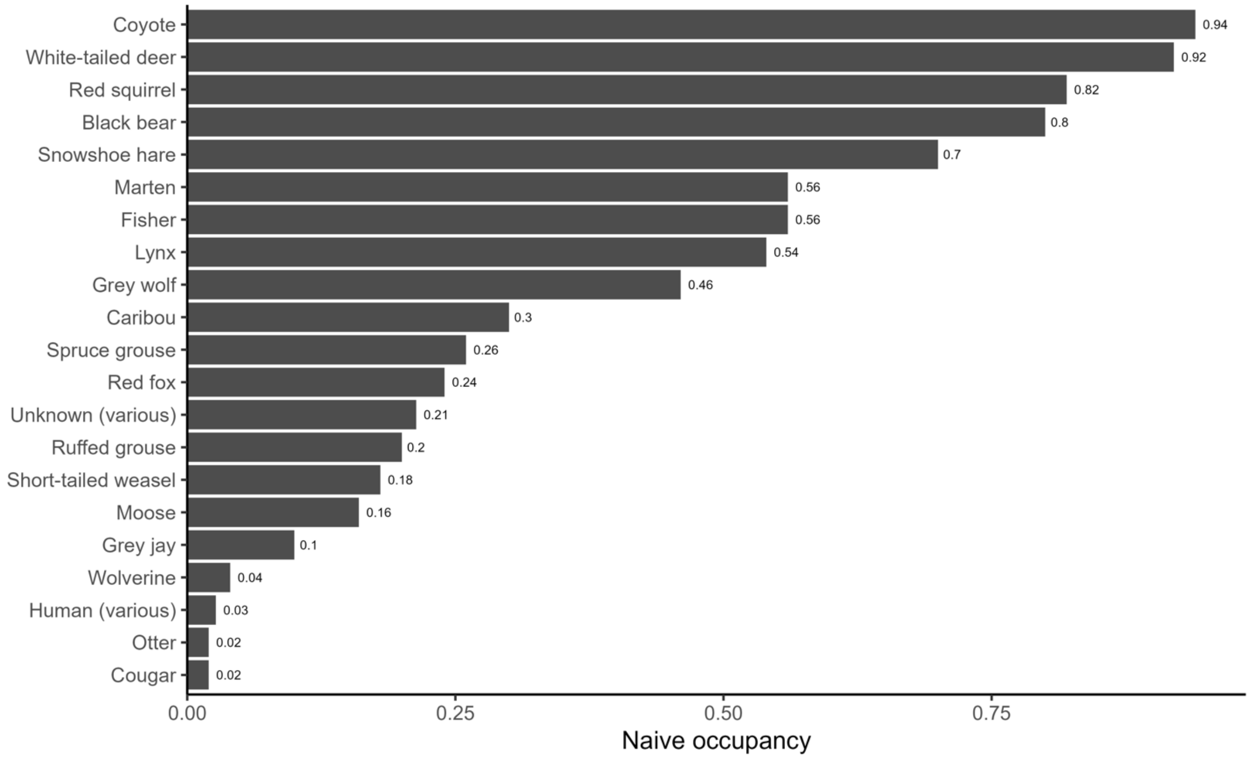
LU16 Array (Mine-Adjacent)

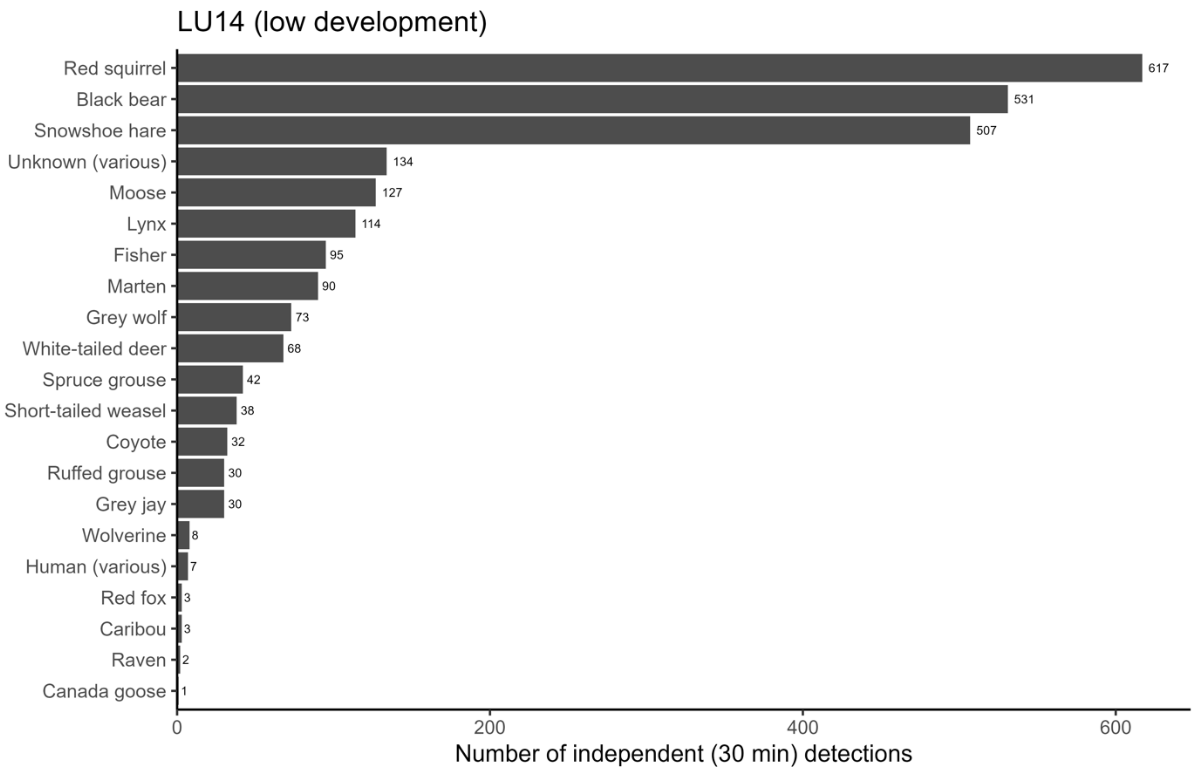
Coyote is the most widespread mammal in this LU (94% occupancy), but white-tailed deer are less so, at 63% occupancy. Red squirrel black bear, and snowshoe hare have the highest relative abundance and high occupancy (92, 86, 82%). Moose have intermediate relative abundance but are widespread (73% occupancy). Furbearers' lynx, marten, red fox, and fisher have low relative abundance but higher occupancy than in-situ landscapes (71, 45, 39, 3%).

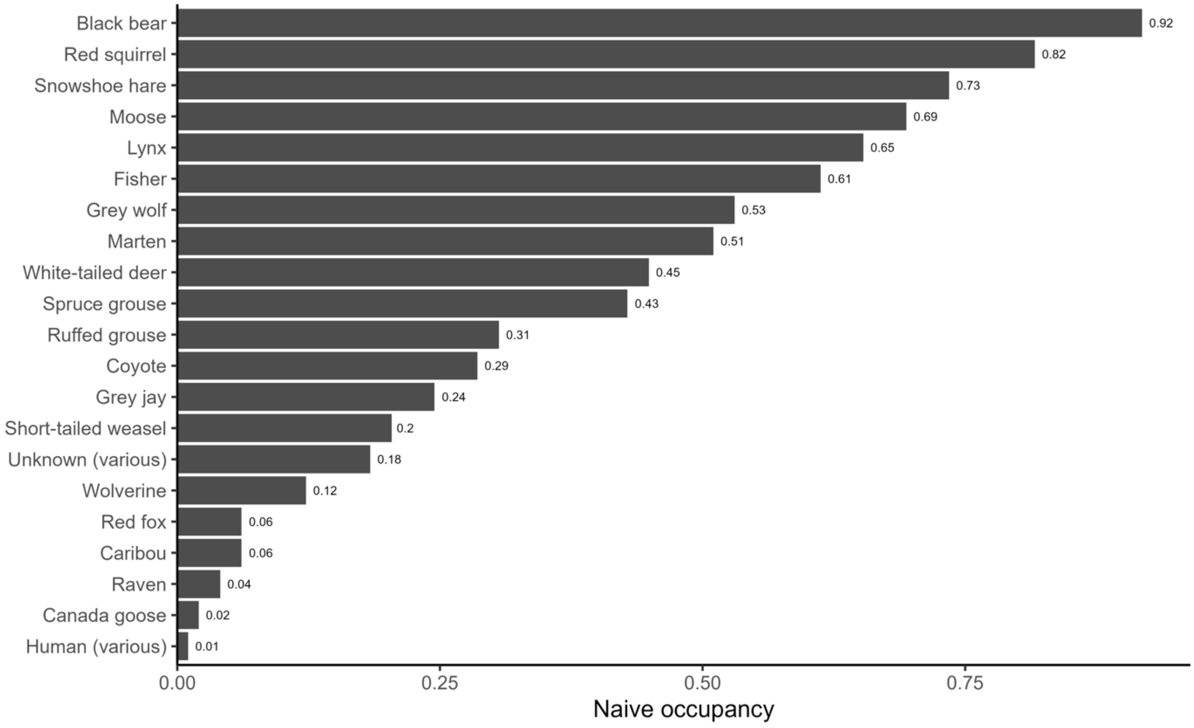
LU22 Array (Pre-in-situ)

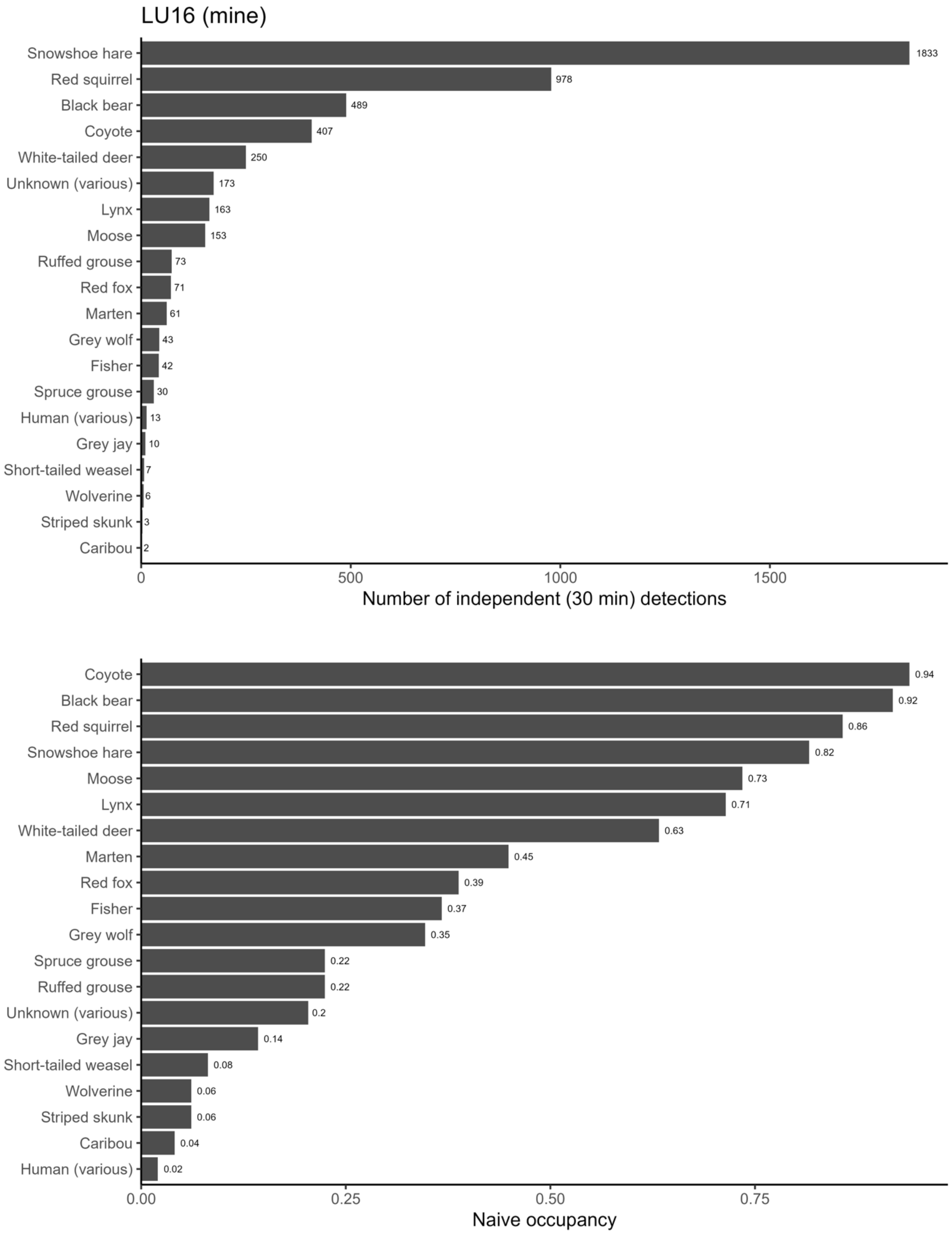
Black bear (90% occupancy), fisher (84% occupancy), snowshoe hare (76% occupancy), and red squirrel (76%) are the most widespread mammal species with the highest relative abundance in this pre-in-situ, relatively low-disturbance LU. Coyote is likewise widespread (82%) but with half the relative abundance compared to the in-situ landscape (218 vs 518 independent detections). White-tailed deer are likewise widespread (74% occupancy) but with 9% the relative abundance than in the in-situ landscape (125 vs 1402 detections) and 1.8 times higher relative abundance than the low-development landscape with (125 vs. 68 detections). Notably, moose are not all widespread here (26% occupancy) and are not abundant (18 detections).

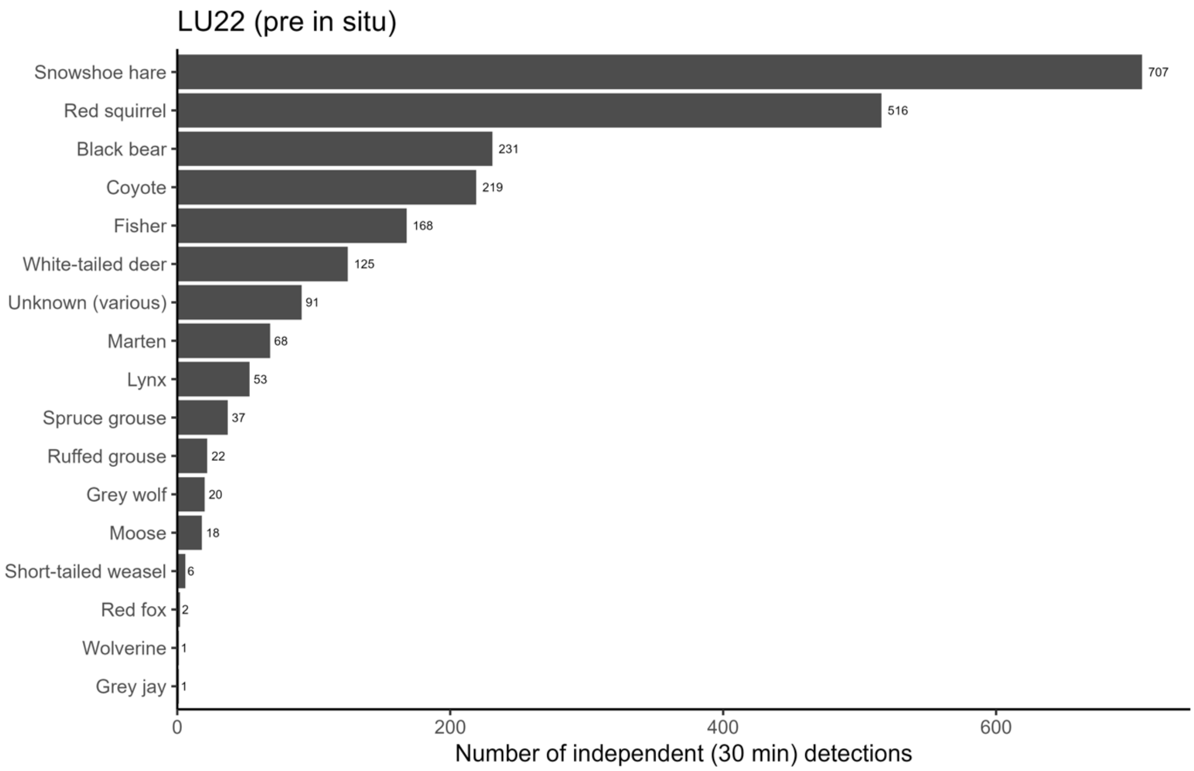

LU9 (in situ)
White-tailed deer 1402
Snowshoe hare 619
Coyote 518
Red squirrel 448
Black bear 166
Unknown (various) 113
Marten 83
Grey wolf 64
Lynx 62
Fisher 51
Caribou 49
Spruce grouse 30
Red fox 22
Human (various) 20
Ruffed grouse 17
Short-tailed weasel 16
Moose 9
Grey jay 5
Wolverine 2
Otter 1
Cougar 1
0
500
1000
Number of independent (30 min) detections

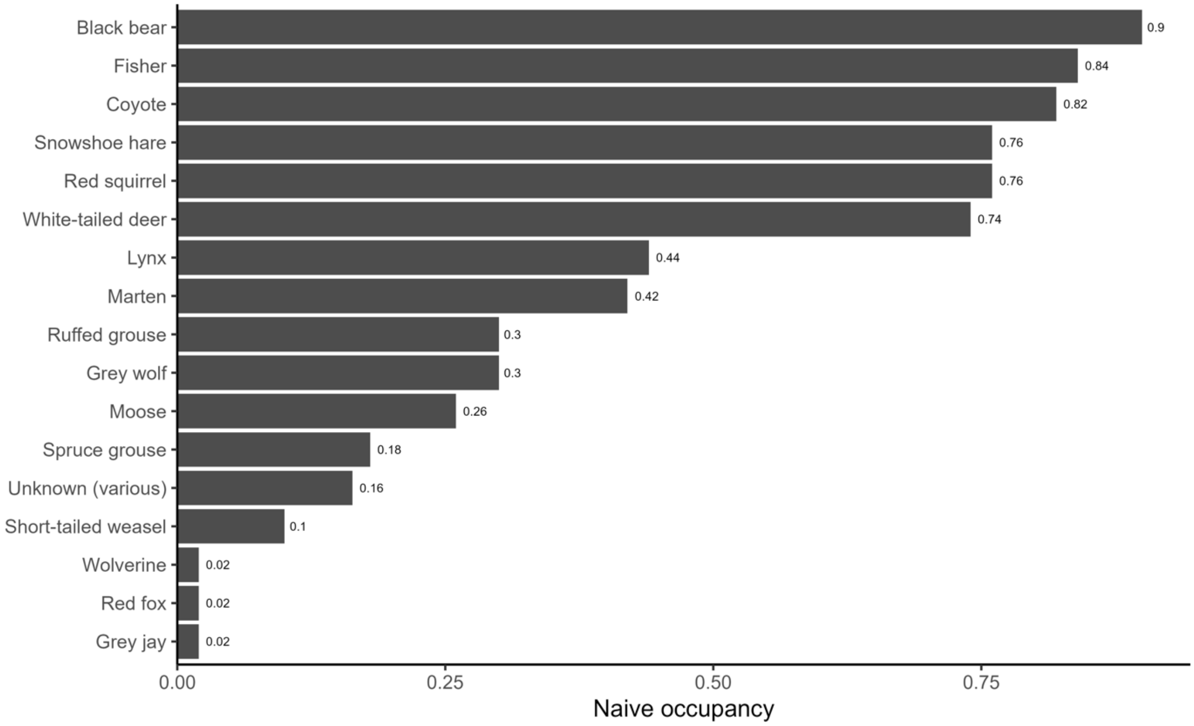

Coyote 0.94
White-tailed deer 0.92
Red squirrel 0.82
Black bear 0.8
Snowshoe hare 0.7
Marten 0.56
Fisher 0.56
Lynx 0.54
Grey wolf 0.46
Caribou 0.3
Spruce grouse 0.26
Red fox 0.24
Unknown (various) 0.21
Ruffed grouse 0.2
Short-tailed weasel 0.18
Moose 0.16
Grey jay 0.1
Wolverine 0.04
Human (various) 0.03
Otter 0.02
Cougar 0.02
0.00
0.25
0.50
0.75
Naive occupancy


LU14 (low development)
Red squirrel 617
Black bear 531
Snowshoe hare 507
Unknown (various) 134
Moose 127
Lynx 114
Fisher 95
Marten 90
Grey wolf 73
White-tailed deer 68
Spruce grouse 42
Short-tailed weasel 38
Coyote 32
Ruffed grouse 30
Grey jay 30
Wolverine 8
Human (various) 7
Red fox 3
Caribou 3
Raven 2
Canada goose 1
0
200
400
600
Number of independent (30 min) detections


Black bear 0.92
Red squirrel 0.82
Snowshoe hare 0.73
Moose 0.69
Lynx 0.65
Fisher 0.61
Grey wolf 0.53
Marten 0.51
White-tailed deer 0.45
Spruce grouse 0.43
Ruffed grouse 0.31
Coyote 0.29
Grey jay 0.24
Short-tailed weasel 0.2
Unknown (various) 0.18
Wolverine 0.12
Red fox 0.06
Caribou 0.06
Raven 0.04
Canada goose 0.02
Human (various) 0.01
0.00
0.25
0.50
0.75
Naive occupancy


LU16 (mine)
Snowshoe hare 1833
Red squirrel 978
Black bear 489
Coyote 407
White-tailed deer 250
Unknown (various) 173
Lynx 163
Moose 153
Ruffed grouse 73
Red fox 71
Marten 61
Grey wolf 43
Fisher 42
Spruce grouse 30
Human (various) 13
Grey jay 10
Short-tailed weasel 7
Wolverine 6
Striped skunk 3
Caribou 2
0
500
1000
1500
Number of independent (30 min) detections
Coyote 0.94
Black bear 0.92
Red squirrel 0.86
Snowshoe hare 0.82
Moose 0.73
Lynx 0.71
White-tailed deer 0.63
Marten 0.45
Red fox 0.39
Fisher 0.37
Grey wolf 0.35
Spruce grouse 0.22
Ruffed grouse 0.22
Unknown (various) 0.2
Grey jay 0.14
Short-tailed weasel 0.08
Wolverine 0.06
Striped skunk 0.06
Caribou 0.04
Human (various) 0.02
0.00
0.25
0.50
0.75
Naive occupancy


LU22 (pre in situ)
Snowshoe hare 707
Red squirrel 516
Black bear 231
Coyote 219
Fisher 168
White-tailed deer 125
Unknown (various) 91
Marten 68
Lynx 53
Spruce grouse 37
Ruffed grouse 22
Grey wolf 20
Moose 18
Short-tailed weasel 6
Red fox 2
Wolverine 1
Grey jay 1
0
200
400
600
Number of independent (30 min) detections


Black bear 0.9
Fisher 0.84
Coyote 0.82
Snowshoe hare 0.76
Red squirrel 0.76
White-tailed deer 0.74
Lynx 0.44
Marten 0.42
Ruffed grouse 0.3
Grey wolf 0.3
Moose 0.26
Spruce grouse 0.18
Unknown (various) 0.16
Short-tailed weasel 0.1
Wolverine 0.02
Red fox 0.02
Grey jay 0.02
0.00
0.25
0.50
0.75
Naive occupancy

ACME Lab Public Data Portal

The ACME Lab's data portal lists maps and metadata for OSM's TBM Mammal Monitoring Program for 2021-2024: (http://www.acmelab.ca/dataportal.html#Boreal).

This portal describes where and when monitoring has occurred. Here, data associated with research is permanently archived with associated DOI's. Each LU is linked as its own project, and each project contains:

1. GIS shapefiles of the deployment sites.
2. Landcover covariates around each camera site, as derived from the ABMI's *Wall-to-Wall Land Cover Inventory* (https://abmi.ca/home/data-analytics/da-top/da-product-overview/Data-Archive/Land-Cover.html).
3. Anthropogenic feature covariates around each camera site, as derived from the ABMI's *Wall-to-Wall Human Footprint Inventory* (https://abmi.ca/home/data-analytics/da-top/da-product-overview/Human-Footprint-Products/HF-inventory.html).
4. Data extracted from camera images using *TimeLapse Image Analyzer* 2.55(Greenberg et al. 2019b) in CSV format.
5. Dataframes for R statistical software(R Core Team 2024b) that merge all the associated datasets and provide code for exploring the modelling the data.

4. SELECTING SPATIAL SCALES FOR UNDERSTANDING SPECIES RESPONSES TO ANTHROPOGENIC LANDSCAPE CHANGE WITH CAMERA TRAP DATA

Marissa A. Dyck, Rebecca M. Smith, Emerald Arthurs, Megan Braun, Shay Marks, Andrew F. Barnas, Jason T. Fisher

OSM SUMMARY

A key question for understanding OS impacts and for managing OS landscapes, is "*Does the density of OS features close by, or aggregated in larger landscapes, affect a species' occurrence within a landscape?*" Does a seismic line just affect the animals on that line, or do the effects of multiple lines accrue as lines increase in density? The same question applies to all anthropogenic features in the OSR. This question is the topic of the ABMI-UVIC joint deliverable, in which we compare the results of JEM-site monitoring on- and near-features, to the LU-scale monitoring which aggregates feature density. Here we dig even deeper into that question by modeling the effects of industrial feature density on multiple mammal species across 20 scales. We find that there is no consistent scale that explains the response of mammals to OS and other features, but that aggregate feature densities are critical to explaining outcomes for mammal in these landscapes. We show that some species respond to local-scale densities whereas others have much larger-scale responses, signalling population outcomes. This information helps us understand *how* OS features affect mammals, to guide recommendations for mitigation and better landscape management.

INTRODUCTION

Anthropogenic landscape change has drastically altered Earth's ecosystems; more than 75% of ice-free land has undergone human-induced modification (Ellis and Ramankutty 2008). This level of landscape change has profound effects on ecological systems, leading to numerous conservation crisis including accelerated rates of species loss and global climate change (Dirzo et al. 2014, Ceballos et al. 2015, Ceballos et al. 2017, Trenberth 2018). Energy development is one driving force of landscape change in the current Anthropocene Epoch, and results of energy exploration and extraction activities create complex landscapes and systems. As energy development activities continue, an overarching ecological unknown is to understand how species respond to these novel disturbance environments. Disentangling the effects of landscape change in these complex systems is challenging especially since species may respond to disturbances in different ways depending on the landscape context (Fidino et al. 2021b, Barnas et al. 2024c). Management decisions to address changes in complex human-altered systems therefore not only require robust data but also replicated samples from which to draw reliable inferences.

In turn, remote camera traps have become a widely used technique particularly for studying wide-ranging terrestrial mammals (Trolliet et al. 2014). Remote camera traps allow for investigation across large spatial scales and temporal extents (Burton et al. 2015a), are minimally-invasive (Kelly et al. 2012, Meek et al. 2014), and facilitate synthetic approaches between groups (Steenweg et al. 2017b, Cove et al. 2021). Data generated from camera trap studies allow for species-specific inferences on behavior (Caravaggi et al. 2017, Barnas et al. 2022b), habitat use and density (Jacques et al. 2019, Dyck et al. 2022, Iosif et al. 2022, Ethier et al. 2024a), and allow for estimating how these factors change with landscape change (Fisher and Burton 2018).

Species occurrence data from camera traps are often used to examine relationships between species and their environment, where occurrence is analyzed in relation to spatial resource availability (Shurin et al. 2002, Wiewel et al. 2007). The theoretical basis for these analyses stems from optimal foraging and risk-reward theories (Pyke 1984, Holbrook and Schmitt 1988a), which assume that animals select habitat based on available resources and perceived risks. However, applying these concepts to camera trap data introduces challenges, particularly in defining the spatial scale at which landscape features influence habitat selection. Mammal responses to landscape features depends on the scale at which the features are measured in relation to camera trap placement. For example (Figure 1), a camera placed in dense forest directly adjacent to a forestry cutblock may provide abundant early forage for moose (*Alces alces*) and nearby escape cover (Johnson and Rea 2023). If we consider only this small spatial scale, we may predict high relative moose abundance. However, when considering the larger spatial extent around the camera site, high-density anthropogenic linear features will facilitate predator incursion into the area, and we may predict lower relative moose abundance as a result.

This problem of scale is central to ecological inquiry (Levin 1992), and ecologists recognized its existence as early as the 1930s (Urban 2014). The early theoretical groundwork helped establish landscape ecology as a field (MacArthur and Levins 1964, Sarkar 1984, Wiens 1989, Allen and Hoekstra 1992) and many empirical studies have aimed to assess how species respond to stressors at different scales and the relative roles of factors operating at each scale (Turner 1989, Chave 2013, Lawler and Torgersen 2020). The knowledge that ecological processes operate at different scales is now well established and critical to our understanding of ecological systems (Levin 1992, Lawler and Torgersen 2020). Therefore, several theories have emerged in the field of landscape ecology attempting to characterize predictable patterns of scale to which species respond to their environment (Holland et al. 2004, Holland et al. 2005, Nams et al. 2006, Fisher et al. 2011, Holland and Yang 2016). Holland et al. (2004) posited that there is a characteristic scale at which a species interacts with its environment, while Wiens (1989) posited that there may be domains of scale (a spatial range) where ecological patterns and processes are consistent. Early work on beetles (Holland et al. 2004, Holland et al. 2005) and mammals (Nams et al. 2006, Fisher et al. 2011) suggested support for these characteristic scales, but the emerging body of research suggests that best-supported scales are not predictable, but rather context-specific (Stuber and Fontaine 2019). Investigating scale-dependence is important to understand an identify how mammal-habitat relationships change across spatial scales to best inform conservation practices.

One biogeoclimatic region where the problem of scale need be considered is the western Cordillera of North America, where the western boreal forest is changing rapidly due to resource extraction creating landscapes without global or historical analogs (Pickell et al. 2014, Pickell et al. 2015, Pickell et al. 2016b). Mammal species respond to oil sands -generated landscape features, and the cumulative effects of ancillary disturbances, in various ways (Fisher and Burton 2018, 2021, Wittische et al. 2021b, Fisher and Ladle 2022a, Roberts et al. 2022, Fuller et al. 2023). Linear features, such as seismic lines and roads, facilitate wolf (*Canis lupus*) travel (Dickie et al. 2017) which then increases encounter and predation rates, affecting caribou (*Rangifer tarandus*) and moose (McKenzie et al. 2012, Boucher et al. 2022). Concurrently, polygonal anthropogenic features, such as cutblocks and well sites, provide early-seral forage subsidy (Fisher and Burton 2018, Routh and Nielsen 2021, McKay and Finnegan 2022) for herbivores, which then attracts carnivores, also altering predator-prey dynamics (Fisher and Ladle 2022a). Forestry cutblocks attract large herbivores (Fisher and Wilkinson 2005), and the role of well sites has recently been revealed as additional sources of early-seral forage for many species, and an aggregator of prey for carnivores (Fisher et al. 2021b, Fuller et al. 2023). Clearly, different disturbance features evoke variable responses from large mammals, but it is unknown whether species interact with these features at some “characteristic” scale (Holland et al. 2004) or if these scales are predictable.

Here, we examined habitat relationships at multiple spatial scales for several boreal mammal species. We used a multi-scale information-theoretic approach to understand the effect of spatial scale on species responses to landscape features an area of heavy habitat disturbance, the Athabasca oil sands. We used camera traps to quantify species' relative abundance (O'Connell et al. 2011, Fisher 2025), and then modelled each species against natural and anthropogenic landscape variables across multiple spatial scales. We hypothesized (1) domains of scale would emerge for each species, such that habitat measured at spatial scales of similar sizes would perform comparably to explain a species' relative abundance; (2) the best-supported spatial scale would vary between the type of processes being measured (e.g., anthropogenic and natural landscape features); (3) best-supported spatial scales would vary among species and not be predictable (e.g., by body size or trophic level).

MATERIALS AND METHODS

Study area

Our study frame is the Western Sedimentary Basin (Porter et al. 1982), a vast portion of the western Canadian boreal forest underlain by the world's 3rd-largest petroleum deposits (Figure 2) (Government of Alberta, 2023) including the Athabasca Oil Sands Regions (OSR), which aggregate three independently managed oil sands areas (ABMI, 2014). Covering a total area of 140,000 km², the OSR is characterized by a mosaic of upland and lowland forests, wetlands, and anthropogenic features resulting from natural resource extraction, particularly energy development and agriculture, which together comprise 15.5% of the total area (ABMI, 2014). This diverse landscape supports a high diversity of mammals, including grey wolf (*Canis lupus*; hereafter wolf), caribou, moose, black bear (*Ursus americanus*), white-tailed deer

(*Odocoileus virginianus*), Canada lynx (*Lynx canadensis*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), fisher (*Pekania pennanti*), and marten (*Martes americana*).

Sampling design

Our work was part of the joint Canada-Alberta Oil Sands Monitoring program (Roberts et al. 2022), and our design follows the terrestrial Biological Monitoring Program's BADR design We stratified this region according to the degree of anthropogenic development (high, medium, and low development) (Smith 2018, Bayne et al. 2021a) and selected six landscape units (LUs) defined by hydrologic boundaries and each covering 1000-2000 km² (Figure 2). To quantify large mammal relative abundance in each LU, we employed a constrained stratified sampling design wherein LUs were stratified into upland (>50% upland deciduous forest) and lowland (>50% wet coniferous forest) categories. Within each LU, we divided the area into 2 km² hexagonal grid cells using ArcGIS (Version 10.3; ESRI 2014), ensuring that the cells were located within 100 m of accessible roads or trails, as identified in the Alberta Biodiversity Monitoring Institute's 'Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region' (hereafter ABMI HFI) (Alberta Biodiversity Monitoring 2021).

From this candidate set of 60 cells per LU, we randomly selected 40-50 cells for each LU, adjusting the selection criteria to ≥25% for either upland or lowland strata if 30 cells were not identifiable. One remote infrared wildlife camera (Reconyx PC900 Hyperfire™, Holmen, WI, USA) was deployed within each selected cell, positioned at least 100 m from active human-use roads and trails and at least 1 km from other camera locations in adjacent cells. Cameras were strategically placed along active wildlife trails to enhance the probability of detecting species (MacKenzie et al. 2003, MacKenzie and Royle 2005, MacKenzie et al. 2017b). Additionally, a scent lure (O'Gorman's™ Long Distance Call, O'Gorman's MT) was applied to a bait tree at each camera location to further increase the likelihood of mammal detection and reduce the frequency of false absences (Stewart et al. 2019b). Images were identified to species by trained reviewers using Timelapse Image Analyzer 2.0 (Greenberg et al. 2019a).

In this design, we deployed remote cameras across these six LUs from 2021 to 2023 (Figure 2). Each LU was monitored for approximately 12 months, with two LUs observed from 2021 to 2022 and four LUs from 2022 to 2023; however, some monitoring periods were limited due to logistical constraints.

Quantifying natural and anthropogenic landscape features around cameras

We quantified anthropogenic disturbance features from the ABMI HFI dataset (Alberta Biodiversity Monitoring 2021)grouping together ecologically similar features (Table S1). We quantified natural landscape features using landcover data from the ABMI Wall-to-wall Land Cover Map 2010 Version 1.0 (Alberta Biodiversity Monitoring 2010). We employed our multi-scale analysis by extracting landscape data at 20 buffer widths ranging from 250-meter radius to 5000-m radius, in 250-meter increments surrounding the camera locations.

To assess multicollinearity among covariates, we conducted pairwise Pearson's correlation tests within each spatial scale. Variables with a correlation coefficient (r) exceeding 0.6 were either excluded from a model or merged into a single variable if ecologically justified (Zuur et al. 2010b). The final selection of HFI and land cover variables used for subsequent analyses is summarized in Table 1.

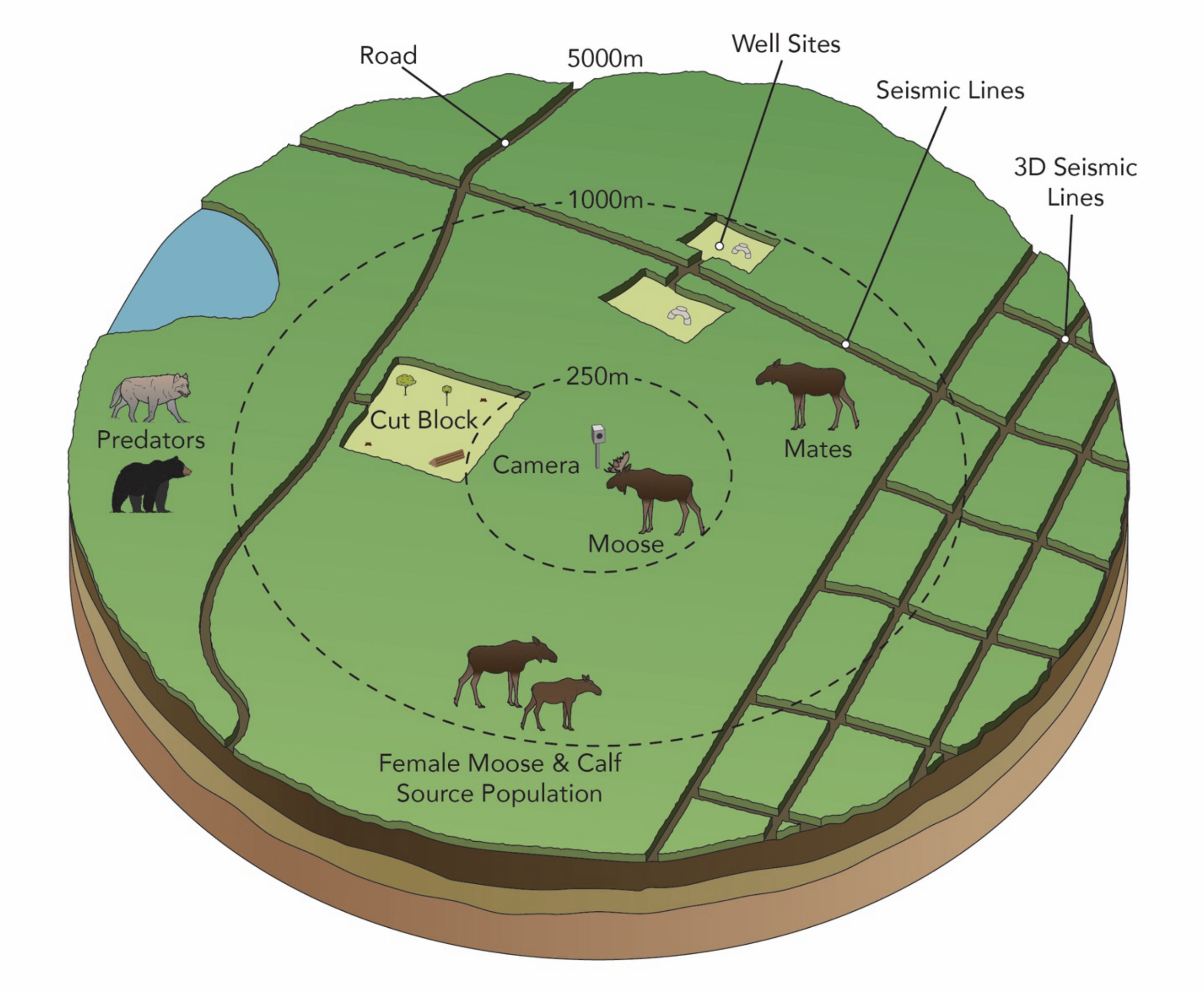


Figure 1. Schematic of a camera site within a Landscape Unit, and the features surrounding it. Within a 250-m radius of a camera the site is predominantly conifer forest (green), with some cutblock. Different features are captured as the spatial scale increases. So too does the ecological "neighborhood" of the moose, as its occurrence at a site can depend on the presence of conspecifics, competitors, and predators, which are cueing into landscape features aggregated at different scales.

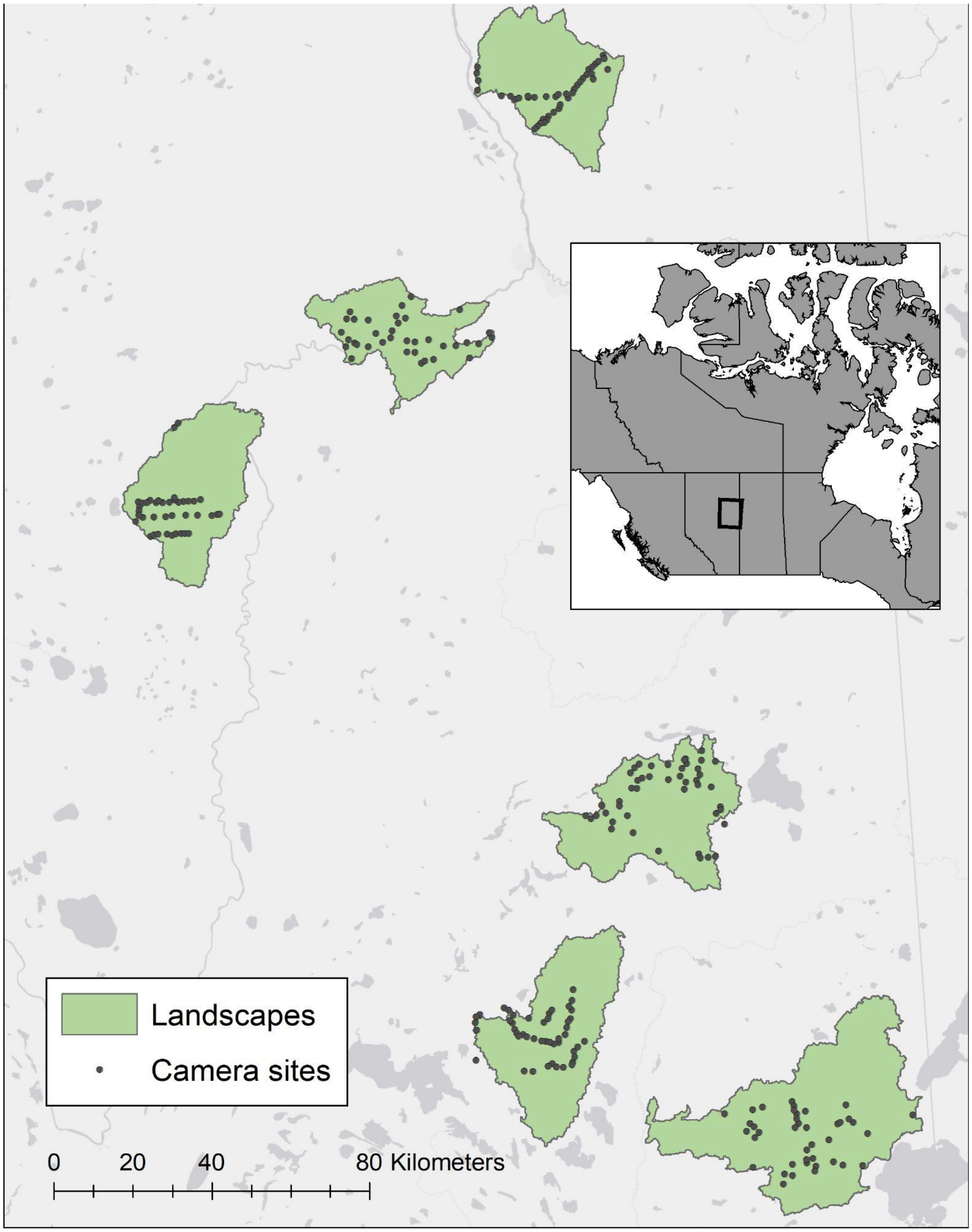


Figure 2: Map of study area in the Oil Sands Region (OSR) of Alberta, Canada with landscape units (LUs; in green) and camera deployment sites within each LU (black points).

Model framework

We define an “optimal spatial scale” as one at which quantified habitat explains species’ occurrence better than other scales (Holland et al. 2004, Fisher et al. 2011), as measured by AIC weight and model validation (Burnham and Anderson 2002a). To evaluate how the optimal spatial scale varies with species and different types of landscape processes (e.g., anthropogenic versus natural), we performed three distinct analyses. First, we assessed the best-fitting spatial scale for each species using only anthropogenic (HFI) covariates; in the second, we used only natural (landcover) covariates; and in the third, we employed a mixed approach incorporating both landscape types (i.e., global models). For all analyses, we constructed generalized linear mixed models (GLMMs) for the global models according to Equation 1, which was modified for the anthropogenic and natural landcover models (see below)

Equation 1:

$$\begin{aligned}\eta_{ij} = \beta_0 + B_1 Harvest_{ij} + \beta_2 Industrial_{ij} + \beta_3 Pipelines/TransmissionLines_{ij} \\ + \beta_4 SeismicLines_{ij} + \beta_5 3DSeismic_{ij} + \beta_6 Trails_{ij} + \ \beta_7 Wells_{ij} \\ + \ \beta_8 Developed_{ij} + \beta_9 Forest_{ij} + \beta_{10} Grassland_{ij} + \ \beta_{11} Shrub_{ij} + LU_j\end{aligned}$$

$$\text{logit}(\theta_{ij}) = \ \eta_{ij}$$

$$Monthly\ species\ occurrence_{ij} \sim \text{Bernoulli}(\theta_{ij})$$

$$LU_j \sim \text{Gaussian}(0, \sigma^2)$$

Monthly species occurrence is represented as the i^{th} observation at LU *j*, where LU is a random intercept with j^{th} level *j*= individual landscape unit. Monthly species occurrence was assumed to follow a Bernoulli distribution, whereby each month was considered an independent trial where a species was detected (1) or not detected (0) within a calendar month. Mammal occurrence was modeled as a proportional binomial response variable, and calculated as the proportion of months a species was present for all months that had 15 (approximately 0.5 month) or more fully operational camera days, with the months of December through March excluded from black bear occurrence calculations to account for their hibernation period. Note we treated 0's a true and not as in occupancy models (MacKenzie et al. 2002), which partition 0 in an e.g. 0101 detection history as error. Mammals temporarily emigrate from sites and the time spent in patch is a part of the biological process we are measuring. A non-detection of a species on a wildlife trail, with lure, in an entire month, is confidently treated as a true absence.

To enhance computational efficiency and facilitate comparisons of effect sizes, continuous variables were standardized (mean = 0, standard deviation = 1) for each spatial scale independently. For the anthropogenic analysis equation 1 was reduced to include harvest, industrial, pipelines/transmission lines, seismic lines, 3D seismic lines, trails, and wells as fixed effects while the natural landcover analysis included forest, grassland, and developed landcover types.

Models were constructed using the glmmTMB package in R version 4.2.1 (Brooks et al. 2017). To determine the most appropriate model (i.e., spatial scale) for each species, we used Akaike Information Criterion corrected for small sample size (AICc) and selected the lowest AICc as the most supported model (i.e., spatial scale) from each of the three analyses (Akaike 1998, Burnham and Anderson 2002a), using the MuMIn package (Bartoń 2020).

RESULTS

Camera operability and mammal detections

The study generated a total 208,655 non-blank images across all six LUs and 82,027 camera trap nights. Of those 178,730 images were of 22 different mammal species identifiable to the species level; the most common species detected on cameras was white-tailed deer (hereafter deer) with 67,643 images and the least common was the North American porcupine (*Erethizon dorsatum*) with 7 images. Other species detected in decreasing order of images included, black bear (46,306), moose (28,692), coyote (10,355), snowshoe hare (*Lepus americanus*; 10,218), wolf (4,482), North American red squirrel (*Tamiasciurus hudsonicus*; 3,798), lynx (2,344), caribou (1,452), fisher (1,188), red fox (782), marten (637), cougar (*Puma concolor*; 442), wolverine (*Gulo gulo*; 137), striped skunk (*Mephitis mephitis*; 66), river otter (*Lontra canadensis*; 38), long-tailed weasel (*Mustela frenata*; 38), elk (36), short-tailed weasel (*Mustela erminea*; 25), mule deer (*Odocoileus hemionus*; 9), and North American beaver (*Castor canadensis*; 9).

Evidence for domains of scale

Spatial scale domains emerged for some species but not all and differed between natural and anthropogenic landcover (Figure 3-5). For example, when considering both landcover types (i.e., global models) coyote, fisher, wolf, red fox, and white-tailed deer - to a lesser degree - all showed evidence of a domain, whereby spatial scales within ± 250m - 500m of the best-fit spatial scale had similar AICc scores and model weights to the best-fit buffer (Figure 3). However, when considering solely anthropogenic disturbance features, fisher, wolf, moose, and coyote - to a lesser degree - showed evidence of a domains (Figure 4); while moose, red fox, white-tailed deer with wolf and lynx - to a lesser degree - showed evidence of a characteristic scale when modeled with natural landcover features (Figure 5). Several species showed evidence of domains of scale with all three analyses; AICc scores for the best-fit models for coyote, fisher, and wolf were all <1 AICc from subsequent models of similar spatial scales (Table 2).

Optimal spatial scales for natural and anthropogenic landcover

Optimal spatial scales for each species – that which was best supported by weight of information-theoretic evidence – were also dependent on the types of landcover heterogeneity (Table 2). All three analyses – anthropogenic, natural, and combined landcover – were not in agreement on the optimal spatial scale for any species, although the optimal buffer for the global analysis aligned closely (e.g., optimal buffers were the same or within 250m) with either the anthropogenic or landscape analysis for all species except fishers (where the optimal global model was at a spatial scale between the optimal models for the other two analyses; Figure 6)). Additionally, the relative size of best-supported spatial scales varied across analyses, with no consistent pattern in spatial scale differences between anthropogenic, global, and landcover models. For example, fishers, wolf, lynx, red fox, and white-tailed deer all had smaller optimal spatial scales for anthropogenic models relative to the landcover models while black bear, caribou, coyote, and moose all had smaller optimal spatial scales for anthropogenic models relative to the landcover models (Figure 6).

Species-specific spatial scales

Within an analysis, the optimal spatial scale varied across species and encapsulated a large range of sizes with a minimum size of 250 meters for black bears (global and landcover models), lynx (global and anthropogenic), moose (global and landcover) and caribou (landcover) to 5,000m for coyote (global) (Figure 6). There were no discernable trends in best-supported spatial scales across species relating to either body size or trophic level. For example, our four largest species (black bear, white-tailed deer, caribou, and moose) had optimal spatial scales ranging from 250m – 4500m across the three analyses and our four smallest species (fisher, red fox, lynx, and coyote) had optimal spatial scales ranging from 250m – 5000m (Table 2).

DISCUSSION

Habitat loss is a major driver of global biodiversity loss, but the impacts of loss echo well beyond the patch or stand removed. In this multi-landscape analysis across the western boreal forest oil sands, the density of landscape change as far 4500-m away from a camera trap affected mammal species' relative abundance there. This is expected under theory; landscape supplementation, complementation, and other landscape processes appear as altered (e.g. harvested, removed, or fragmented) patches but manifest as population processes (Addicott et al. 1987, Pulliam and Danielson 1991, Dunning et al. 1992). Here, we show that landscape change amplifies well beyond the local patch, or the amount of habitat altered, to affect species' spatial distribution and relative abundance, and this is true of the entire mammal community we analyzed.

The spatial scale at which natural and anthropogenic heterogeneity best explained species' relative abundance varied among species, and not predictably. The optimal spatial scale was not related to body mass, as observed in the single-landscape study by Fisher et al. (2011) based on Hollings' spatial discontinuity hypothesis (Holling 1992). Nor was the optimal spatial scale related to trophic level, as expected since predators generally have larger home-range sizes than prey (Lindstedt et al. 1986, Kelt and Van Vuren 2001).

Moreover, the optimal scale differed among natural and anthropogenic features for all species except white-tailed deer. There was no directionality to these differences. We predicted that anthropogenic features, being a novel intrusion, would have spatially farther-reaching influence on species' space-use than do natural features. This was the case only for four of the nine species we analyzed (black bear, caribou, coyote, and moose), so does not hold generally.

Domains of scale – a series of spatial scales similar in size at which species-habitat relationships hold constant (Wiens 1989, Wiens and Milne 1989) – were not apparent across the community, observed only for a few species, and these domains varied among natural and anthropogenic models. In global (combined natural and anthropogenic models), evidence for scale domains was observed for five of nine species: coyote, fisher, wolf, red fox, and white-tailed deer. Anthropogenic disturbance models showed scale domains for only four species, and natural heterogeneity models showed scale domains for a different four species. We had hoped that this empirical analysis would follow theory and reveal some general laws (Lawton 1999, Allen and Hoekstra 2015) wherein optimal spatial scales are indeed "characteristic" sensu (Holland et al. 2004, Fisher et al. 2011), but this is not supported.

Nonetheless, optimal scales do plainly merge from multi-scale species-habitat models, as shown for multiple other taxa including beetles (Holland et al. 2005) and birds (Mahon et al. 2016, Stuber and Fontaine 2019, Mazziotta et al. 2024). The ramification for modelling is that is insufficient to choose a single spatial scale and then assume that habitat quantified at this scale provides the best explanation for habitat selection and spatial distribution. We echo former researchers in advocating for a multi-scale approach whenever possible.

The ramification for ecological conservation is that for many mammal species, the effects of anthropogenic landscape change on point estimates of relative abundance is manifested at spatial scales encompassing the "ecological neighborhood" (Addicott et al. 1987) around a camera site. Thu, the impact is more than habitat loss per se – whether it be cutting of mature forest for timber, replacement of natural habitat with early-seral vegetation as in well sites or building a road – but instead a change in the relative value of the surrounding landscape. This net value can be positive or negative, providing subsidies or risks, creating winners and losers

(Fisher and Burton 2018, Mahon et al. 2019). Mitigating the effects of development through restoration will therefore require large-scale planning that recovers multiple forms of disturbance, not simply seismic lines as is currently practiced (Tattersall et al. 2020b, Beirne et al. 2021a, Dickie et al. 2022).

Table 1: Names and descriptions of 11 Human Footprint Inventory (HFI) and land cover (LC) covariates used in generalized linear mixed effects models (GLMMs) of nine boreal mammal species in the Oil Sands region of Alberta, Canada. Descriptions for covariates were derived from the metadata documentation for Alberta Biodiversity Monitoring Institute's 'Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region' (HFI) and Alberta Biodiversity Monitoring Institute's 'Wall-to-Wall Land Cover Map 2010 Version 1.0'

Variable name	Variable type	Units	Unit description	Variable Description
Harvest	HFI	Proportion	The proportion of harvested areas within the buffer area.	Harvest is defined as, areas where forestry operations have occurred (clear-cut, selective harvest, salvage logging, etc.)
OSM industrial	HFI	Proportion	The proportion of various industrial features (i.e. borrowpits, clearings, facilities, and mines) within the buffer area.	Borrowpits, clearings, facilities, and mines are all defined in detail in Table S1 of the supporting information.
Pipelines and transmission lines	HFI	Proportion	The proportion of both pipelines and transmission lines within the buffer area.	Pipelines and transmission lines are defined in detail in Table S1 of the supporting information.
Seismic lines	HFI	Proportion	The proportion of seismic lines within the buffer area.	Seismic lines are defined as cleared corridors created during hydrocarbon exploration. They are a polygon feature class derived from a 3-meter buffer (6-meter total width) of a pre-low-impact-seismic centerline.
Seismic lines 3D	HFI	Proportion	The proportion of 3D seismic lines within the buffer area.	3D seismic lines are defined as cleared corridors created during hydrocarbon exploration. They are a polygon feature class derived from a 1.5-meter buffer (3-meter total width) of a pre-low-impact-seismic centerline.
Trails	HFI	Proportion	The proportion of trails within the buffer area	Trails are defined as cleared corridors surfaced with dirt or low vegetation for human/vehicle access.
Wells	HFI	Proportion	The proportion of wellsites within the buffer area	Wellsites are defined as, ground cleared for an oil/gas well pad where at least one well is currently active
Lc_developed	LC	Proportion	The proportion of developed land within the buffer area	Developed land is defined as urban and built-up areas (including industrial sites), impervious artificial surfaces (e.g. airport runaways), railways and roads.

Lc_forest	LC	Proportion	The proportion of coniferous, broadleaf, and mixed forests	Treed areas with at least a 10% crown closure of trees of any kind.
Lc_grassland	LC	Proportion	The proportion of grassland within the buffer area	Grasslands are defined as predominantly native grasses and other herbaceous vegetation with a minimum of 20% ground cover.
Lc_shrub	LC	Proportion	The proportion of shrubland within the buffer area	Shrubland is defined as at least 20% ground cover which is at least one-third shrub, with no or little presence of trees (<10% crown closure)

Table 2: Data for the most supported models (e.g. spatial scale) at predicting mammal presence/absence from three analyses (global, anthropogenic features, and landscape features) for nine mammal species in the oil sands region, Alberta, Canada. The most supported model (lowest AIC) from each analysis is listed along with the weight for that model and the delta Akaike Information Criterion (ΔAIC) for the next best performing model. Models in bold were >2 AIC lower than the next model.

Species	Top global model	Weight	ΔAIC*	Top anthropogenic model	Weight	ΔAIC*	Top landcover model	Weight	ΔAIC*
Black bear	**250m**	**0.678**	**5.15**	4000m	0.174	0.17	**250m**	**0.915**	**9.19**
Caribou	**1000m**	**0.796**	**4.63**	**1000m**	**0.884**	**5.16**	250m	0.222	1.23
Coyote	5000m	0.444	0.41	4750m	0.268	0.26	3750m	0.192	0.12
Fisher	1000m	0.266	0.84	250m	0.395	0.38	2500m	0.205	0.28
Grey wolf	3500m	0.303	0.45	2000m	0.245	0.09	3500m	0.243	0.26
Lynx	**250m**	**0.982**	**8.36**	**250m**	**0.996**	**12.94**	500m	0.207	1.40
Moose	**250m**	**0.941**	**7.02**	750m	0.526	0.90	**250m**	**0.988**	**11.28**
Red fox	4750m	0.367	0.03	**1750m**	**0.733**	**3.08**	4750m	0.325	0.26
White-tailed deer	1500m	0.234	0.16	**1500m**	**0.732**	**2.64**	**4500m**	**0.611**	**2.73**

*The delta AIC is presented for the next best model rather than the most supported model itself as the weight for all most supported models is zero, the delta AIC for the next best model is included to be transparent about the certainty of any one model.

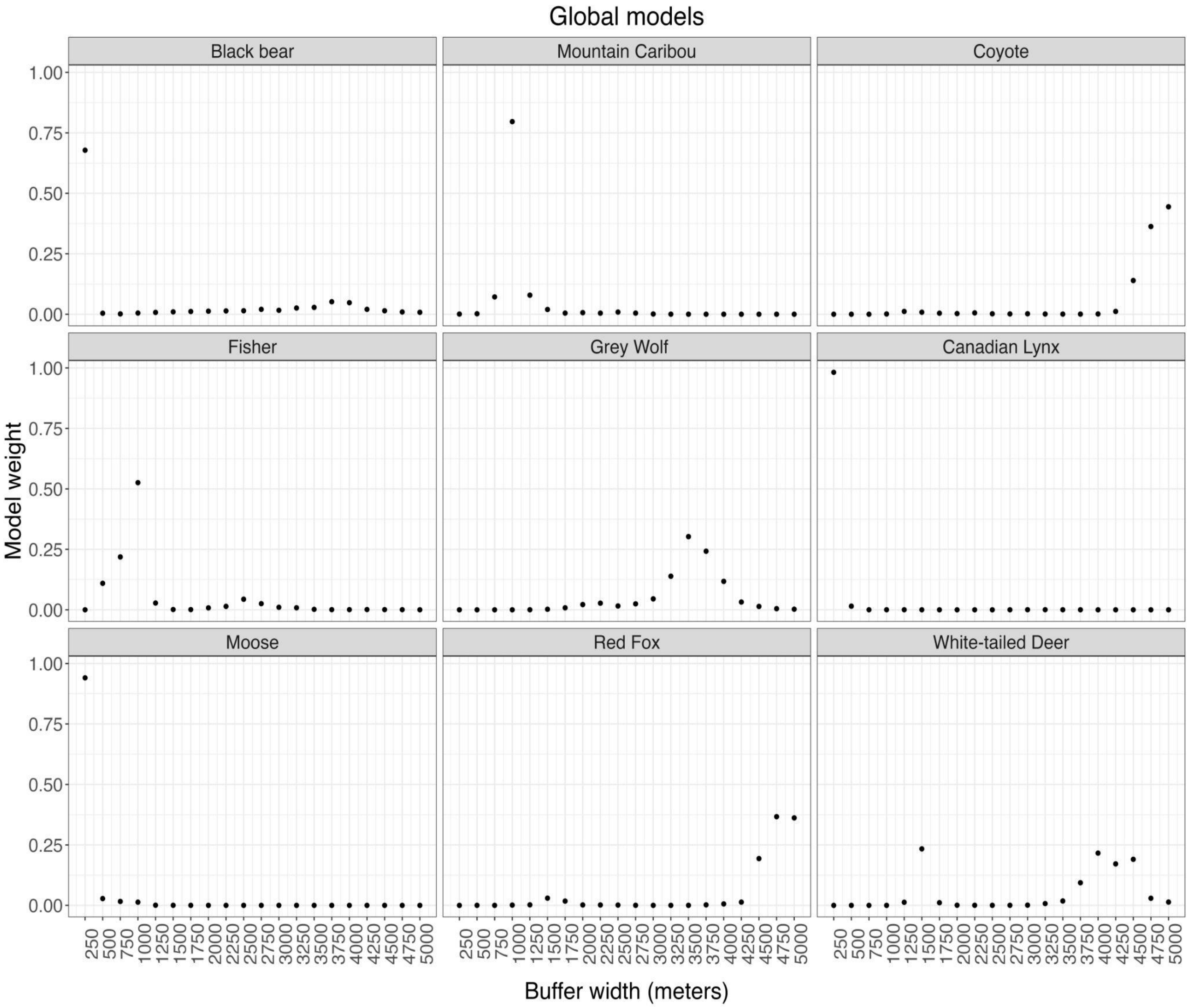


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Figure 3: Model weights plotted for each model at predicting mammal presence/absence for nine mammal species in the oil sands region, Alberta, Canada. Results are from model selection for global models (i.e., models that included both anthropogenic and landscape variables). All models included the same variables extracted at different buffer widths from the camera.

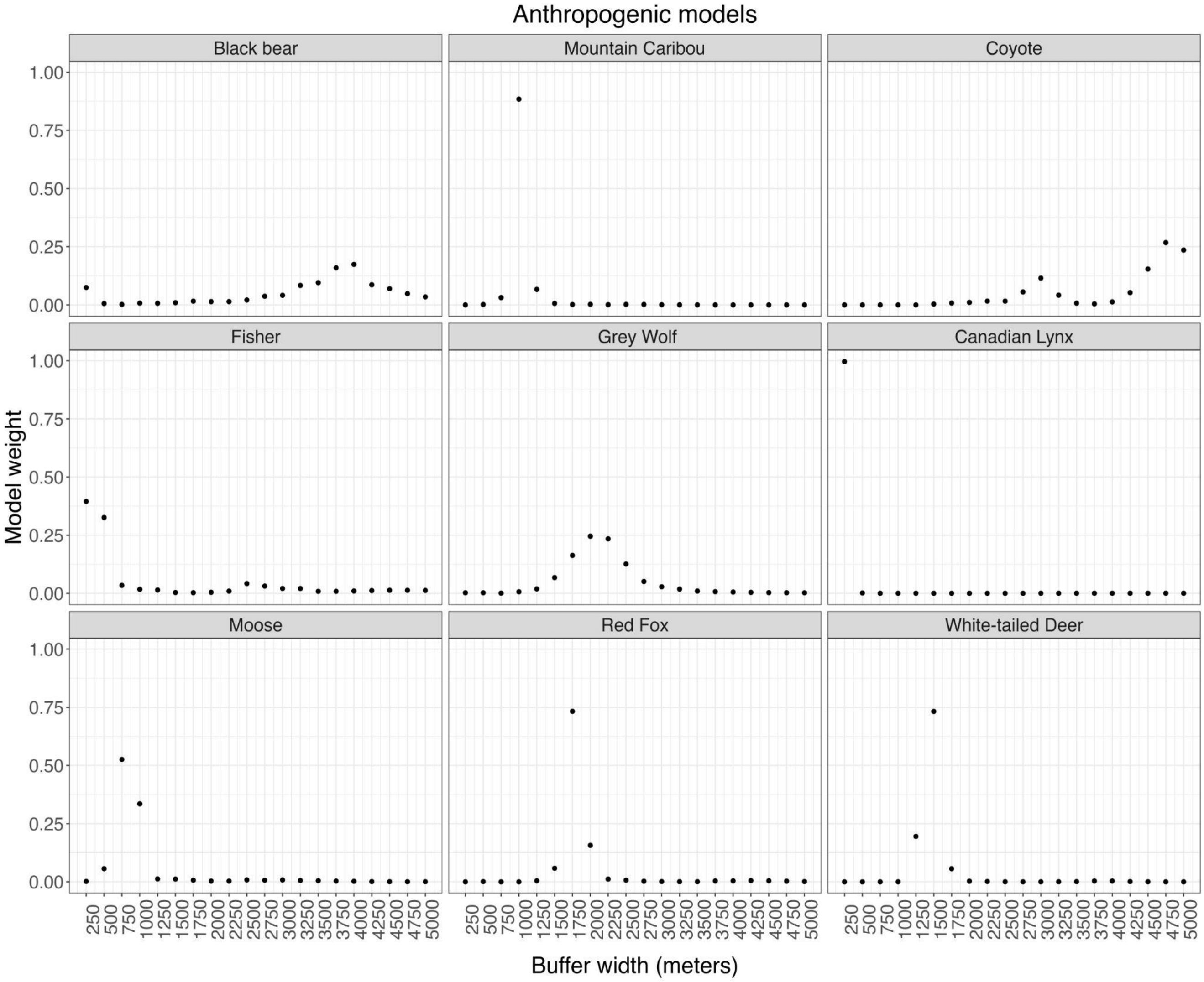

Figure 4: Model weights plotted for each model at predicting mammal presence/absence for nine mammal species in the oil sands region, Alberta, Canada. Results are from model selection for anthropogenic models (i.e., models that included only anthropogenic variables). All models included the same variables extracted at different buffer widths from the camera.

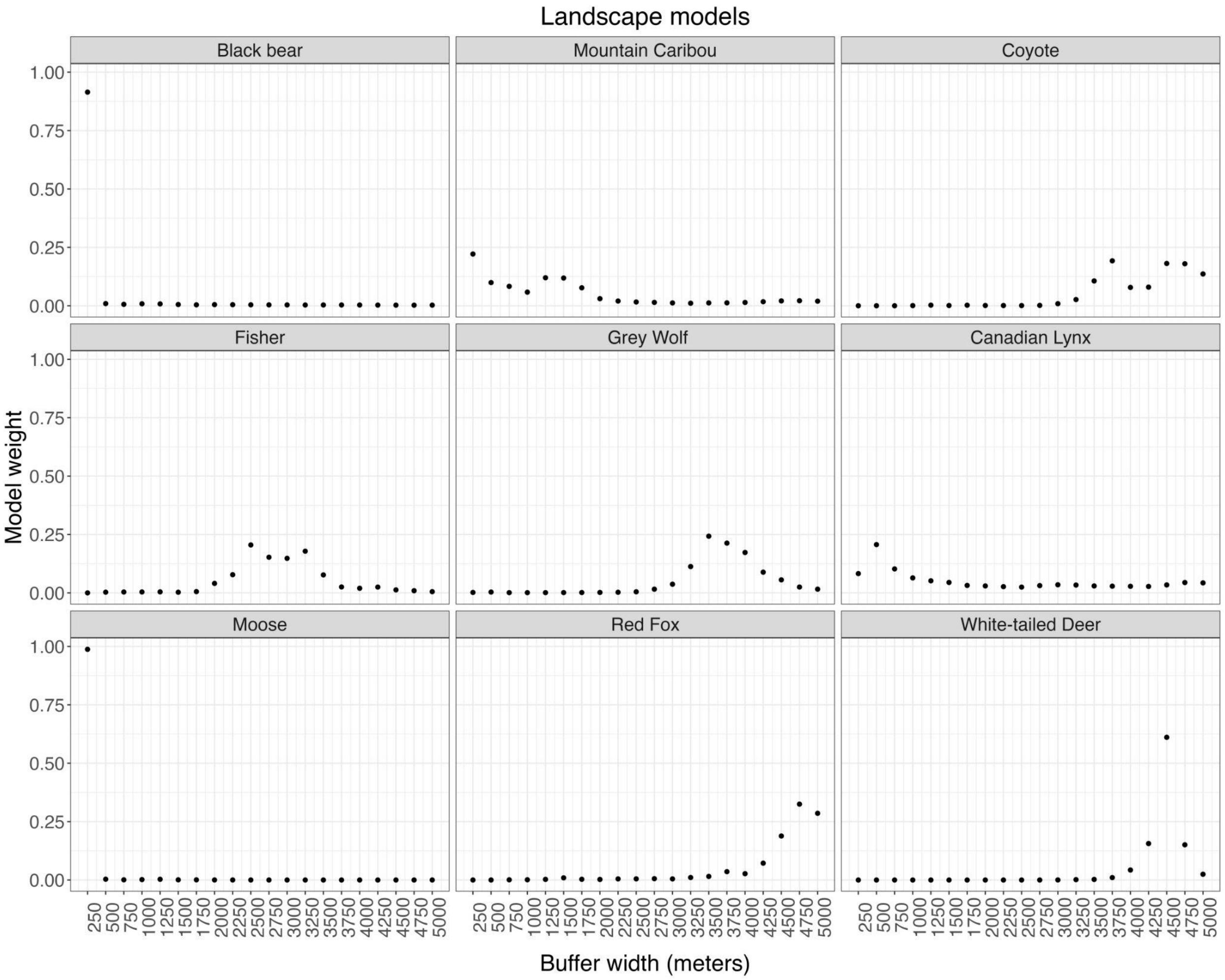

Figure 5: Model weights plotted for each model at predicting mammal presence/absence for nine mammal species in the oil sands region, Alberta, Canada. Results are from model selection for landscape models (i.e., models that included only landscape variables). All models included the same variables extracted at different buffer widths from the camera.

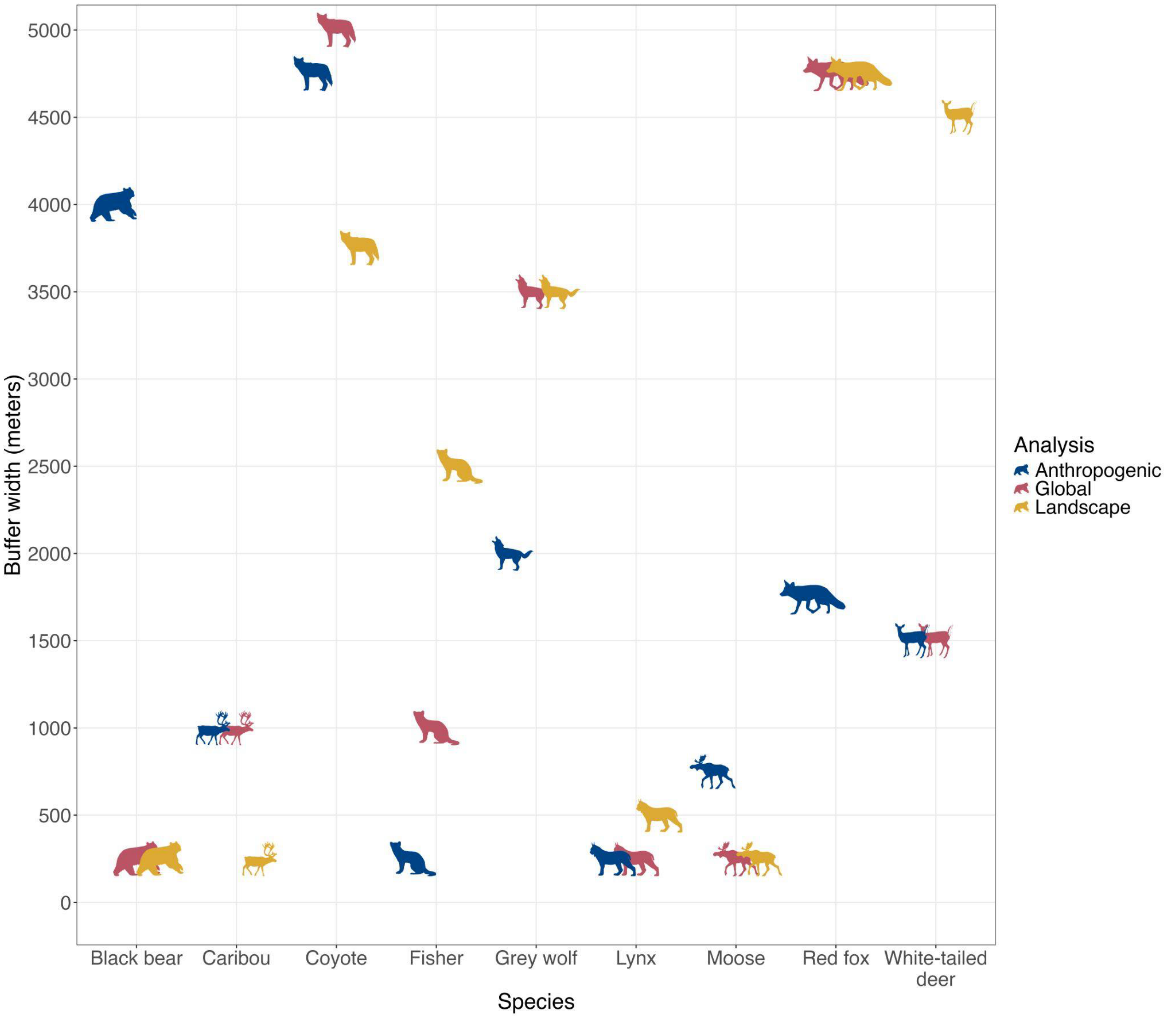

Figure 6: The best-supported spatial scales at which landscape features predicted mammal presence/absence, from three analyses plotted for each of nine mammal species in the oil sands region, Alberta, Canada. The anthropogenic analysis (blue) includes only Human Footprint Inventory (HFI) covariates, while the landscape analysis (yellow) includes only land cover types, and the global (pink) includes both types of variables. All models within an analysis included the same variables, the only difference was the buffer width used to calculate the proportions of each variable around a camera.

REFERENCES

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos:340-346.

Akaike, H. 1998. Information Theory and an Extension of the Maximum Likelihood Principle. Pages 199-213 *in* E. Parzen, K. Tanabe, and G. Kitagawa, editors. Selected Papers of Hirotugu Akaike. Springer, New York, NY.

Alberta Biodiversity Monitoring, I. 2010. Wall-to-wall Land Cover Inventory.

Alberta Biodiversity Monitoring, I. 2021. Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region.

Allen, T. F., and T. W. Hoekstra. 2015. Toward a unified ecology. Columbia University Press.

Allen, T. F. H., and T. Hoekstra. 1992. Toward a unified ecology New York (NY) Columbia University Press.

Barnas, A. F., B. J. Darby, D. T. Iles, D. N. Koons, R. F. Rockwell, C. A. D. Semeniuk, and S. N. Ellis-Felege. 2022. Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance. Journal of Avian Biology **2022**:e02840.

Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J. Paczkowski, F. E. C. Stewart, E. Tattersall, and J. T. Fisher. 2024. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Science of The Total Environment **915**:169285.

Bartoń, K. 2020. MuMIn: Multi-Model Inference.

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dillegeard, D. Farr, J. Fisher, M. Freemark, K. Foster, C. Godwin, C. Herbert, D. Huggard, D. McIssac, T. Narwani, S. Nielsen, B. Pauli, S. Prasad, D. Roberts, S. Slater, S. Song, S. Swanson, P. Thomas, J. Toms, C. Twitchell, S. White, F. Wyatt, and L. Mundy. 2021. A Before-After Dose-Response (BADR) Terrestrial Biological Monitoring Framework for the Oil Sands. OSM Technical Report Series 7.

Beirne, C., C. Sun, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2021. Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics. Journal of Applied Ecology **58**:2821-2832.

Boucher, N. P., M. Anderson, A. Ladle, C. Procter, S. Marshall, G. Kuzyk, B. M. Starzomski, and J. T. Fisher. 2022. Cumulative effects of widespread landscape change alter predator–prey dynamics. Scientific Reports **12**:11692.

Brooks, M. E., K. Kristensen, K. J. v. Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal **9**:378.

Burnham, K., and D. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach 2nd EditionSpringer-Verlag. New York, New York.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.

Caravaggi, A., P. B. Banks, A. C. Burton, C. M. V. Finlay, P. M. Haswell, M. W. Hayward, M. J. Rowcliffe, and M. D. Wood. 2017. A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation **3**:109-122.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances **1**:e1400253.

Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences **114**:E6089-E6096.

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology letters **16**:4-16.

Cove, M. V., R. Kays, H. Bontrager, C. Bresnan, M. Lasky, T. Frerichs, R. Klann, T. E. Lee Jr, S. C. Crockett, A. P. Crupi, K. C. B. Weiss, H. Rowe, T. Sprague, J. Schipper, C. Tellez, C. A. Lepczyk, J. E. Fantle-Lepczyk, S. LaPoint, J. Williamson, M. C. Fisher-Reid, S. M. King, A. J. Bebko, P. Chrysafis, A. J. Jensen, D. S. Jachowski, J. Sands, K. A. MacCombie, D. J. Herrera, M. van der Merwe, T. W. Knowles, R. V. Horan Iii, M. S. Rentz, L. S. E. Brandt, C. Nagy, B. T. Barton, W. C. Thompson, S. P. Maher, A. K. Darracq, G. Hess, A. W. Parsons, B. Wells, G. W. Roemer, C. J. Hernandez, M. E. Gompper, S. L. Webb, J. P. Vanek, D. J. R. Lafferty, A. M. Bergquist, T. Hubbard, T.

Forrester, D. Clark, C. Cincotta, J. Favreau, A. N. Facka, M. Halbur, S. Hammerich, M. Gray, C. C. Rega-Brodsky, C. Durbin, E. A. Flaherty, J. M. Brooke, S. S. Coster, R. G. Lathrop, K. Russell, D. A. Bogan, R. Cliché, H. Shamon, M. T. R. Hawkins, S. B. Marks, R. C. Lonsinger, M. T. O'Mara, J. A. Compton, M. Fowler, E. L. Barthelmess, K. E. Andy, J. L. Belant, D. E. Beyer Jr, T. M. Kautz, D. G. Scognamillo, C. M. Schalk, M. S. Leslie, S. L. Nasrallah, C. N. Ellison, C. Ruthven, S. Fritts, J. Tleimat, M. Gay, C. A. Whittier, S. A. Neiswenter, R. Pelletier, B. A. DeGregorio, E. K. Kuprewicz, M. L. Davis, A. Dykstra, D. S. Mason, C. Baruzzi, M. A. Lashley, D. R. Risch, M. R. Price, M. L. Allen, L. S. Whipple, J. H. Sperry, R. H. Hagen, A. Mortelliti, B. E. Evans, C. E. Studds, A. P. K. Sirén, J. Kilborn, C. Sutherland, P. Warren, T. Fuller, N. C. Harris, N. H. Carter, E. Trout, M. Zimova, S. T. Giery, F. Iannarilli, S. D. Higdon, R. S. Revord, C. P. Hansen, J. J. Millspaugh, A. Zorn, J. F. Benson, N. H. Wehr, J. N. Solberg, B. D. Gerber, J. C. Burr, J. Sevin, A. M. Green, Ç. H. Şekercioğlu, M. Pendergast, K. A. Barnick, A. J. Edelman, J. R. Wasdin, A. Romero, B. J. O'Neill, N. Schmitz, J. M. Alston, K. M. Kuhn, D. B. Lesmeister, M. A. Linnell, C. L. Appel, C. Rota, J. L. Stenglein, C. Anhalt-Depies, C. Nelson, R. A. Long, K. Jo Jaspers, K. R. Remine, M. J. Jordan, D. Davis, H. Hernández-Yáñez, J. Y. Zhao, and W. J. McShea. 2021. SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. Ecology **102**:e03353.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology **54**:253-263.

Dickie, M., G. G. Sherman, G. D. Sutherland, R. S. McNay, and M. Cody. 2022. Evaluating the impact of caribou habitat restoration on predator and prey movement. Conservation Biology **37**:e14004.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science **345**:401-406.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos:169-175.

Dyck, M. A., R. Iosif, B. Promberger–Fürpass, and V. D. Popescu. 2022. Dracula's ménagerie: A multispecies occupancy analysis of lynx, wildcat, and wolf in the Romanian Carpathians. Ecology and Evolution **12**:e8921.

Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment **6**:439-447.

Ethier, C. A., A. F. Barnas, N. P. Boucher, K. Baillie-David, and J. T. Fisher. 2024. Lethal wolf control elicits change in moose habitat selection in unexpected ways. The Journal of Wildlife Management **88**:e22620.

Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. M. Kay, H. A. Sander, B. Macdougall, C. M. Salsbury, T. J. Ryan, J. L. Angstmann, J. Amy Belaire, B. Dugelby, C. J. Schell, T. Stankowich, M. Amaya, D. Drake, S. H. Hursh, A. A. Ahlers, J. Williamson, L. M. Hartley, A. J. Zellmer, K. Simon, and S. B. Magle. 2021. Landscape-scale differences among cities alter common species' responses to urbanization. Ecological Applications **31**.

Fisher, J. T. 2025. Ecological Insights From Camera Trapping Span Biological Taxa, and the Globe. Ecology and Evolution **15**:e70947.

Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution **1**:517-528.

Fisher, J. T., and A. C. Burton. 2018. Wildlife winners and losers in an oil sands landscape. Frontiers in Ecology and the Environment **16**:323-328.

Fisher, J. T., and A. C. Burton. 2021. Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. Ecology and Evolution **11**:900-911.

Fisher, J. T., F. Grey, N. Anderson, J. Sawan, N. Anderson, S.-L. Chai, L. Nolan, A. Underwood, J. Amerongen Maddison, H. W. Fuller, and S. Frey. 2021. Indigenous-led camera-trap research on traditional territories informs conservation decisions for resource extraction. FACETS **6**:1266-1284.

Fisher, J. T., and A. Ladle. 2022. Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. Science of The Total Environment **822**:153432.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal Review **35**:51-81.

Fuller, H. W., S. Frey, and J. T. Fisher. 2023. Integration of aerial surveys and resource selection analysis indicates human land use supports boreal deer expansion. Ecological Applications **33**:e2722.

Greenberg, S., T. Godin, and J. Whittington. 2019. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution **9**:13706-13730.

Holbrook, S. J., and R. J. Schmitt. 1988. The Combined Effects of Predation Risk and Food Reward on Patch Selection. Ecology **69**:125-134.

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. Bioscience **54**:227-233.

Holland, J. D., L. Fahrig, and N. Cappuccino. 2005. Body size affects the spatial scale of habitat–beetle interactions. Oikos **110**:101-108.

Holland, J. D., and S. Yang. 2016. Multi-scale studies and the ecological neighborhood. Current Landscape Ecology Reports **1**:135-145.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Iosif, R., V. D. Popescu, L. Ungureanu, C. Şerban, M. A. Dyck, and B. Promberger-Fürpass. 2022. Eurasian lynx density and habitat use in one of Europe's strongholds, the Romanian Carpathians. Journal of Mammalogy **103**:gyab157.

Jacques, C. N., R. W. Klaver, T. C. Swearingen, E. D. Davis, C. R. Anderson, J. A. Jenks, C. S. Deperno, and R. D. Bluett. 2019. Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps. Wildlife Society Bulletin **43**:256-264.

Johnson, C. J., and R. V. Rea. 2023. Response of moose to forest harvest and management: a literature review. Canadian Journal of Forest Research **54**:366-388.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling for carnivores. Carnivore ecology and conservation: a handbook of techniques:47-69.

Kelt, D. A., and D. H. Van Vuren. 2001. The ecology and macroecology of mammalian home range area. The American Naturalist **157**:637-645.

Lawler, J. J., and C. E. Torgersen. 2020. Assessing the Relative Importance of Factors at Multiple Spatial Scales Affecting Terrestrial and Aquatic Wildlife. Current Landscape Ecology Reports **5**:12-24.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos:177-192.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology **73**:1943-1967.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology **67**:413-418.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences **51**:1207-1210.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**:2200-2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248-2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier.

Mackenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105-1114.

Mahon, C. L., G. Holloway, P. Sólymos, S. G. Cumming, E. M. Bayne, F. K. Schmiegelow, and S. J. Song. 2016. Community structure and niche characteristics of upland and lowland western boreal birds at multiple spatial scales. Forest Ecology and Management **361**:99-116.

Mahon, C. L., G. L. Holloway, E. M. Bayne, and J. D. Toms. 2019. Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. Ecological Applications **29**:e01895.

Mazziotta, A., A. Lindén, K. Eyvindson, S. Bianchi, A. Kangas, M. Melin, L. Ruha, and J. T. Forsman. 2024. Unraveling the characteristic spatial scale of habitat selection for forest grouse species in the boreal landscape. Forest Ecology and Management **563**:122008.

McKay, T. L., and L. A. Finnegan. 2022. Predator–prey co-occurrence in harvest blocks: Implications for caribou and forestry. Conservation Science and Practice **4**:e12847.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface Focus **2**:205-216.

Meek, P. D., G.-A. Ballard, P. J. S. Fleming, M. Schaefer, W. Williams, and G. Falzon. 2014. Camera Traps Can Be Heard and Seen by Animals. PLOS ONE **9**:e110832.

Nams, V. O., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes–an example with grizzly bears. Biological Conservation **128**:109-119.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera traps in animal ecology: methods and analyses. Springer.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. 2015. The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. Canadian Journal of Forest Research **45**:732-743.

Pickell, P. D., N. C. Coops, S. E. Gergel, D. W. Andison, and P. L. Marshall. 2016. Evolution of Canada's boreal forest spatial patterns as seen from space. PLOS ONE **11**:e0157736.

Pickell, P. D., S. E. Gergel, N. C. Coops, and D. W. Andison. 2014. Monitoring forest change in landscapes under-going rapid energy development: challenges and new perspectives. Land **3**:617-638.

Porter, J., R. Price, and R. McCrossan. 1982. The western Canada sedimentary basin. Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences **305**:169-192.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**:S50-S66.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual review of ecology and systematics **15**:523-575.

Roberts, D. R., E. M. Bayne, D. Beausoleil, J. Dennett, J. T. Fisher, R. O. Hazewinkel, D. Sayanda, F. Wyatt, and M. G. Dubé. 2022. A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. Integrated Environmental Assessment and Management **18**:388-406.

Routh, M. R., and S. E. Nielsen. 2021. Dynamic patterns in winter ungulate browse succession in the Boreal Plains of Alberta. Forest Ecology and Management **492**:119242.

Sarkar, S. 1984. Hierarchy: Perspectives for Ecological Complexity. JSTOR.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785-791.

Smith, R. 2018. Evaluating the impacts of anthropogenic development on large mammals across protected and industrialized landscapes in Western Canada. University of Victoria.

Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. T. Fisher, C. Burton, S. E. Townsend, C. Carbone, J. M. Rowcliffe, J. Whittington, J. Brodie, J. A. Royle, A. Switalski, A. P. Clevenger, N. Heim, and L. N. Rich. 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**:26-34.

Stewart, F. E. C., J. P. Volpe, and J. T. Fisher. 2019. The Debate About Bait: A Red Herring in Wildlife Research. The Journal of Wildlife Management **83**:985-992.

Stuber, E. F., and J. J. Fontaine. 2019. How characteristic is the species characteristic selection scale? Global Ecology and Biogeography **28**:1839-1854.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020. Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape. Biological Conservation **241**:108295.

Trenberth, K. E. 2018. Climate change caused by human activities is happening and it already has major consequences. Journal of Energy & Natural Resources Law **36**:463-481.

Trolliet, F., C. Vermeulen, M.-C. Huynen, and A. Hambuckers. 2014. Use of camera traps for wildlife studies: a review. Biotechnologie, Agronomie, Société et Environnement **18**.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual review of ecology and systematics:171-197.

Urban, D. 2014. On Scale and Pattern. The Bulletin of the Ecological Society of America **95**:124-125.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.

Wiens, J. A., and B. T. Milne. 1989. Scaling of ‘landscapes’ in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology **3**:87-96.

Wiewel, A. S., W. R. Clark, and M. A. Sovada. 2007. Assessing Small Mammal Abundance with Track-Tube Indices and Mark–Recapture Population Estimates. Journal of Mammalogy **88**:250-260.

Wittische, J., S. Heckbert, P. M. A. James, A. C. Burton, and J. T. Fisher. 2021. Community-level modelling of boreal forest mammal distribution in an oil sands landscape. Science of The Total Environment **755**:142500.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. . Methods in Ecology and Evolution **1**:3-14.

5. WHAT'S UP WITH BLACK BEARS? SEASON AND DEMOGRAPHIC DRIVE OCCURRENCE ON OIL SANDS DISTURBANCE FEATURES

Megan Braun, Andrew F. Barnas, Jason T. Fisher

OSM SUMMARY

Black bears are one the indicators signalled by Indigenous community members as being culturally important. The effects of OS development on black bears have been very ambiguous, with a few studies showing contextual and contrasting responses (Tigner et al. 2014, Fisher and Burton 2018, Fisher and Ladle 2022b). We hypothesized that because previous studies have lumped together different age-classes and seasons, that approach may be obscuring responses to OS features if these differ among those members of the population and through time. We split up our data into seasons and identified bears with and without cubs, and our hypotheses were confirmed: bears react to OS features differently in different seasons and depending on whether they have a cub or not. Thus, we show that OS features do indeed have demonstrable and strong effects on this important mammal species, as do other features, and that perceived risk of humans is a likely mechanism for some of these responses. This knowledge will help guide an understanding of *how* OS features affect bears, to inform any mitigation actions and future landscape planning.

Abstract

Habitat selection by wildlife can depend on trade-offs between the spatiotemporal distribution of perceived risks and rewards, both of which anthropogenic disturbance may alter. In the western Nearctic boreal forest, landscape changes associated with petroleum extraction

have altered habitat availability for multiple mammals in clear patterns. However, one species - black bear – presents unique challenges. Black bear habitat selection in relation to disturbance lacks consensus, with contrasting results indicating that response to disturbance remain largely unknown. However, previous research has not considered potential seasonal and demographic influences on behaviour. Here, we hypothesized that feature use by black bears depends on a trade-off between associated benefits and risks, which vary seasonally, and that different bear demographics (i.e., solitary adults versus females with young) weigh these benefits and risks differently, manifesting as differential habitat selection. Using data from 233 camera-traps deployed across six landscapes across a gradient of disturbance, we constructed a candidate set of generalized linear mixed models with predictors hypothesized to influence bear occurrence. In support of our hypothesis, we found that bear occurrence in relation to disturbance features varied seasonally and between demographic groups. Most notably, solitary adult occurrence was negatively affected by roads in spring and fall but not summer, indicating a potential risk response to hunting activity in the former seasons. Solitary adult occurrence was also positively influenced by moose in spring (likely from calf predation), and negatively by linear features used by off-highway vehicles in summer and fall. Female with young occurrence was negatively influenced by roads in all seasons, and by linear features in spring and fall. This study was conducted as part of the Oil Sands Monitoring Program, and results will directly inform conservation initiatives. Broadly, the work provides key insights into how changing risk-reward trade-offs drives variation in habitat selection by wildlife over time and between demographics.

Introduction

Habitat selection by wildlife can depend on a trade-off between the spatial distribution of perceived risks and rewards across a landscape. In this trade-off, if high reward food-rich habitats also have high risk (e.g. abundant predators), then lower reward food-poor habitats with less risk may be preferred (Holbrook and Schmitt 1988b). Further, risk-reward trade-offs are not static, but rather dynamic and fluctuate over an animal's lifespan. Trade-offs in habitats may vary temporally when risks and rewards themselves vary temporally: for example, predation risk changing along with the diurnal pattern of predator activity (Lima and Dill 1990), or forage availability fluctuating by season. The willingness of an animal to take risks can also shift though time based on life history stage. For example, under parental investment theory (Trivers, 1972), animals with offspring may prioritize avoiding risks to increase chances of offspring survival (Ben-David et al. 2004).

Dynamic assessment of trade-offs by animals is further complicated by anthropogenic disturbance, which can alter the spatiotemporal distributions of risks and rewards on the landscape. Anthropogenic disturbances present a number of new perceived risks, such as roads with noisy vehicles and collision risk (Poulin et al. 2023), but also benefits such as food availability from waste disposal near settlements. For prey species, human disturbance can also confer an interesting benefit known as the "human shield" effect, where prey may occur close to disturbances/human activity to buffer against predators if they avoid these risky areas (Berger 2007).

Within the Nearctic western boreal forest lies Alberta's Oil Sands Region (OSR), where largescale anthropogenic landscape change associated with petroleum extraction, timber harvest, and transportation has influenced mammal habitat selection (Pickell et al. 2013, Roberts et al.

2022). These landscape disturbances are typically categorized as polygonal features (e.g., oil well sites) and linear features (e.g., seismic lines), which act differently on different mammal species (Roberts et al. 2022). Depending on species-specific resource requirements, features result in "winner" species that generally benefit from the disturbances, and "losers" which are negatively impacted (Fisher and Burton 2018). Numerous studies have investigated the responses of individual species, and the mammal community as a whole, to disturbance features, ultimately to direct industrial activities and restoration efforts (Fisher and Burton 2018, Beirne et al. 2021b, Wittische et al. 2021a). Although clear and consistent patterns have emerged for some species, such as the use of linear features by canids (Wittische et al. 2021a), there is still uncertainty regarding the responses of some community members, especially the large, omnivorous black bear (*Ursus americanus*).

Black bear habitat selection in relation to linear and polygonal disturbances in the OSR is largely inconsistent, with research indicating either a positive (Mosnier et al. 2008, Bayne 2011, Latham et al. 2011a, Tigner et al. 2014, Demars and Boutin 2018, Dickie et al. 2020b), negative (Fisher and Burton 2018, Fisher and Ladle 2022c, Cuveira-Santos 2024), or negligible attraction to disturbance features (Beirne et al. 2021b). Ultimately, this lack of consensus signifies that overall, black bear preference and use of these features is unknown, making it impossible to draw informative conclusions for management actions. However, it is possible that these analyses were performed at scales inadequate to discern extant relationships. Studies on black bear habitat selection in the OSR have largely considered feature response over the entire active season (i.e., the period where bears are not undergoing hibernation) and without demographic discernment (with the exception of select telemetry work, ex. Latham et al. (2011a)). However, black bear behaviour is both highly seasonal (Pelchat and Ruff 1986) and varies by demographic group (Gantchoff et al. 2019). Consequently, important patterns of feature response could have been previously overlooked due to a lack of consideration of bear biology, warranting a finer scale investigation into potential mechanisms (i.e., risks and rewards) that dictate both feature attraction and avoidance.

Several factors could mediate black bear attraction to linear and polygonal features. First, forage subsidies are provided throughout the active season in both feature types. Black bears are opportunistic omnivores, consuming primarily vegetation and tending to select available food with the highest nutrient content (Pelchat and Ruff 1986). Past research into the plant component of their diet by Pelchat and Ruff (1986) in the Alberta boreal forest suggests that this can be divided temporally into several stages. Upon emergence from hibernation, bears start by consuming green vegetation, shifting to early ripening berries by mid-July and then to late-ripening berries by mid-August until hibernation onset. Other diet analyses conducted throughout the boreal forest are consistent with these general stages (Raine and Kansas 1990, Mosnier et al. 2008, Romain et al. 2013, Lesmerises et al. 2015). Most plants in their diet are abundant in early-seral vegetation communities such as on linear and polygonal features (Fisher and Wilkinson 2005, Dabros et al. 2018), and the spring green-up may occur earlier relative to forested landcover due to higher solar irradiation (Mosnier et al. 2008). Berry species also appear to thrive in disturbance features: Velvet leaf blueberry (*Vaccinium myrtilloides*) was found to have significantly greater vigour and fruit production on seismic lines relative to adjacent forest (Dawe et al. 2017) and significantly higher berry production in open canopies (Nielsen et al. 2020).

Second, linear features provide movement subsidies. Seismic lines facilitate travel between vegetation patches and can enhance the search for animal prey (Bastille-Rousseau et al.

2011, Dickie et al. 2020b, Tattersall et al. 2023b). In the western Nearctic boreal forest, mammalian prey species of black bears include snowshoe hare and neonates of ungulates like white-tailed deer, caribou, and moose (Latham et al. 2011a, Lesmerises et al. 2015). These movement benefits may be particularly important in the spring when there are newborn fawns and calves, and when vegetation is both scarcer and nutrient-poor, thus requiring more frequent movements between patches (Young and Ruff 1982).

Although disturbance features provide forage and movement subsidies throughout the active season, feature use may depend on weighting these benefits with associated risks. One risk that could result in feature avoidance is the presence of human hunters on and near features. In Alberta, there are both spring and fall hunting seasons for black bears, and hunting is the primary source of mortality (Alberta Government 2016). During these periods, hunting risk may cause black bears to avoid linear features, which are used as access routes for hunters (Dabros et al. 2018), as well as polygonal features, where bears could easily be spotted. Stillfried et al. (2015) support this conjecture, wherein black bears increased avoidance of non-paved roads (which were used as hunter access routes) during the hunting season relative to the non-hunting season. Ordiz et al. (2012) also found evidence that bears are aware of hunting risk, altering their behaviour and movement patterns during hunting seasons.

Risk of feature use may, however, vary by demographic group. For females with dependent young, another risk that drives habitat selection is the presence of solitary male and female black bears. Infanticide can be a major source of cub mortality in bear populations, and females with young have been shown spatially segregate themselves from other bears even if this means selecting habitats with poorer food resources (Ben-David et al. 2004, Czetwertynski 2008, Gantchoff et al. 2019). If solitary adult bears are using the disturbance features for the forage and movement subsidies, it is therefore possible that females with cubs will avoid them despite these benefits. However, this pattern may reverse temporally if solitary adult bears avoid the features during the spring and fall hunts. Females with cubs are protected from harvesting (Alberta Government 2016) and there is evidence that they could be aware of this protection. Ordiz et al. (2012) found that movement patterns of females with cubs were barely altered by the hunting season relative to solitary adult bears. Additionally, Stillfried et al. (2015) found that female black bears selected habitat much closer to the unpaved roads during the hunting season than males. They suggested this could be due to cub presence, and that females may be using hunter proximity as a human shield against other bears (Stillfried et al. 2015). It is possible that a similar phenomenon occurs with OSR disturbance features.

The objective of this study is to weigh evidence for competing hypotheses about black bear habitat selection in relation to OSR disturbance features. It is also to determine the importance of disturbance features in driving habitat selection relative to other predictors, such as prey abundance and natural landcover. We hypothesize that (1) bear use of features varies seasonally as risks and subsidies are differentially present, and (2) feature use varies for bears with dependent young, versus solitary adult bears, due to susceptibility to different risks (hunting for the former, infanticide for the latter). We predict that solitary adult bears will avoid linear and polygonal disturbance features during the spring and fall hunting seasons but will use features in the summer to benefit from forage and movement subsidies. Conversely, we predict that females with young will be attracted to linear and polygonal features during the hunting seasons to benefit from subsidies and the "shield" against infanticide risk but will avoid them in the summer due to the presence of solitary adult bears.

Methods

Study area

This study was situated in the boreal ecozone of northeastern Alberta, Canada. The landscape here is characterized by a mixture of upland forests composed of jack pine, white spruce, aspen, and lodgepole pine, and lowland muskegs dominated by larch and black spruce (Pickell et al. 2013). Forests present as a patchwork of different stand ages due to the occurrence of frequent natural disturbances including insects and wildfire (Pickell et al. 2013). Underlying this landscape is one of the worlds' largest hydrocarbon deposits, which initially spurred the establishment of the OSR (Alberta Government 2023). The OSR is composed of three administrative regions that together account for 21% of the province's land area (Bayne et al., 2021) Throughout the OSR, there is significant industrial development that has resulted in widespread landscape change (Pickell et al. 2016a). With respect to bitumen extraction, surface mining is restricted to a relatively small portion of the Athabasca region, while in situ mining is prevalent throughout the rest of the area, resulting in dense networks of disturbance features including roads, seismic lines, pipelines, and well pads (Bayne et al., 2021).

Camera trap arrays

To investigate black bear habitat selection, detection data was acquired from camera traps placed within six different study landscapes ("landscape units") throughout the OSR (Fig. 1.). Defined by watershed boundaries, each landscape unit was approximately 1000 km^2, and varied in their respective level of anthropogenic disturbance to span a gradient of low to high intensity (Bayne 2021). To select camera deployment locations (i.e., camera "sites"), landscapes were first stratified by dominant forest class (>50%; conifer, deciduous, and mixed wood) to account for natural variability in sampling locations. Then, each landscape unit was overlain by a grid of 2-

km^2 hexagonal cells in ArcGIS Desktop (ESRI 2014) with the cell size chosen to enable sufficient spacing between cameras for independence in species-habitat models (Zuckerberg et al. 2020b). 30 cells were randomly selected from each stratum. For ease of site access, cells were constrained to within 100 meters of accessible roads (when possible), except for LU21 where all sites were reached via helicopter.

Among the selected cells in each landscape, 40 – 50 Reconyx PC900 Hyperfire infrared remote digital cameras (Holmen, WI) were deployed, with one camera per cell. Detection probability for wildlife was enhanced by placing cameras along an active game trail (Fisher and Burton 2018) and by administering scent lure (O'Gorman's™ Long Distance Call) on a tree 4-7 meters in front of each camera. Cameras were also placed approximately 1 meter from the ground, and a minimum of 100 meters from active roads and 1 kilometer from other cameras. Additionally, cameras were set to high sensitivity, and once triggered, were programmed to take a single photograph with no delay between consecutive triggers. A 'timelapse' photo was programmed to be taken at the same time daily to ensure functionality.

In two arrays, cameras were deployed in July 2021 and retrieved in either February or September 2022 due to logistical constraints. In the other four arrays, cameras were deployed in September/October 2022 and retrieved in September/October 2023. Once collected, images (Fig. 2.) were manually classified by trained reviewers using Timelapse Image Analyzer 2.0 (Greenberg et al. 2019b) to determine species identities and characteristics and demographic information. All further analyses on these data were performed in R V4.4.1 (R Core Team 2024a).

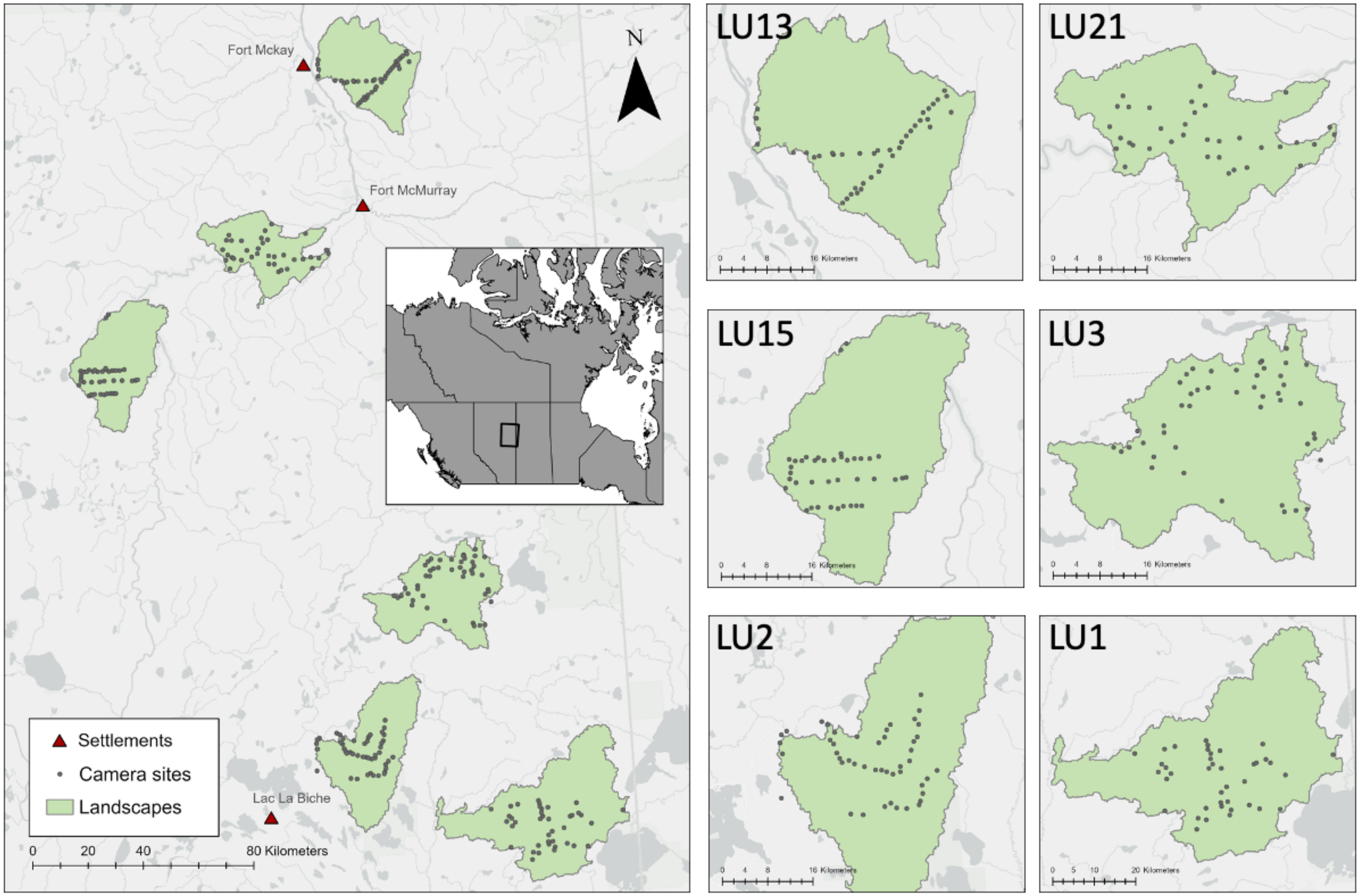

Figure 1. The six landscapes surveyed in northeastern Alberta and individual camera sites (left). The inset map indicates the extent of the OSR in Alberta. LU13) n = 41, LU21) n = 36, LU15) n = 39, LU3) n = 36, LU2) n = 42, LU1) n = 39.

Figure 2. Camera images of black bears in the study landscapes. Top to bottom: adult, cubs, yearling.

Bear demographic data

To examine patterns in black bear habitat selection, we evaluated habitat use separately for two demographic groups: (1) females with young and (2) solitary adults, within each of the three seasons during the active period. We first used the Timelapse images to obtain independent detection events for bears, which were those that occurred a minimum of 30 minutes apart, and recorded the age class data (i.e., whether the bear(s) detected in images were young of year, young of last year, or adults). One error that needed to be accounted for during this step was false cub absences. This can occur due to the way that independent detection events are classified, by taking the tagged information of the individual(s) in only one of the images or episodes (series of images that occur less than one minute apart) of those that occur within 30 minutes of each other. It is possible that a female bear could be detected without her cubs first, resulting in the detection being classified as a solitary adult, but her cubs appear in subsequent photos. To minimize this error, we determined the max group count for each age class within an independent detection event and used this value to define demographic values. We classified females with young as episodes having a group count of cubs or yearlings greater than zero, and solitary adults as episodes with a group count of adults greater than zero, and a group count of cubs or yearlings equal to zero.

We then constructed a proportional binomial response variable (hereafter "occurrence frequency") for whether a bear demographic group was detected (1) or not (0) at a site during an occasion period (15 days). The number of occasion periods with presences/absences were summed for each demographic within three seasons with seasonal boundaries defined by hunting/vegetation seasons: spring (April 1st – June 14th), summer (June 15th – August 28th), and fall (August 29th – November 11th). Winter was not considered because bears are hibernating and thus not usually active during this period. Since not all cameras were active throughout all occasion periods, only occasion periods with a camera active for greater than 6 days (half of the occasion period) were considered.

Predictor variables

For predictors of bear occurrence, we examined four categories of predictors hypothesized to influence habitat selection: 1) prey species, 2) polygonal disturbance features, 3) linear disturbance features, and 4) natural landcover. In terms of prey, we calculated total independent detections for three species: hare, moose, and white-tailed deer, at each site within each season. We did not consider other prey species (ex., caribou) due to lack of detections.

We obtained anthropogenic landcover data from the current version of the Alberta Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory (Alberta Biodiversity Monitoring Institute 2019). In terms of linear features, we retained roads, seismic lines, 3D seismic lines, pipelines, transmission lines, and trails. For polygonal features, we considered well sites and harvest blocks. Natural landcover data on the distribution of shrubland, grassland, broadleaf forest, coniferous forest, and mixed-wood forest was obtained from the most recent version of ABMI's Wall-to-wall Land Cover Map (Alberta Biodiversity Monitoring Institute 2010). Since the scale at which the analysis is performed around camera sites is important for species habitat selection (Fisher et al. 2011), we extracted the proportion of natural and anthropogenic landcover features within a series of concentric circular buffers around each camera site (ranging from 250m to 1500m, increasing at 250m increments).

Assessing correlation of predictors

At each spatial scale, we assessed collinearity among predictor variables using Pearson's correlation coefficient, ensuring that all pairwise combinations were below a threshold value of

0.7 (Zuur et al. 2010a). We removed coniferous forest due to collinearity with broadleaf forest, since forest cover in this region is typically one or the other. Pipelines and transmission lines were also highly collinear, so we combined these features since they share similar ecological function. The 1500m buffer was chosen as the largest buffer size because roads and well pads became highly correlated at greater distances, and both covariates were key parameters of interest that could not be removed from the analysis.

Model structure and candidate set

To evaluate which predictor variable(s) best explain black bear distributions, we created a candidate set of generalized linear mixed models (GLMMs) with binomial distribution and logit-link function (Table 1). Each model in the set was founded upon a hypothesis of what could best explain bear occurrence considering the four predictor categories. We had models within each category (ex., a "polygonal features" model containing well sites and harvest blocks). For linear features, we had a model for roads and a separate model for features commonly used by off-highway vehicles (OHVs) containing seismic lines, 3D seismic lines, pipelines/transmission lines, and trails, due to difference in disturbance type and degree of vegetation. For natural landcover, we considered a "forest model" (broadleaf and mixed-wood forest) and an "open habitat model" (grassland and shrubland). We also had several combination models where predictor categories were combined for a reason (ex., a "total anthropogenic disturbance features" model that combined linear and polygonal features) as well as global and null models. To ensure comparability, all predictor variables included in models were z-scaled (mean = 0, sd. = 1) using the 'scale' function in R.

For both demographic groups, out of the range of buffer distance, the spatial scale that produced the lowest AIC score for the global model was 250-m, so we proceeded to evaluate candidate models at this scale. For solitary adults, candidate models were evaluated separately within each season. Additionally, for comparison of a seasons-based approach versus the approach of disregarding season as done in many past studies, model selection was performed for the three seasons combined. In the case of females with young, there were not enough detections within individual seasons to perform separate analyses, so models were evaluated for the seasons combined with season as an interaction (see Table 2 for modified model set). This approach was not ideal as it did not identify a top model for each season, but was the best option given data limitations. To reduce the complexity of models containing interaction terms, the model set was modified to create the predictor variable "OHV linear features" which combined linear features used by off-highway vehicles together. Each model including season as an interaction with predictors was paired with an identical model without season to determine whether occurrence near predictors varied temporally. A model with solely season as a predictor was also added to the model set, and the global model was eliminated due to complexity.

Random effect structure

For solitary adults, "landscape unit" was considered as a random effect in each model as these were spread across space and defined by varying degrees of disturbance. The fit of this random effect was evaluated using AIC, which indicated that for summer and combined season models, including random effect was better supported than omitting it (Appendices Table 4), suggesting there is variation to be accounted for between landscape units. Although for spring and fall the model without landscape unit as a random effect emerged on top, the random effect was retained across all seasons for consistency. For females with young, the data frame was structured differently, consisting of three observations per site (one per season), so a nested random effect structure with "array" and "site" was used to avoid pseudoreplication. The nested random effect structure was also better supported via AIC in comparison of intercept only models with just array, just site, and the null model.

Model validation and predictions

For each analysis, models were ranked in an information-theoretic framework, and AIC scores were calculated to evaluate the strength of empirical support for each. Top models were evaluated by generating diagnostic plots (package "DHARMa") and calculating VIF values (package "performance"). Odds ratios were calculated and plotted for the top models to visualize the effect of these predictors on bear occurrence.

Table 1. Candidate model set used to determine the influence of predictor variables on solitary adult occurrence. The model set was evaluated for each season, and for all seasons combined.

Bear occurrence best explained by:	**Candidate model name**	**Predictor variables**
Roads	Roads	Roads
Linear features used by OHVs	OHV	Seismic lines + 3D seismic lines + pipelines and transmission lines + trails
All linear features (Roads + OHV)	Linear	Roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails
Polygonal features	Polygonal	Harvest sites + wells
Linear and polygonal features	Linear + Polygonal	Roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + harvest sites + wells
Open natural habitat	Open natural	Grassland + shrubland
Open foraging areas	Polygonal + Open natural	Harvest sites + wells + grassland + shrubland
Forest	Forest	Broadleaf forest + mixed forest
All natural landcover	Open natural + Forest	Grassland + shrubland + broadleaf forest + mixed forest
Prey species	Prey	Moose + white-tailed deer + hare

Prey and linear features	Prey + Linear	Moose + white-tailed deer + hare + roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails
Prey and roads	Prey + Roads	Moose + white-tailed deer + hare + roads
Food sources (forage and prey)	Prey + Linear + Polygonal	Moose + white-tailed deer + hare + roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + harvest sites + wells
Food sources without roads	Prey + OHV + Polygonal	Moose + white-tailed deer + hare + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + harvest sites + wells
Global	Global	Moose + white-tailed deer + hare + roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + harvest sites + wells + grassland + shrubland + broadleaf forest + mixed forest
Null	Null	1

Table 2. Candidate models used to determine the influence of predictor variables on female with young occurrence. “OHV linear features” combines traditional seismic lines, 3D seismic lines, pipelines/transmission lines, and trails together into one variable. Candidate models are

otherwise identical to solitary adult models, but each has a duplicate model with season as an interaction with each predictor variable. An additional model with only season is also present.

Bear occurrence best explained by:	**Candidate model name**	**Predictor variables**
Roads	Roads	Roads
Roads with season interaction	Roads*Season	Roads*season
Linear features used by OHVs	OHV	OHV linear features
Linear features used by OHVs with season interaction	OHV*Season	OHV linear features*season
All linear features (Roads + OHV)	Linear	Roads + OHV linear features
All linear features (Roads + OHV) with season interaction	Linear*Season	Roads*season + OHV linear features*season
Polygonal features	Polygonal	Harvest sites + wells
Polygonal features with season interaction	Polygonal*Season	Harvest sites*season + wells*season
Linear and polygonal features	Linear + Polygonal	Roads + OHV linear features + harvest sites + wells
Linear and polygonal features with season interaction	Linear*Season + Polygonal*Season	Roads*season + OHV linear features*season + harvest sites*season + wells*season
Open natural habitat	Open natural	Grassland + shrubland
Open natural habitat with season interaction	Open natural*Season	Grassland*season + shrubland*season
Open foraging areas	Polygonal + Open natural	Harvest sites + wells + grassland + shrubland
Open foraging areas with season interaction	Polygonal*Season + Open natural*Season	Harvest sites*season + wells *season + grassland*season + shrubland*season
Forest	Forest	Broadleaf forest + mixed forest
Forest with season interaction	Forest*Season	Broadleaf forest*season + mixed forest*season
All natural landcover	Open natural + Forest	Grassland + shrubland + broadleaf forest + mixed forest

All natural landcover with season interaction	Open natural*Season + Forest*Season	Grassland*season + shrubland*season + broadleaf forest*season + mixed forest*season
Prey species	Prey	Moose + white-tailed deer + hare
Prey species with season interaction	Prey*Season	Moose*season + white-tailed deer*season + hare*season
Prey and linear features	Prey + Linear	Moose + white-tailed deer + hare + roads + OHV linear features
Prey and linear features with season interaction	Prey*Season + Linear*Season	Moose*season + white-tailed deer*season + hare*season + roads*season + OHV linear features*season
Prey and roads	Prey + Roads	Moose + white-tailed deer + hare + roads
Prey and roads with season interaction	Prey*Season + Roads*Season	Moose*season + white-tailed deer*season + hare*season + roads*season
Food sources (forage and prey)	Prey + Linear + Polygonal	Moose + white-tailed deer + hare + roads + OHV linear features + harvest sites + wells
Food sources (forage and prey) with season interaction	Prey*Season + Linear*Season + Polygonal*Season	Moose*season + white-tailed deer*season + hare*season + roads*season + OHV linear features*season + harvest sites*season + wells*season
Food sources without roads	Prey + OHV + Polygonal	Moose + white-tailed deer + hare + OHV linear features + harvest sites + wells
Food sources without roads with season interaction	Prey*Season + OHV*Season + Polygonal*Season	Moose*season + white-tailed deer*season + hare*season + OHV linear features*season + harvest sites*season + wells*season
Season	Season	Season
Null	Null	1

Results

Detections

Across the six landscapes, images were collected from 233 sites with each camera operational for approximately one year beginning in either 2021 or 2022. Images resulted in a total of 459 independent detections of cubs or yearlings, and 1471 independent detections of solitary adults. By season, independent detections of solitary adults were as follows: spring, 309; summer, 746; and fall, 416. For females with young, these were: spring, 63; summer, 235; fall, 78. Proportion of detections in each season varied (Figure 3).

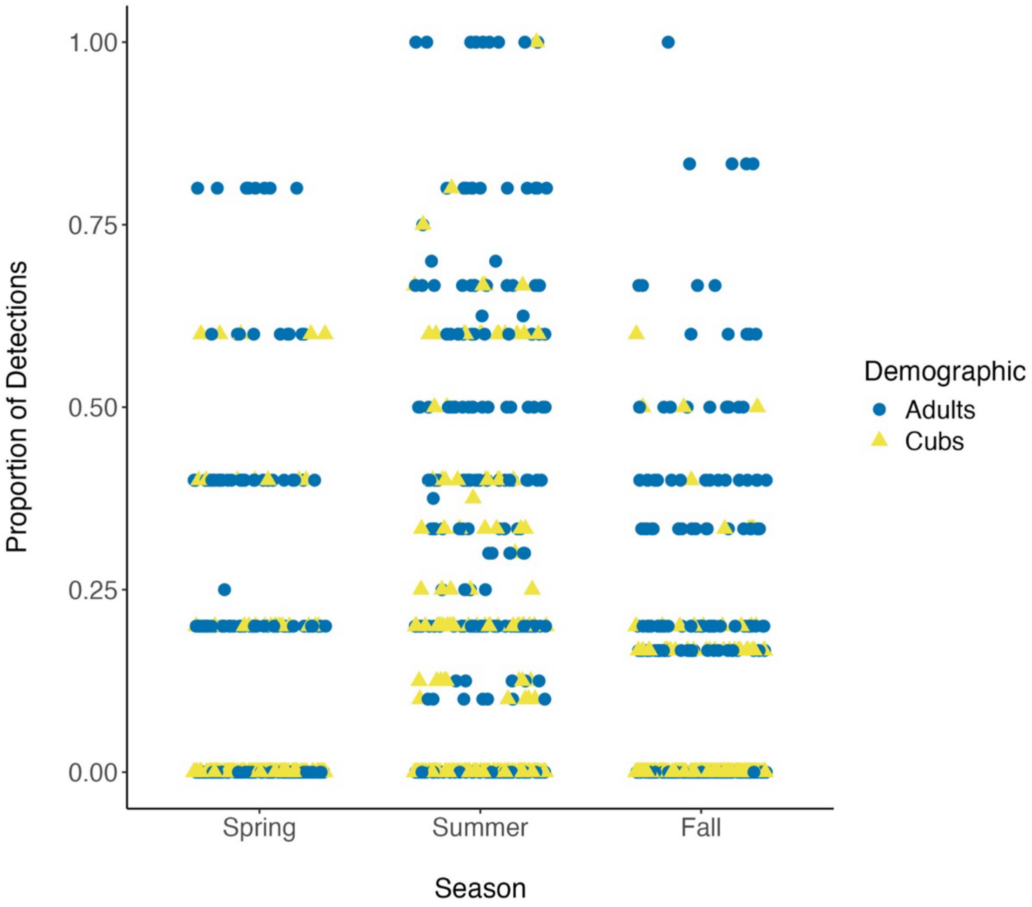

Fig. 3. Proportion of detections (occasion periods present/total number of occasions) of solitary adults and females with young within each season. Detections were greatest in the summer for both demographics.

Solitary adult habitat selection

Within each season, the 250-meter buffer distance was the best supported scale for habitat selection by solitary adults. In spring, the prey and roads model best explained solitary adult occurrence (AICw = 0.83; Table 3). Solitary adults exhibited a strong negative association with roads (β = -0.37, [95% CI: -0.55 – -0.17], P < 0.001; Figure 4; Figure 5; Table 7) but were positively associated with all three prey species, most strongly with moose (β = 0.29, [95% CI: 0.15 – 0.44], P < 0.001; Figure 4; Figure 6; Table 7) and white-tailed deer (β = 0.16, [95% CI: 0.01 – 0.32], P = 0.037; Figure 4; Table 7).

In summer, the OHV linear features model was best supported (AICw = 0.67; Table 3). The linear features model (Roads + OHV) was within 2 ΔAIC, indicating that the addition of roads to OHV linear features provides some explanatory power, but not enough to overcome the parameter penalty. In summer, solitary adults associated negatively with 3D seismic lines (β = -0.17 [95% CI: -0.34 – -0.01], P = 0.04; Figure 4; Table 7) and pipelines/transmission lines (β = -0.17 [95% CI: -0.34 – 0.00], P = 0.05; Figure 4; Table 7), but positively with trails (β = 0.17 [95% CI: 0.06 – 0.29], P = 0.0037; Figure 4; Table 7). Interestingly, upon examining the summer linear features model bears no longer avoided roads (β = -0.04 [95% CI: -0.18 – 10], P = 0.61; Figure 5).

In fall, the prey and linear features model was best supported (AICw = 0.43; Table 3). The linear features model was within 2 ΔAIC indicating that despite the parameter penalty, the addition of prey species to this model is important for explaining occurrence. Solitary adults exhibited a strong negative response to roads (β = -0.37 [95% CI: -0.55 – -0.19], P < 0.001; Figure 4; Figure 5; Table 7). They also associated negatively with other linear features: traditional seismic lines (β = -0.19 [95% CI: -0.35 – -0.03], P = 0.021; Figure 4; Table 7) and pipelines/transmission lines (β = -0.30 [95% CI: -0.53 – -0.07], P = 0.01; Figure 4; Table 7). In terms of prey species, solitary adults positively associated with hare (β = 0.14 [95% CI: 0.01 – 0.27], P = 0.029; Figure 4; Table 7) and white-tailed deer (β = 0.12 [95% CI: -0.02 – 0.26], P = 0.10; Table 7), but were indifferent to moose.

Model selection was also performed across all seasons combined to compare these results to those of a seasonal approach. In the combined approach, the prey and linear features model was the best predictor of solitary adult occurrence (AICw = 0.69; Table 3) with the global model second. In terms of linear features, solitary adults negatively associated with roads (β = -0.14 [95% CI: -0.25 – -0.04], P = 0.0066; Figure 7; Table 7), traditional seismic lines (β = -0.12 [95% CI: -0.21 – -0.03], P = 0.0063; Figure 7; Table 7), 3D seismic lines (β = -0.17 [95% CI: -0.28 – -0.06], P = 0.0018; Figure 7; Table 7), and pipelines/transmission lines (β = -0.10 [95% CI: -0.20 – 0.01], P = 0.070; Figure 7; Table 7), and positively associated with trails (β = 0.09, [95% CI: 0.02 – 0.17],P = 0.018; Figure 7; Table 7). With respect to prey, solitary adults positively associated with moose (β = 0.15 [95% CI: 0.07 – 0.23], P < 0.001; Figure 7; Table 7) and hare (β = 0.08 [95% CI: 0.01 – 0.15], P = 0.028; Figure 7; Table 7).

Table 3. Top models (within 2 ΔAIC) for occurrence of solitary adults within each season and for females with young. See Table 6 (Appendices) for rankings of all models in each analysis.

Demographic	Season	Top buffer (m)	Top models	df	log-lik	AIC	ΔAIC	AICw
Solitary adults	Spring	250	Prey + Roads	6	-244.06	500.58	0.00	0.83
	Summer	250	OHV	6	-395.47	803.31	0.00	0.67
			Linear	7	-395.34	805.18	1.87	0.26
	Fall	250	Prey + Linear	10	-302.66	626.31	0.00	0.43
			Linear	7	-306.57	627.63	1.33	0.22
	All	250	Prey + Linear	10	-577.77	1176.54	0.00	0.69
Females with young	All	250	Linear*Season	11	-483.19	988.78	0.00	0.77

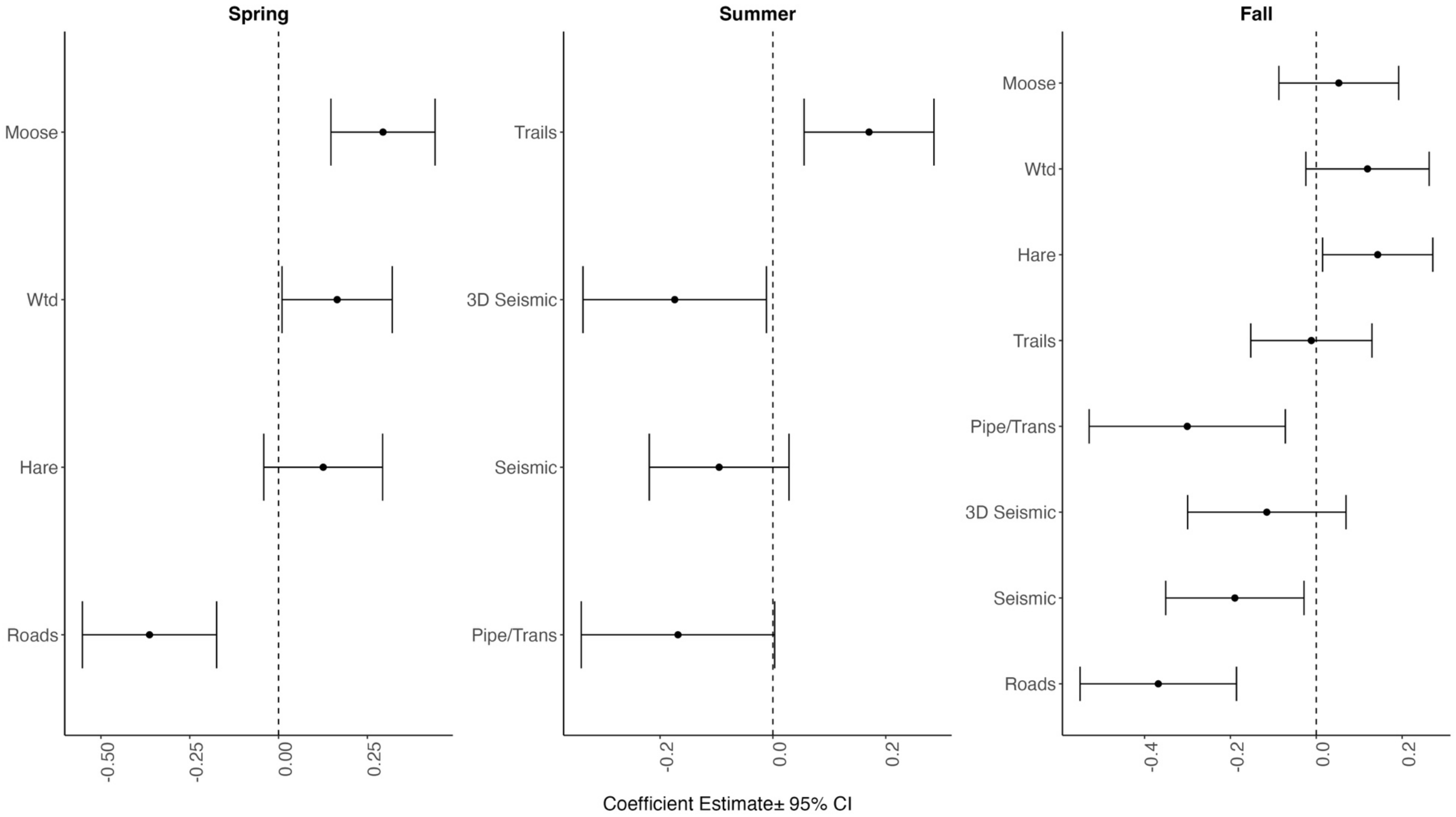

Figure 4. Beta coefficient plots of best supported model of solitary adult occurrence in each season (spring: prey and roads; summer: OHV linear features; fall: prey and linear features). Values <1 indicate a negative predictor of occurrence, values >1 indicate a positive predictor of occurrence. Bars represent 95% confidence intervals.
*Wtd = White-tailed deer
*Pipe/Trans = Pipelines and transmission lines

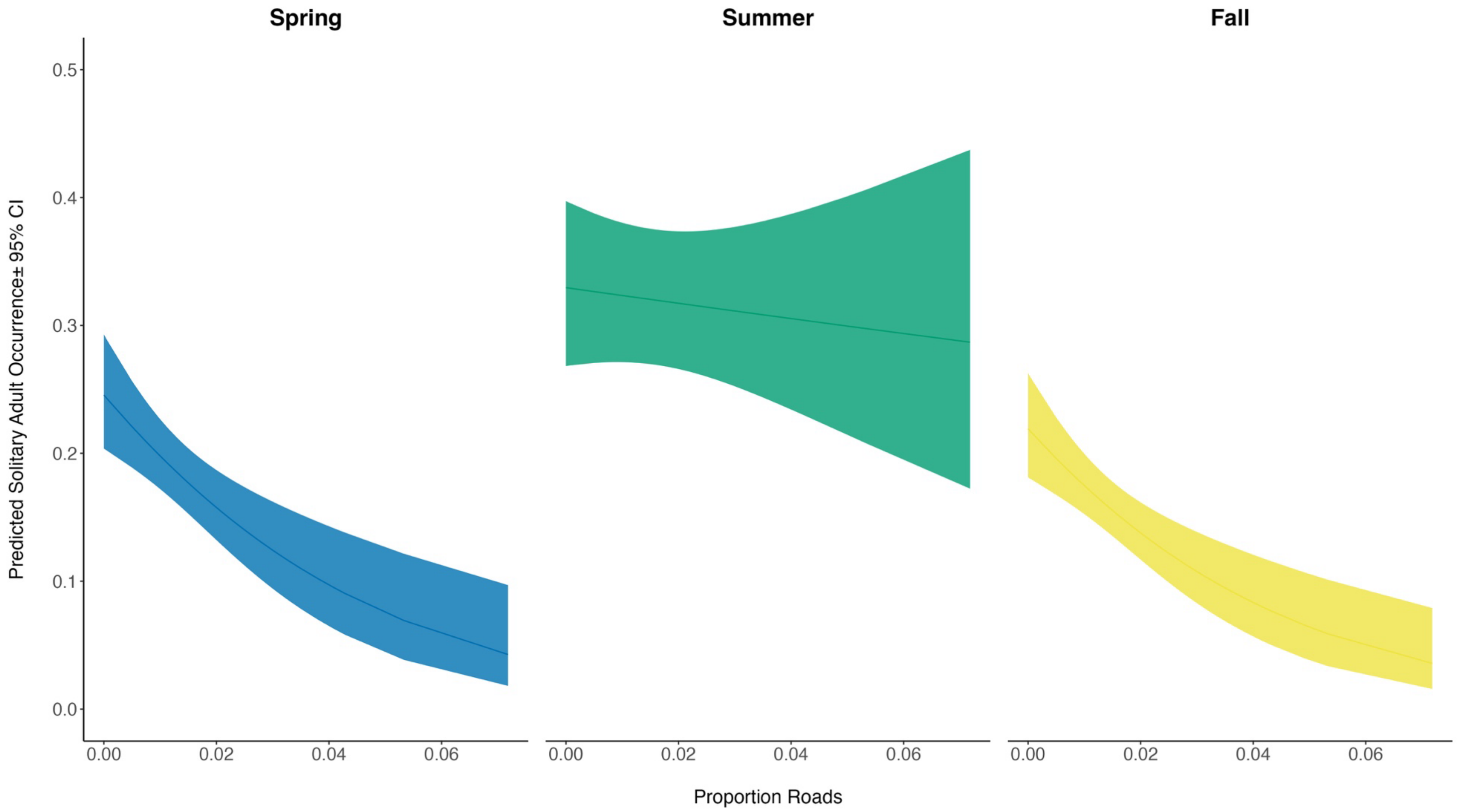

Figure 5. Predictive plots of changes in solitary adult occurrence with increasing road density (proportion of the 250-meter buffer designated as roads) for each season. The ribbon around each line represents the 95% confidence interval. Solitary adult occurrence is expected to decrease with increasing road density in the spring and fall but be relatively unaffected by road density in the summer, which is also the non-hunting season.

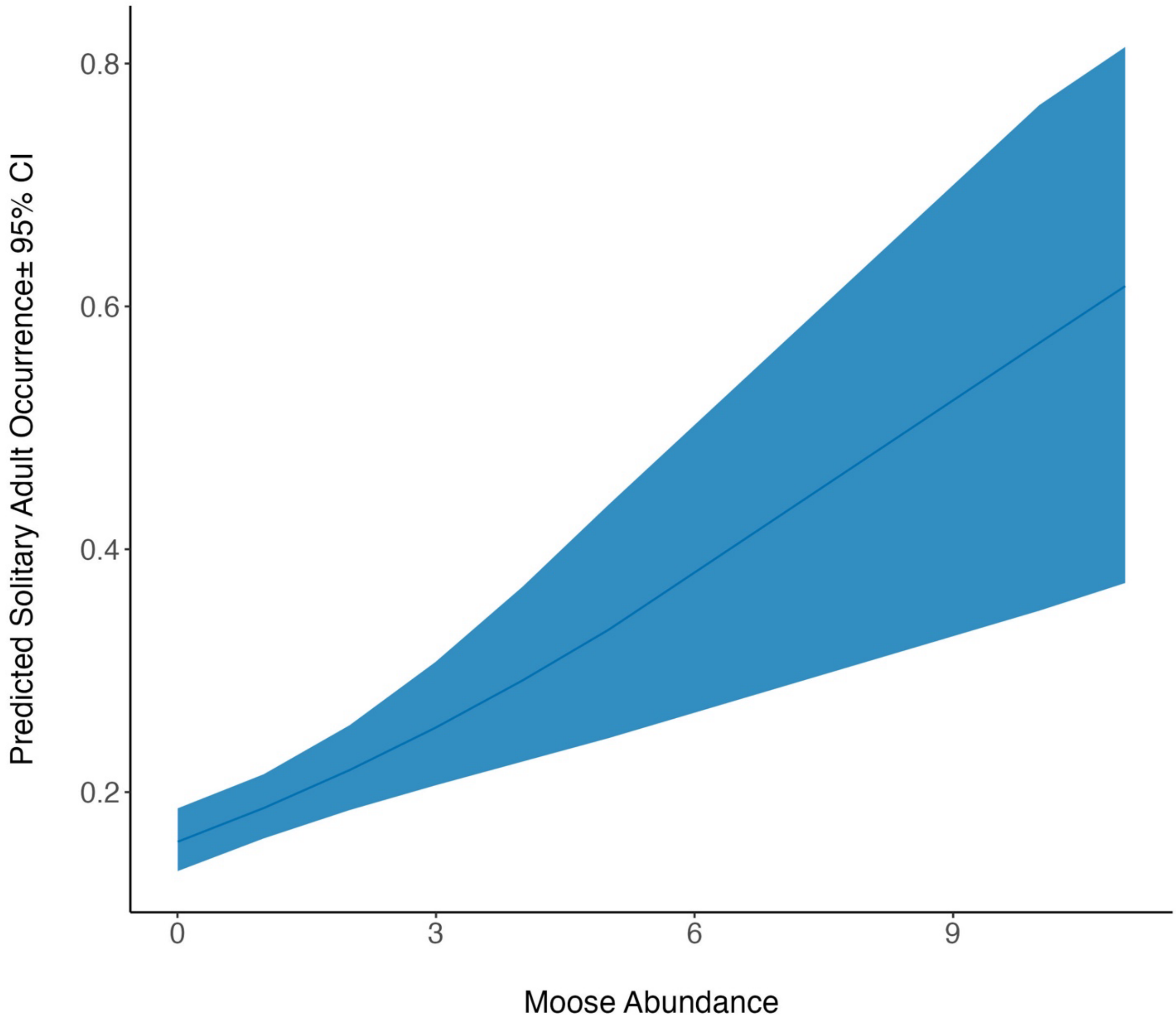

Figure 6. Predictive plot indicating that solitary adult occurrence is expected to increase with increasing moose abundance in spring. The ribbon represents the 95% confidence interval.

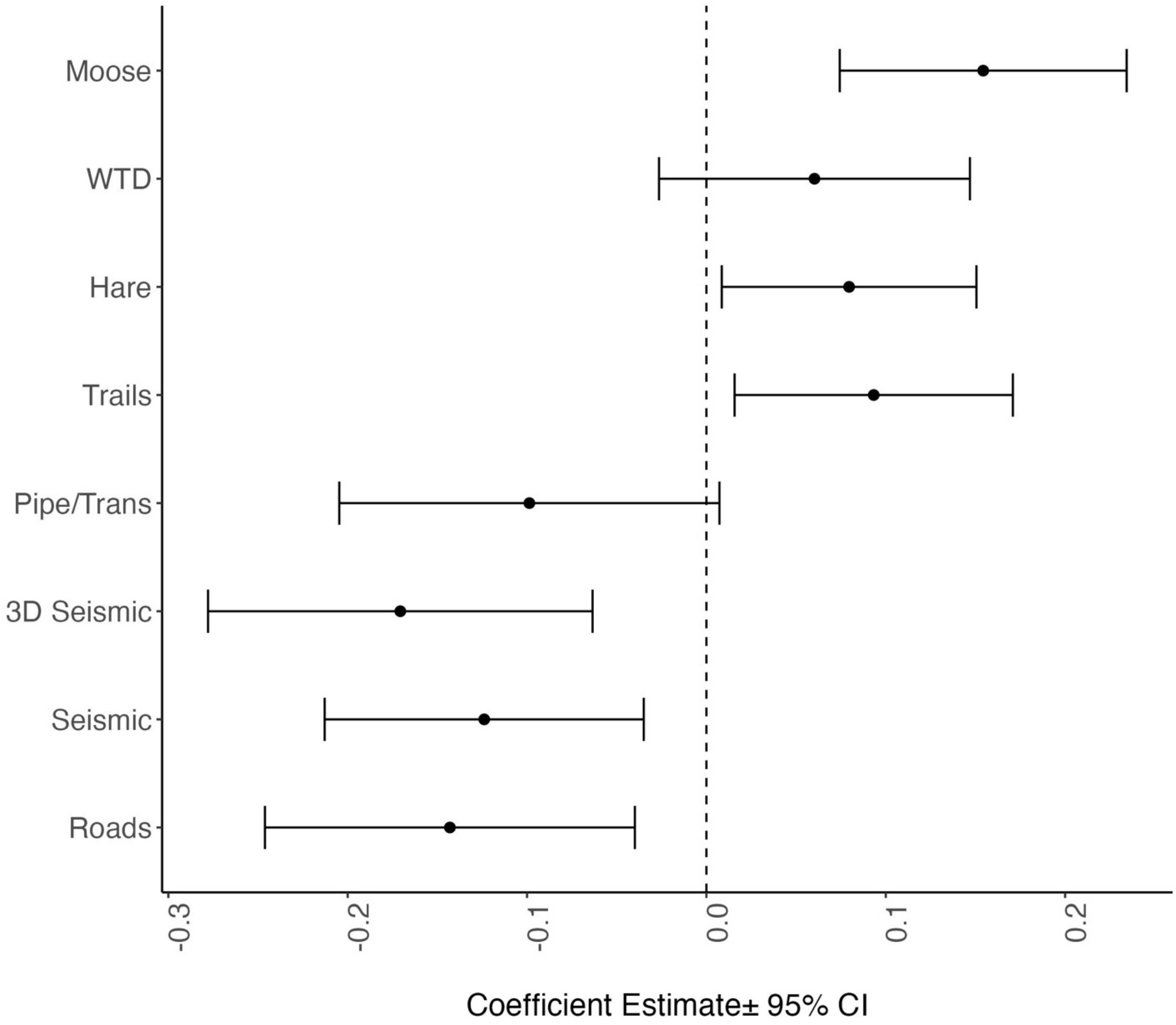

Figure 7. Beta coefficient plots of best supported model for solitary adults across all seasons combined (the prey and linear features model). Values <1 indicate a negative predictor of occurrence, values >1 indicate a positive predictor of occurrence. Bars represent 95% confidence intervals.

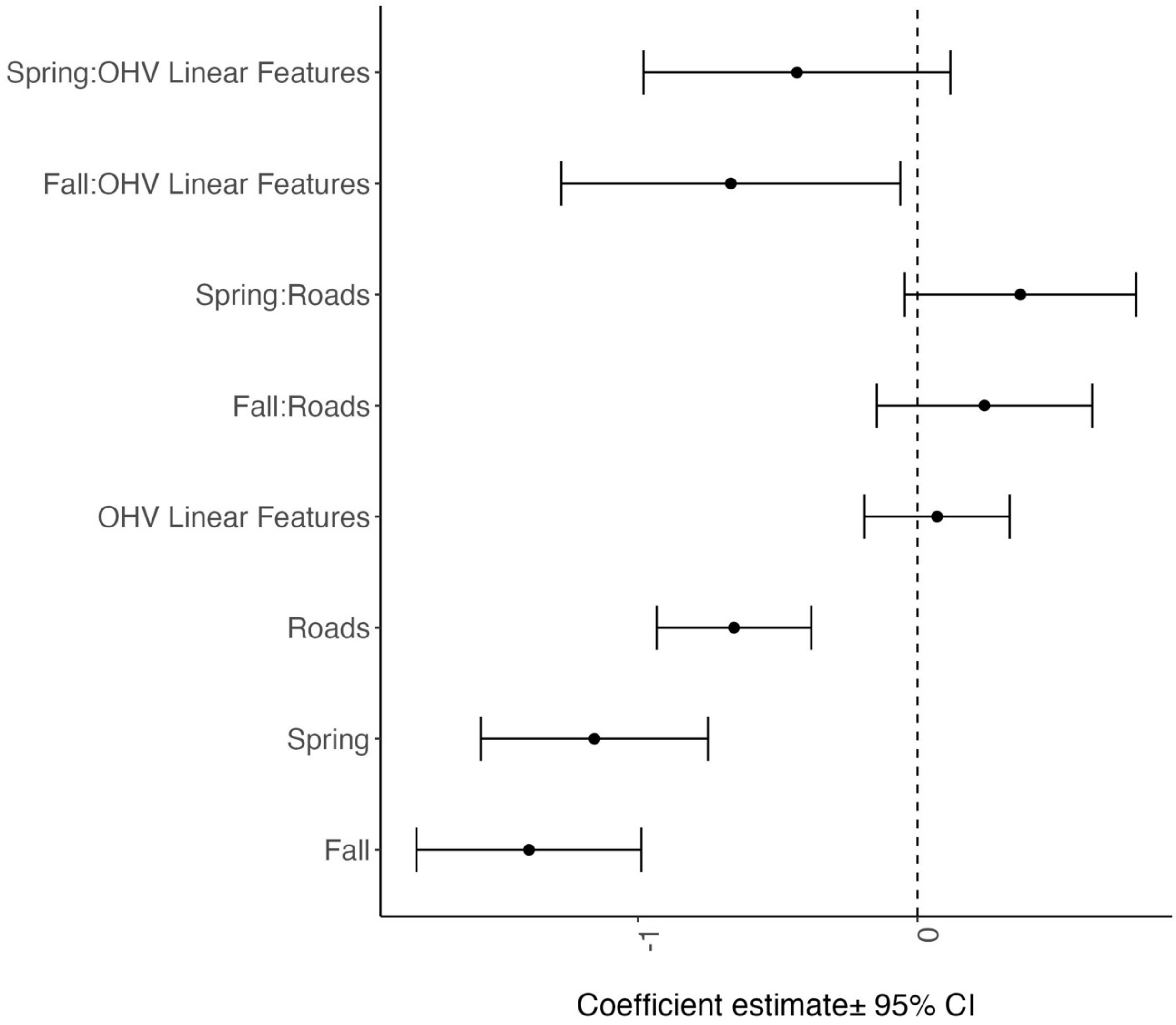

Figure 8. Beta coefficients plotted for predictors in the best supported model for cubs (the Linear*Season model). “Summer” was selected as the reference season. Bars represent 95% confidence intervals.

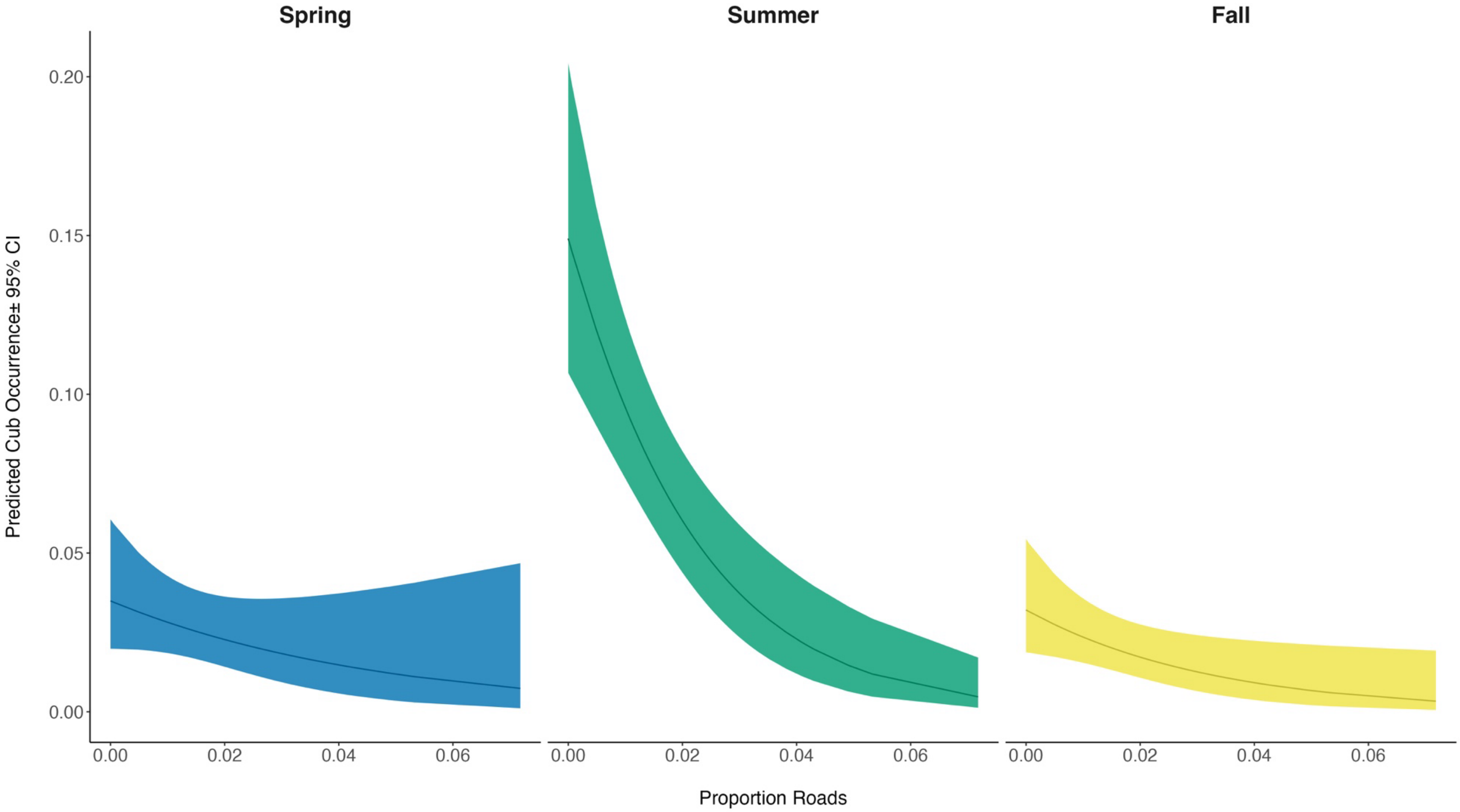

Figure 9. Predictive plot indicating that female with young occurrence is expected to decrease with increasing road density in each season. The ribbon represents the 95% confidence interval.

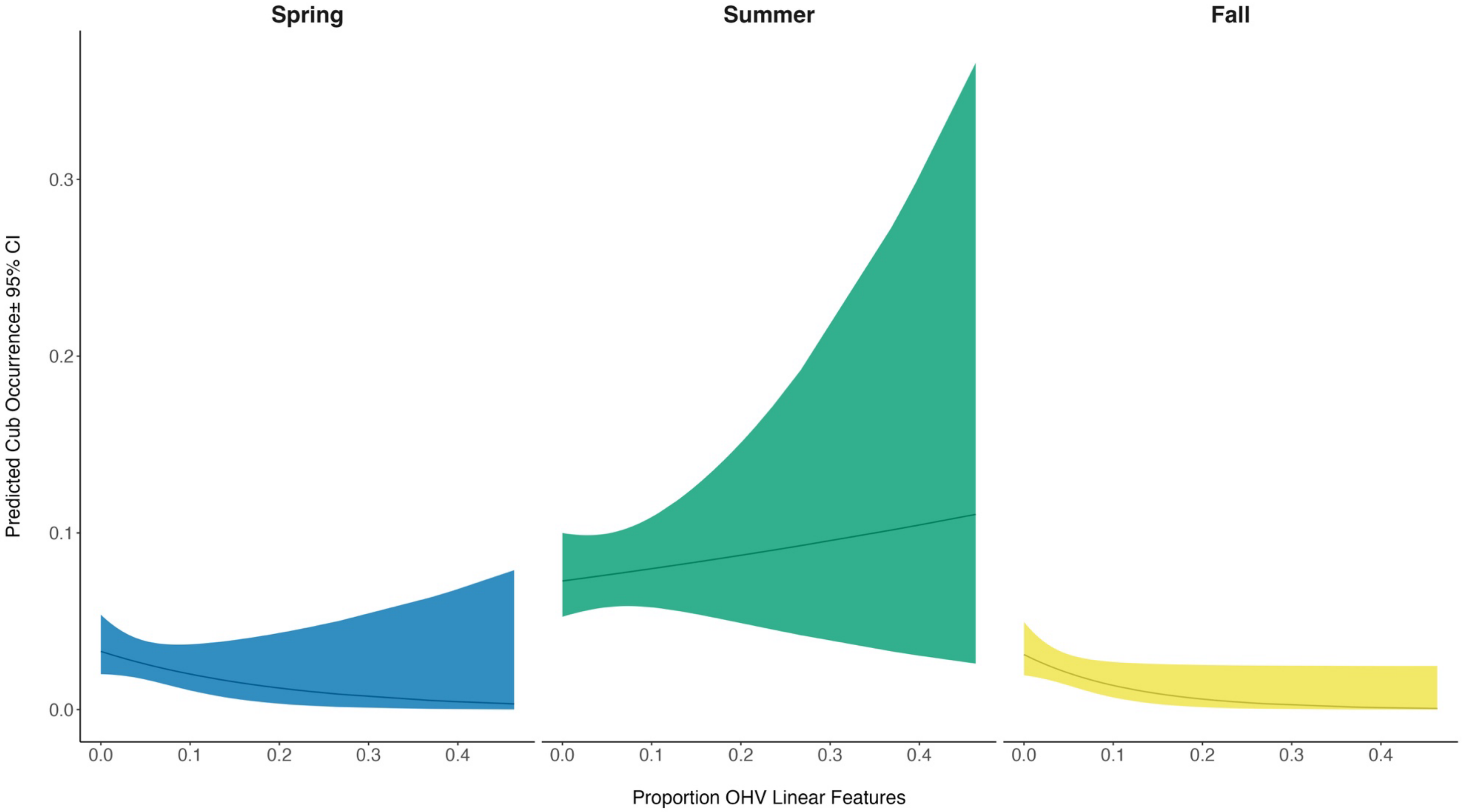

Figure 10. Predictive plot of changes in female with young occurrence with increasing density of OHV linear features in each season. Occurrence is expected to decrease in the spring and fall but slightly increase in the summer. The ribbon represents the 95% confidence intervals.

Female with young habitat selection

The 250-meter buffer distance was also the best supported scale for habitat selection by females with young. The linear features model with season as an interaction best explained cub/yearling occurrence across the three seasons (AICw = 0.77; Table 3). Occurrence was strongly negatively associated with roads in the reference (non-hunting) season, summer (β = -0.66, [95% CI: -0.93 – -0.38], P < 0.001; Figure 8; Figure 9; Table 7), and this remained negative in the spring and fall with effect sizes not different from zero (P spring = 0.08, P fall = 0.22). Occurrence was not altered by OHV linear features in the summer (β = 0.07, [95% CI: -0.19 – 0.33], P = 0.59; Figure 8; Figure 10; Table 7), however the interaction terms signalled a strong negative association in the spring (β = -0.43, [95% CI: -0.98 – 0.12], P = 0.12) and fall (β = -0.67, [95% CI: -1.27 – -0.06], P = 0.03).

Discussion

In support of our first hypothesis, we found that bear occurrence in relation to predictor variables, including disturbance features, varied seasonally. Our second hypothesis was also supported, as mothers with young responded differently to disturbance features than solitary adults. These findings highlight the importance of considering season and demographic when analyzing black bear habitat selection to identify fine-scale patterns that would otherwise be missed. Although our hypotheses were supported, the relationship of occurrence to disturbance features did not always correspond with our predictions. This will be discussed for the different predictor categories.

Linear features

Occurrence of both demographics was strongly influenced by linear features across seasons. For solitary adults, roads and/or OHV linear features were consistently retained in the top model explaining occurrence in each season, and the "linear features" model was the top model for females with cubs.

Solitary adult bear's seasonal association with roads was in accordance with our prediction bears strongly avoided roads during the spring and fall, but did not avoid roads in the summer. As roads serve as major access routes for hunters in the spring and fall hunting seasons, road avoidance during these periods could be a risk response. This would support the findings of Stillfried et al. (2015), who found that bears increase road avoidance during hunting seasons. Ordiz et al. (2012) and Price et al. (2024) also found bears appear to be aware of hunting threat, altering their behaviour to avoid hunter encounters. However, solitary adult occurrence relative to other linear features that hunters might access via OHV did not follow the exact same pattern. In fall, in accordance with our prediction of hunting risk aversion, bears strongly avoided traditional seismic lines and pipelines/transmission lines. But in spring, bear occurrence was not influenced by any of these features except a slight avoidance of seismic lines. This could be because when forage is scarce in the spring, bears need to move about more in search of vegetation and prey (Young and Ruff 1982), and might be more prone to use linear features for movement subsidies despite hunting risk. In summer, we expected bears to be attracted to linear features for forage subsidies in the absence of hunting risk. However, solitary adults were only attracted to trails and avoided 3D seismic lines and pipelines/transmission lines. This suggests that there could be a risk response to linear features in summer as well, perhaps to avoid recreational vehicle activity, that outweighs any forage subsidies linear features might provide.

Linear feature use has also been shown to be driven by fine scale characteristics such as the presence of certain forage species and height of online vegetation (Tattersall et al. 2023b), which we did not consider in this analysis.

Females with young strongly avoided roads in all seasons. This suggests that roads could be perceived as risky to mothers from high human use in all seasons, despite the benefit they may have for vegetation subsidies and as a human shield from infanticide (especially when solitary adults are avoiding roads in the spring and fall). One explanation is that females with young are not aware of their protection from hunting as some sources suggest (Ordiz et al. 2012, Stillfried et al. 2015), and the risk is amplified with cubs in their protection. A review of black bear life history traits found that hunting best explained adult female mortality, even over food resource availability (Metthé et al. 2025). However, females with young only avoided OHV linear features in the spring and fall, but not in the summer. If linear feature avoidance is a risk response to hunting activity/human presence, then this change in pattern relative to road avoidance could be explained by the fact that roads experience consistent human use in all seasons, whereas use of OHV linear features likely is decreased or less disruptive (i.e., no gunshots) in the summer relative to spring and fall.

Polygonal features

Wells and harvest sites did not have a strong influence on occurrence of either demographic or were not retained in any of the top models. For solitary adults, there was no response to these features in any season. This ran counter to our prediction that solitary adults would avoid polygonal features during the hunting season (due to exposure) and utilize them for forage in the summer. It is especially interesting that bears were not attracted to polygonal features in the non-hunting season since many sources indicate these areas support berryproducing species (Brodeur et al. 2008, Nielsen et al. 2020), many of which are shade-intolerant, and found bears used them for foraging (Brodeur et al. 2008, Mosnier et al. 2008, Lesmerises et al. 2015). There was also no association with polygonal features in any season for females with young. We came up with a several explanations that could explain this lack of relationship. First, it is possible that across the landscape polygonal features are subject to varying levels of human presence. This could especially be true for well pads, where some receive frequent servicing and others are entirely abandoned. Then, bears may be utilizing polygonal features with less human activity, and avoiding those with more activity, resulting in a net zero relationship. Second, a management practice is to apply herbicide (ex., glyphosate) to cut blocks post-harvest, which could reduce forage availability and quality, and is suggested as a possible reason for moose avoiding these features (Carroll et al. 2024). Finally, it is possible that there are other areas, like open pine stands (Pelchat and Ruff 1986), with an abundance of berries, and polygonal features are thus not that attractive as forage sites.

Prey

Prey species presented in the top models for solitary adults in the spring and fall. In spring, solitary adults were positively associated with all three species, and most strongly with moose. Animal prey may serve as a more important source of calories during spring when vegetation quality is poorer, and berries have not yet emerged (Young and Ruff 1982, Zager and Beecham 2006). It was expected that bears would be positively associated with moose as many sources indicate calf predation (Garneau et al. 2007, Bastille-Rousseau et al. 2011, Moore et al. 2024), especially during the period of 0 - 5 weeks of age (Moore et al. 2024). In fall, solitary adult bears were positively associated with hare, suggesting that hare may also be of dietary importance in this season. However, the three prey species were not present in the top model for females with young, and even upon examining the best-supported model that included prey (the prey*season + linear*season model), occurrence was not influenced seasonally by these species. It is possible that bears with young in tow are not as able to effectively hunt prey and prioritize other food resources.

Comparing the seasons-based approach to combined seasons analysis for solitary adults

When the same model set was run across all seasons combined for solitary adults, the top model was the prey and linear features model, with the global model coming in second (ΔAICc = 2.78). The high ranking of the global model indicates that in the absence of seasonal considerations, patterns of bear occurrence are less clear. The beta coefficients of the predictor variables in the top model also masked fine-scale seasonal patterns: for example, the model indicates a negative association with roads, but this is not true in the summer and is more negative than suggested in the spring and fall. Similarly, occurrence is positively related to moose in this model, but our analysis found this to be false in the summer and fall. These findings highlight the value of a seasonal approach to identify temporal patterns associated with species biology that are otherwise masked.

Limitations

Several limitations of this study must be noted. First, although the error of false cub absences was statistically addressed, it is still possible that a female was detected by a camera, but her cubs never passed in front of the field of view. This would result in the female still being classified incorrectly as a solitary adult. Second, due to the lack of female with young detections, we were not able to run candidate models separately for each season. In the case of greater detections, it would be interesting to take this approach and identify top models per season to increase the resolution of results. Third, the strength of our conclusions is limited by the lack of data on hunter distributions across the study area. The Alberta Open Government website has records of bear harvests per wildlife management unit (WMU) each year (Alberta Government 2024). However, there is no finer scale metric of where hunters concentrate efforts within each WMU, and no quantitative data to back the assumption of linear features as a proxy for hunting intensity. Future work could pair cameras with ARUs to monitor gunshot and OHV noise, creating a noisescape to incorporate into the analysis of bear occurrence. Fourth, it is possible that bear feature use could depend on whether it is the day or night. Ordiz et al. (2012) demonstrated that after the onset of hunting, brown bears moved more during the dark hours and reduced movement during daylight hours. It would be interesting to investigate diel activity in relation to feature use, and if this varies seasonally. Last, although we segregated black bears by demographic, it is likely that as generalists, there is significant individual variation in behaviour that affects habitat use, as well as territorial boundaries that may impede habitat selection (Latham et al. 2011a).

Conclusion

In summary, we found that black bear habitat selection in the OSR in relation to anthropogenic disturbance features is both influenced by season and demographic and identified better defined trends in each subcategory. Since some seasonal changes of feature avoidance (ex., roads) appears to be linked to hunting activity, future work should incorporate a variable of hunting effort into the analysis. Understanding black bear habitat selection in the OSR is important to realize their spatial distributions in relation to woodland caribou, as bears are predators of this at-risk species. Broadly, this study provides key insights into how changing risk-reward trade-offs drives variation in habitat selection by wildlife over time and between demographics.

References

Alberta Biodiversity Monitoring Institute. (2010). Wall-to-wall Land Cover Map.

Alberta Biodiversity Monitoring Institute. (2019). *Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region* (

Alberta Government. (2016). *Management plan for black bears in Alberta*. Edmonton, Alberta: Alberta Environment and Parks. Retrieved from https://open.alberta.ca/dataset/3274cf4f-3cd5-430a-9a6b-20813737642f/resource/79507b50-af50-4b1a-bfcb-00ff614f4fc2/download/2016-managementplan-blackbear-jan2016.pdf

Alberta Government. (2023). *About oil sands*. Retrieved 19 Mar from https://www.alberta.ca/about-oil-sands.aspx

Alberta Government. (2024). *Hunter harvest report : black bear*. Retrieved Mar 20 from https://open.alberta.ca/publications/hunter-harvest-report-black-bear-estimated-resident-harvest-for-black-bear

Bastille-Rousseau, G., Fortin, D., Dussault, C., Courtois, R., & Ouellet, J.-P. (2011). Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? *Ecography (Copenhagen)*, *34*(4), 588-596. https://doi.org/10.1111/j.1600-0587.2010.06517.x

Bayne, E., Dennett, J., Kohler, M., Ball, J., Bidwell, M., Braid, A., Chetelat, J., Dillegeard, E., Farr, D., Fisher, J., Freemark, M., Foster, K., Godwin, C., Hebert, C., Huggard, D., McIssac, D., Narwani, T., Nielsen, S., Pauli, B., Prasad, S., Roberts, D., Slater, S., Song, S., Swanson, S., Thomas, P., Toms, J., Twichell, C., White, S., Wyatt, F., Mundy, L. (2021). *Oil Sands Monitoring Program: A before-after dose-response (BADR) terrestrial biological monitoring framework for the oil sands* (OSM Technical Report Series No. 7, Issue. https://open.alberta.ca/publications/9781460151341

Bayne, E., Lankau, H., Tigner, J. (2011). *Ecologically-based criteria to assess the impact and recovery of seismic lines: The importance of width, regeneration, and seismic density* (Report No. 192, Issue.

Beirne, C., Sun, C., Tattersall, E. R., Burgar, J. M., Fisher, J. T., & Burton, A. C. (2021). Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics. *Journal of Applied Ecology*, *58*(12), 2821-2832. https://doi.org/10.1111/1365-2664.14020

Ben-David, M., Titus, K., & Beier, L. R. (2004). Consumption of Salmon by Alaskan Brown Bears: A Trade-off between Nutritional Requirements and the Risk of Infanticide? *Oecologia*, *138*(3), 465-474. https://doi.org/10.1007/s00442-003-1442-x

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. *Biology letters (2005)*, *3*(6), 620-623. https://doi.org/10.1098/rsbl.2007.0415

Brodeur, V., Ouellet, J.-P., Courtois, R., & Fortin, D. (2008). Habitat selection by black bears in an intensively logged boreal forest. *Canadian journal of zoology*, *86*(11), 1307-1316. https://doi.org/10.1139/Z08-118

Carroll, K., Grey, F., Anderson, N., Anderson, N., & Fisher, J. (2024). *Indigenous-led analysis of important subsistence species response to resource extraction*. Authorea, Inc. https://dx.doi.org/10.22541/au.173199516.65667642/v1

Cuveira-Santos, G., Marion, S., Sutherland, C., Beirne, C., Herdman, E., Tattersall, E., Burgar, J., Fisher, J., Burton, C. (2024). Disturbance-mediatd changes to boreal mammal spatial networks in industrializing landscapes [DRAFT]. *Ecological Applications*.

Czetwertynski, S. (2008). Effects of hunting on the demographics, movement, and habitat selection of american black bears [Unpublished doctoral dissertation]. University of Alberta

Dabros, A., Pyper, M., & Castilla, G. (2018). Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. *Environmental Reviews*, *26*(2), 214-229. https://doi.org/10.1139/er-2017-0080

Dawe, C. A., Filicetti, A. T., & Nielsen, S. E. (2017). Effects of Linear Disturbances and Fire Severity on Velvet Leaf Blueberry Abundance, Vigor, and Berry Production in Recently Burned Jack Pine Forests. *Forests*, *8*(10), 398. https://doi.org/10.3390/f8100398

Demars, C. A., & Boutin, S. (2018). Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. *Journal of Animal Ecology*, *87*(1), 274-284. https://doi.org/10.1111/1365-2656.12760

Dickie, M., McNay, S. R., Sutherland, G. D., Cody, M., Avgar, T., & Loison, A. (2020). Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *The Journal of animal ecology*, *89*(2), 623-634. https://doi.org/10.1111/1365-2656.13130

ESRI. (2014). ArcGIS Desktop.

Fisher, J. T., Anholt, B., & Volpe, J. P. (2011). Body mass explains characteristic scales of habitat selection in terrestrial mammals. *Ecology and Evolution*, *1*(4), 517-528. https://doi.org/10.1002/ece3.45

Fisher, J. T., & Burton, A. C. (2018). Wildlife winners and losers in an oil sands landscape. *Frontiers in Ecology and the Environment*, *16*(6), 323-328. https://doi.org/10.1002/fee.1807

Fisher, J. T., & Ladle, A. (2022). Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. *The Science of the total environment*, *822*, 153432-153432. https://doi.org/10.1016/j.scitotenv.2022.153432

Fisher, J. T., & Wilkinson, L. (2005). The response of mammals to forest fire and timber harvest in the North American boreal forest. *Mammal review*, *35*(1), 51-81. https://doi.org/10.1111/j.1365-2907.2005.00053.x

Gantchoff, M. G., Beyer, D., & Belant, J. L. (2019). Reproductive class influences risk tolerance during denning and spring for American black bears (Ursus americanus). *Ecosphere (Washington, D.C)*, *10*(4), e02705-n/a. https://doi.org/10.1002/ecs2.2705

Garneau, D. E., Post, E., Boudreau, T., Keech, M., & Valkenburg, P. (2007). Spatio-temporal Patterns of Predation among Three Sympatric Predators in a single-prey System. *Wildlife Biology*, *13*(2), 186-194. https://doi.org/10.2981/0909-6396(2007)13[186:SPOPAT]2.0.CO;2

Greenberg, S., Godin, T., & Whittington, J. (2019). Design patterns for wildlife-related camera trap image analysis. *Ecology and Evolution*, *9*(24), 13706-13730. https://doi.org/10.1002/ece3.5767

Holbrook, S. J., & Schmitt, R. J. (1988). Combined Effects of Predation Risk and Food Reward on Patch Selection. *Ecology (Durham)*, *69*(1), 125-134. https://doi.org/10.2307/1943167

Latham, A. D. M., Latham, M. C., & Boyce, M. S. (2011). Habitat selection and spatial relationships of black bears (Ursus americanus) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. *Canadian journal of zoology*, *89*(4), 267-277. https://doi.org/10.1139/z10-115

Lesmerises, R., Rebouillat, L., Dussault, C., & St-Laurent, M.-H. (2015). Linking GPS Telemetry Surveys and Scat Analyses Helps Explain Variability in Black Bear Foraging

Strategies. *PLOS ONE*, *10*(7), e0129857-e0129857. https://doi.org/10.1371/journal.pone.0129857

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian journal of zoology*, *68*(4), 619-640. https://doi.org/10.1139/z90-092

Metthé, L., Dussault, C., & Hamel, S. (2025). Linking spatial variations in life-history traits to environmental conditions across American black bear populations. *Ecological monographs*, *95*(1). https://doi.org/10.1002/ecm.1650

Moore, S. A., Wolf, T. M., Severud, W. J., Isaac, E. J., & Chenaux-Ibrahim, Y. M. (2024). Spring black bear harvest and predation pressure on moose calves in a multi-predator system. *The Journal of Wildlife Management*, *88*(6), n/a. https://doi.org/10.1002/jwmg.22618

Mosnier, A., Ouellet, J.-P., & Courtois, R. (2008). Black bear adaptation to low productivity in the boreal forest. *Écoscience*, *15*(4), 485-497. https://doi.org/10.2980/15-4-3100

Nielsen, S. E., Dennett, J. M., & Bater, C. W. (2020). Predicting Occurrence, Abundance, and Fruiting of a Cultural Keystone Species to Inform Landscape Values and Priority Sites for Habitat Enhancements. *Forests*, *11*(7), 783. https://doi.org/10.3390/f11070783

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M., & Swenson, J. E. (2012). Do bears know they are being hunted? *Biological conservation*, *152*, 21-28. https://doi.org/10.1016/j.biocon.2012.04.006

Pelchat, B. O., & Ruff, R. L. (1986). Habitat and Spatial Relationships of Black Bears in Boreal Mixedwood Forest of Alberta. *Bears: Their Biology and Management*, *6*, 81. https://doi.org/10.2307/3872809

Pickell, P. D., Andison, D. W., & Coops, N. C. (2013). Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. *Forest ecology and management*, *304*, 243-253. https://doi.org/10.1016/j.foreco.2013.04.031

Pickell, P. D., Coops, N. C., Gergel, S. E., Andison, D. W., & Marshall, P. L. (2016). Evolution of Canada's Boreal Forest Spatial Patterns as Seen from Space. *PLOS ONE*, *11*(7), e0157736-e0157736. https://doi.org/10.1371/journal.pone.0157736

Poulin, M.-P., Cherry, S. G., & Merkle, J. A. (2023). Dynamic balancing of risks and rewards in a large herbivore: Further extending predator-prey concepts to road ecology. *The Journal of animal ecology*, *92*(10), 1954-1965. https://doi.org/10.1111/1365-2656.13985

Price, L. E., Skelly, B. P., Morrison, E. E., Carpenter, C. P., Ryan, C. W., & Rota, C. T. (2024). TWS Journals. *Wildlife Society Bulletin*, *48*(2). https://doi.org/10.1002/wsb.1522

R Core Team. (2024). R: A language and environment for statistical computing.

Raine, R. M., & Kansas, J. L. (1990). Black Bear Seasonal Food Habits and Distribution by Elevation in Banff National Park, Alberta. *Bears, their biology and management*, *8*, 297-304. https://doi.org/10.2307/3872932

Roberts, D. R., Bayne, E. M., Beausoleil, D., Dennett, J., Fisher, J. T., Hazewinkel, R. O., Sayanda, D., Wyatt, F., & Dubé, M. G. (2022). A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. *Integrated Environmental Assessment and Management*, *18*(2), 388-406. https://doi.org/10.1002/ieam.4519

Romain, D. A., Obbard, M. E., & Atkinson, J. L. (2013). Temporal variation in food habits of the American Black Bear (Ursus americanus) in the boreal forest of northern Ontario. *Canadian field-naturalist*, *127*(2), 118-130. https://doi.org/10.22621/cfn.v127i2.1442

Stillfried, M., Belant, J. L., Svoboda, N. J., Beyer, D. E., & Kramer-Schadt, S. (2015). When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. *Behavioural processes*, *120*, 30-39. https://doi.org/10.1016/j.beproc.2015.08.003

Tattersall, E., Pigeon, K., MacNearney, D., & Finnegan, L. (2023). Walking the line: Investigating biophysical characteristics related to wildlife use of linear features. *Ecological solutions and evidence*, *4*(1), n/a. https://doi.org/10.1002/2688-8319.12219

Tigner, J., Bayne, E. M., & Boutin, S. (2014). Black bear use of seismic lines in Northern Canada. *The Journal of Wildlife Management*, *78*(2), 282-292. https://doi.org/10.1002/jwmg.664

Wittische, J., Heckbert, S., James, P. M. A., Burton, A. C., & Fisher, J. T. (2021). Community-level modelling of boreal forest mammal distribution in an oil sands landscape. *The Science of the total environment*, *755*(Pt 2), 142500-142500. https://doi.org/10.1016/j.scitotenv.2020.142500

Young, B. F., & Ruff, R. L. (1982). Population Dynamics and Movements of Black Bears in East Central Alberta. *The Journal of Wildlife Management*, *46*(4), 845. https://doi.org/10.2307/3808217

Zager, P., & Beecham, J. (2006). The role of American black bears and brown bears as predators on ungulates in North America. *Ursus (International Association for Bear Research and Management)*, *17*(2), 95-108. https://doi.org/10.2192/1537-6176(2006)17[95:TROABB]2.0.CO;2

Zuckerberg, B., Cohen, J. M., Nunes, L. A., Bernath-Plaisted, J., Clare, J. D. J., Gilbert, N. A., Kozidis, S. S., Maresh Nelson, S. B., Shipley, A. A., Thompson, K. L., & Desrochers, A. (2020). A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring in Landscape Ecology? *Current landscape ecology reports*, *5*(4), 140-148. https://doi.org/10.1007/s40823-020-00059-4

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3-14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

6. ENERGY INFRASTRUCTURE CLEARS THE WAY FOR COYOTES IN ALBERTA'S OIL SANDS

Jamie F Clarke, Larissa Bron, Madison Carlson, Sophia Labiy, Zoe Penno, Hayley Webster, Jason T Fisher, and Marissa A Dyck

OSM Summary

Oil sands development occurs against the backdrop of other macroecological changes to boreal forest systems. Climate is changing, fire regimes are changing, and so too are some continentally distributed mammal species, such as white-tailed deer and coyotes. Both are neonative to the boreal forest, having expanded from southern ranges for reasons associated with anthropogenic landscape development (and climate) but not necessarily oil sands development. Nonetheless OS does play role in facilitating these expansions into the boreal forest, as clearly illustrated for white-tailed deer (Fisher et al. 2020, Darlington et al. 2022, Fuller et al. 2023, Khan et al. 2023). Coyotes may also play a large role in disrupting normal boreal predator-prey relationships but thus far the effects of OS on coyotes have been examined as part of larger communities (Fisher and Burton 2018, Fisher et al. 2021c). Here we dive deeper into the role that some OS features play in coyote distribution across the OSR. We show that wide linear features play a very strong role, as does the wholesale loss of natural landcover (mature boreal forest canopy). Any management actions aimed to restore natural boreal forest functioning will necessarily have to tackle coyote management, and we provide information to guide those future decisions.

Introduction

People have profoundly changed the Earth's surface. More than 75% of the planet's ice-free land has been anthropogenically modified (Ellis and Ramankutty 2008), affecting both climate and natural life (Steffen et al. 2005). Land use change – leading to habitat loss and fragmentation – has altered ecosystem structure and function, to the detriment of biodiversity and biological interactions (Díaz et al. 2019, Sage 2020).

An example of land use change is Alberta's oil sands region – a 140,000 km^2 stretch of boreal forest, townsites and First Nations reserves in Nearctic Canada that sit atop one of the largest hydrocarbon deposits in the world. The region has undergone intensive resource development in the last 50-plus years, with timber harvest, road infrastructure and energy extraction significantly and rapidly altering the landscape (Schieck et al. 2014, Dabros et al. 2017). Decades of cumulative disturbance has created a landscape without historic or global parallels (Pickell et al. 2015, Fisher and Burton 2018, Dabros and Higgins 2023).

Particularly unique is the density of anthropogenic disturbance. The boreal forest of the oil sands region is a maze of linear (e.g., roads) and polygonal (e.g., well pads) clearings (Figure 1). Large swaths of forest have been ~~levelled~~ removed for surface mining operations, with additional mines exhausted or slated for development (Jordaan 2012). Millions more kilometres have been cleared to locate deep petroleum deposits and service *in-situ* wells, creating novel patterns on the landscape (Timoney and Lee 2001, Jordaan 2012, Roberts et al. 2022). These clearings are mostly linear corridors, and include geo-survey (seismic) lines, pipelines, power transmission lines and access roads. In some parts of the oil sands region, the density of seismic lines alone was estimated to be as high as 40 km/km^2 (Stern et al. 2018). On some leases, grid-patterned 3D seismic lines represent more than 10% of the surface footprint (Kansas et al. 2015).

Such intensive and extensive disturbance affects wildlife species variably. On one hand, wildlife "winners" are able to capitalize on the movement and forage subsidies linear features (LFs) provide (Fisher and Burton 2018, Tattersall et al. 2023a). Grey wolves (*Canis lupus*), for example, show a preference for LFs, using them to travel farther and faster across challenging boreal terrain, potentially increasing kill rates (James and Stuart-Smith 2000a, Fryxell et al. 2007, McKenzie et al. 2012, Dickie et al. 2017). Early-seral vegetation (e.g., grasses, forbs, browse) planted or regrowing along LFs supports non-native, range-expanding white-tailed deer, improving survival and supporting population growth (Dawe et al. 2014, Darlington et al. 2022). Wildlife "losers," on the other hand, struggle under the pressures of forest conversion and hyperconnectivity (Fisher and Burton 2018). The mature, undisturbed forests that threatened-status woodland caribou (*Rangifer tarandus caribou*) rely on for shelter and forage are being fragmented by oil and gas development (Boutin et al. 2012, Lesmerises et al. 2013), with LFs increasing predators' access to caribou habitat (Latham et al. 2011b, Whittington et al. 2011, Demars and Boutin 2018) and potentially shifting caribou distribution (Nellemann et al. 2001).

The influence of energy infrastructure on another member of the oil sands mammal community – the coyote (*Canis latrans*) – is not as well understood. Coyotes are relative newcomers to northeastern Alberta, having dramatically extended their range in the 20th century to become the most widely distributed *Canis* species in North America (Hody and Kays 2018, Ward et al. 2018).

In the western boreal forest, evidence suggests coyotes prefer disturbed sites and landscapes (Barnas et al. 2024b), and particularly areas of high LF density – potentially using them as movement corridors – like wolves do (Fisher and Burton 2018, Toews et al. 2018, Tattersall et al. 2020a). Yet, the kinds of LFs coyotes select for is unclear. Also of interest is the interplay between energy infrastructure and coyotes' interspecific interactions. The increased connectivity and permeability LFs provide (Dickie et al. 2017), coupled with coyotes' recent expansion into and success in the region (Burgar et al. 2019), could have important consequences on other species' behaviour and distribution (Heim et al. 2017, Lendrum et al. 2018, Mumma et al. 2019, Chow-Fraser et al. 2022, Fisher and Ladle 2022b, Boczulak et al. 2023).

To better understand which kinds LFs coyotes are using in the oil sands region – and how predation and competition influence coyote LF use – we used camera trapping (O'Connell et al. 2011, Burton et al. 2015b) to measure coyote relative abundance across six landscapes with different degrees of development western boreal forest. Generalized linear models informed by these data, employed an information-theoretic approach, weighed evidence for additive and interactive models representing several competing hypotheses, sensu Burnham and Anderson (2002a). We hypothesized that coyote occurrence would 1) increase with LF density; 2) increase with increasing relative abundance of large and small herbivores, as coyote prey species; and 3) decrease with increasing relative abundance of wolves and bears as coyote competitor species. We predicted that coyote occurrence would increase with LF density since LFs provide movement subsidies for canids (Dickie et al. 2017) and forage subsidies for herbivore prey (Finnegan et al. 2019, Wittische et al. 2021b, Darlington et al. 2022). We further predicted that coyote occurrence would increase with higher relative abundance of prey species and decrease with higher relative abundance of competitor species, as coyotes would frequent prey-rich areas but avoid overlap with competitors (Ballard et al. 2003).

Methods

Study Area

Our study frame was the vast portion of the western boreal forest known as the western sedimentary basin (Porter et al. 1982), and within this frame our study extent was Canada's oil sands region, in northeastern Alberta. The region's topography is flat-to-undulating and is composed of upland forests – filled with white pine (*Picea glauca*), black spruce (*Picea mariana*), trembling aspen (*Populus tremuloides*) and jack pine (*Pinus banksiana*) – and Labrador tea- (*Rhododendron groenlandicum*) dominated lowland muskegs. Winters are typically long and cold, and summers short and warm; mean temperature of the coldest month is about -19º C, and 16º C in the hottest month, with about 450 mm of annual precipitation (Downing and Pettapiece 2006). The boreal forest supports a diversity of mammal species, including wolves, coyotes, lynx (*Lynx canadensis*), red foxes (*Vulpes vulpes*), black bear (*Ursus americanus*), fishers (*Pekania pennanti*), wolverines (*Gulo gulo*), martens (*Martes americana*), woodland caribou, moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*).

This research was conducted under the joint Canada-Alberta Oil Sands Monitoring program (Roberts et al. 2022). The study design for this program divides the region into ~1,000 km^2 landscape units (LUs) based on hydrological boundaries, with each representing a differing degree of cumulative development from forestry, roading, and oil and gas exploration and extraction (Bayne et al. 2021b). LUs were characterized as 1) currently developed for *in-situ* or mine extraction, 2) proposed for *in-situ* development or mine site, or 3) low disturbance reference site (Bayne et al. 2021b). A subset of LUs representing all three disturbance levels were selected for this project.

Sampling Design

A total of 233 Reconyx Hyperfire 2X camera traps (Reconyx, Homen, WI) were deployed in six LUs (Figure 2): one mine site, one proposed *in-situ* site, two active *in-situ* sites and two low-disturbance sites. Camera traps were deployed using a constrained stratified sampling design. Each LU was divided into 60 2-km^2 hexagonal cells using ArcGIS (version 10.3); cells were then categorized as upland (> 50% deciduous) or lowland (> 50% wet coniferous) forest. About 40 cells (actual range: 36-42) were selected for camera trap deployment, with forest types represented roughly equally. We chose a constrained stratified design to control for natural variability, to tease out the effects of industrial development on mammal communities.

In each selected cell, a was deployed at least 100 m from roads or trails and 1 km from other camera stations. Cameras were set about 0.5 m off the ground and pointing down a well-used wildlife trail. Ca. 40 mL of scent lure (Long Distance Call, O'Gorman's, MT) was spread on a tree within each camera's viewshed. Our design maximizes accessibility and probability of medium-to-large mammal detections while maintaining site independence (Diniz-Filho et al. 2003, Hawkins et al. 2007). Cameras were set to take 1 image per motion sensor trigger to prolong battery life and storage capabilities. 78 cameras were set across two LUs from October 2021-2022 and 155 were set across four LUs from fall 2022-2023, for a maximum duration of 13 months per camera trap.

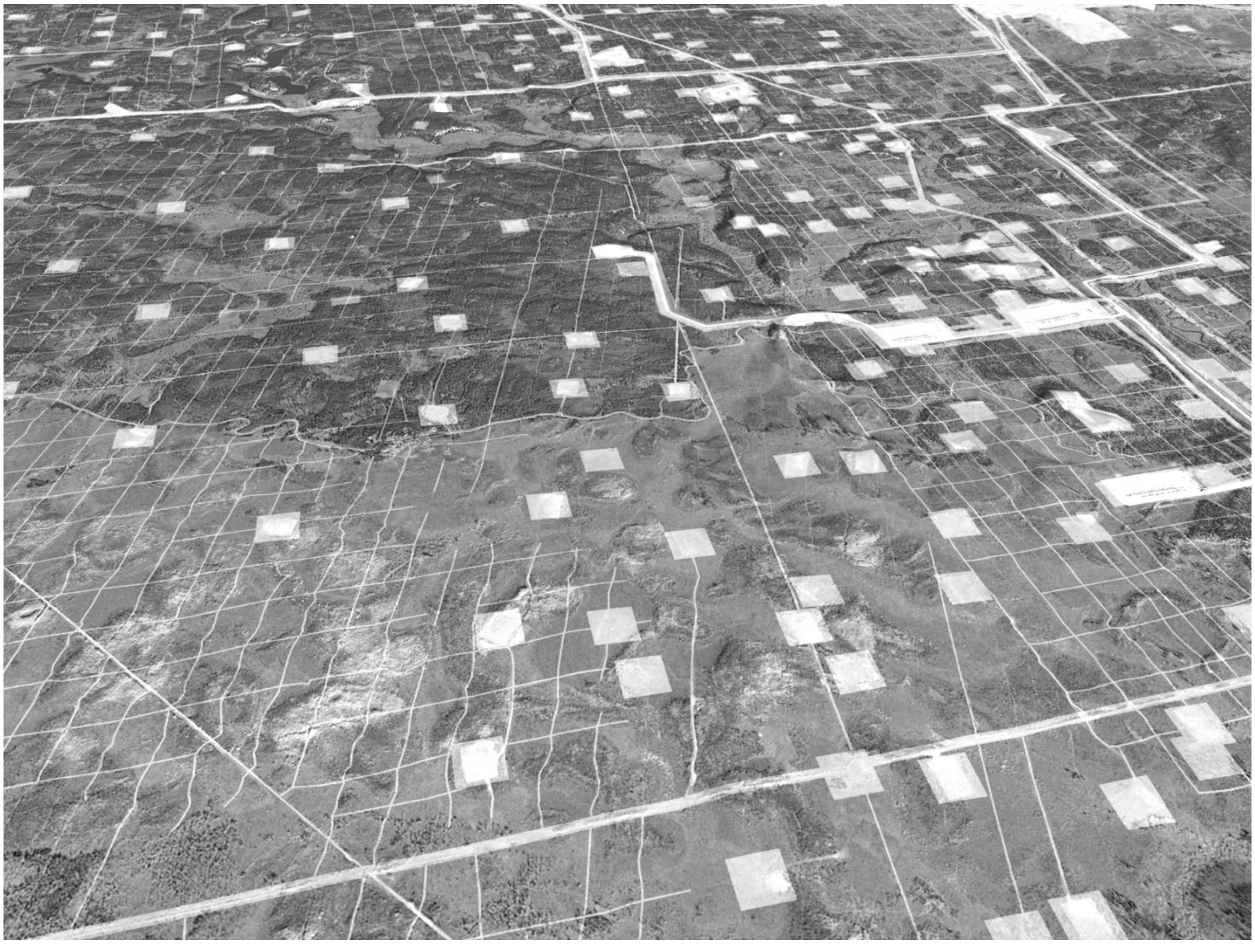

Figure 1. Aerial depiction of oil sands disturbances, including industrial facilities (large polygons), well pads (squares), roads (wide lines), conventional seismic lines (straight narrow lines) and 3D seismic lines (crosshatched, wavy lines). By Scott Heckbert.

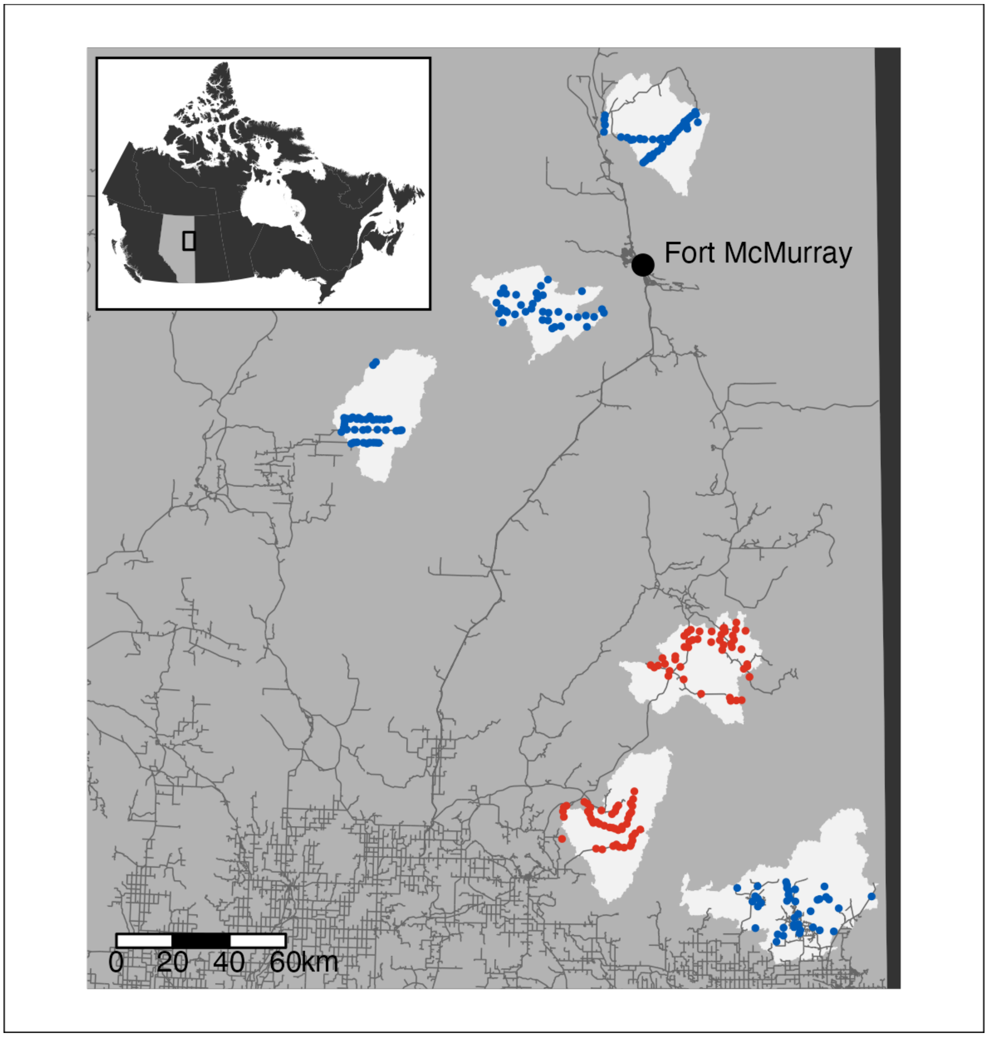

Figure 2. Map of camera trap deployments across 6 LUs (light polygons) in the oil sands region of Alberta. Red dots represent cameras active 2021-2022 (n = 93); blue dots represent cameras active 2022-2023 (n = 155). Grey lines show road networks, including unpaved roads. Inset: map of Canada, with Alberta in light grey and the study area enclosed in the black box.

Defining Variables

Diet studies show that coyotes mostly consume small mammals, ungulates, vegetation, and anthropogenic "by-catch" like pets and livestock (Todd et al. 1981, Lukasik and Alexander 2012, Shi et al. 2021, Jensen et al. 2022, Hayward et al. 2023). Analyses of coyote scat from Alberta indicate that snowshoe hares, rodents and ungulates are some of the most important food sources for coyotes in the region (Todd et al. 1981, Murray et al. 2015). Although deer and moose are coyotes' preferred ungulate prey, there have also been reports of "spill-over" predation on caribou (Boisjoly et al. 2010, Latham et al. 2011c). We therefore considered snowshoe hares, red squirrels, white-tailed deer, caribou and moose as potential coyote prey species in our analyses.

Interspecific competition is challenging to quantify (Murray et al. 2023), but there is some evidence of interference and exploitative competition between coyotes and felids, mustelids and other canids. Coyotes share prey species – including snowshoe hares – with lynx, for example (Ruggiero 1994, Krebs et al. 2001b). Coyotes and cougars also minimize spatial and temporal overlap to reduce conflict (Jensen et al. 2024). LFs increase competition between coyotes and wolverines (Chow-Fraser et al. 2022), while fishers and coyotes both preferentially prey on small mammals (Weir et al. 2005). Similarly, coyotes appear to be limited by competition with grey wolves (Berger and Gese 2007). We therefore classified lynx, cougars, wolverines, fishers and wolves as competitor species.

For interaction models: we chose the single prey and competitor species we believed exerted the most influence on coyote occurrence, given previous findings. We selected snowshoe hares as the main prey species, as lagomorphs are a key component of coyote diet (Prugh 2005, Shi et al. 2021, Hayward et al. 2023), especially in their boreal range (Todd et al. 1981) where they overlap with wolves (Petroelje et al. 2021). Likewise, we selected wolves as the main competitor species. Wolves are competitively dominant to coyotes (Merkle et al. 2009), harassing and sometimes killing coyotes in areas of high wolf-use and density (Miller et al. 2012, Flagel et al. 2017). Other competitor species (e.g., lynx) do not appear to compete as directly or intensely.

Coyotes are expected to spatially distribute relative to available natural resources, proxied by habitat measure using hyperspectral imagery. To quantify natural boreal heterogeneity, landscape data were derived from the Alberta Biodiversity Monitoring Institute's wall-to-wall landcover map (Alberta Biodiversity Monitoring Institute 2024). Landscape features within a 4,750 m radius of each camera station were considered, since it was the top-performing buffer distance for coyotes in anthropogenically-disturbed areas (Dyck et al., in prep). To avoid overparameterization in our models, and given coyotes are habitat generalists, we grouped natural landcover variables (grasslands, shrubland, and coniferous/broadleaf/mixed forest) into a single covariate (Mastro et al. 2019, Petroelje et al. 2021).

Model Framework

432,391 images (including blanks) were captured across the entire study. Of these, 184,985 were images of mammals (excluding people and domestic dogs). Image data was processed by trained technicians using Timelapse software (Greenberg and Godin 2012), with images of the same species captured within 30-minute intervals grouped into independent detections, not corrected for camera activity. Independent detections of coyotes were also used to calculate monthly occurrence (hereafter, occurrence) of coyotes at every camera site. Only cameras with ≥ 15 operational days per month were used to calculate coyote occurrence, to account for occasional camera failures (Fisher and Ladle 2022b). The response metric was thus the number of months a coyote was detected, and the number of months a coyote was not detected, to inform a proportional binomial model wherein each month is a Bernoulli trial (Crawley 2012, Faraway 2016). Here we considered a zero as a true zero and not partitioned as error, as is the case with occupancy models (MacKenzie et al. 2002) – if we do not detect a coyote in a month on a lured wildlife trail we are confident of its absence.

We carried out a two-step model selection to 1) explore which LFs to include in analyses and 2) test our hypotheses on coyote occurrence. In step 1, we competed different groupings of LFs (Table S1). In step 2, we tested the effects of LFs, natural landcover, and independent prey and competitor detections – including interactions between prey and competitor species and LFs – on coyote occurrence. We used a generalized linear mixed model (GLMM) framework with a binomial distribution, and set LU as a random effect, for all analyses, such that:

$$\eta = \beta_0 + \beta_1 * X_1 + \beta_2 * X_2 + \cdots + \beta_n * X_n + \tau$$

where η is the linear predictor, β_0 is the intercept, $\beta_n * X_n$ is a covariate of interest and τ is a random effect. The link function,

$$\text{logit}(\theta) = \eta$$

was used to predict the effect of covariates on coyote occurrence. Coyote occurrence was assumed to follow a Bernoulli distribution,

$$\text{monthly coyote occurrence} \sim \text{Bernoulli}(\theta)$$

whereby each month was considered an independent “trial” and coyotes were either detected (1) or not (0), with each camera site considered a unique replication (Fisher and Ladle 2022b). We included LU as a random effect to account for inherent variability between sampling sites (Supplementary Information). LU was assumed to follow a normal distribution, such that

$$\text{LU} \sim \text{Normal}(0, \sigma^2).$$

Models were constructed using the *lme4* package (Bates et al. 2024) and ranked using the Akaike Information Criterion (AIC; Akaike 1973) using the *MuMIn* package (Bartoń 2024) in R (version 4.3.2). The best-supported models had the lowest AIC scores by Δ AIC of ≥ 2 (Burnham and Anderson 2002a). Variables were scaled for standardized comparison between estimated model coefficients.

Before modelling, we tested multicollinearity between covariates using pairwise Pearson and Spearman's correlation tests. Covariates with a correlation coefficient $(r) \geq 0.6$ were not included in the same models. We then calculated variance inflation factor (VIF) in the package *car* (Fox et al. 2019) to test for collinearity between covariates in our best fit model. VIFs report how much of a given covariate's variability is explained by other covariates, owing to correlation (Craney and Surles 2002). A VIF value of 1 indicates no correlation, with larger values (e.g., > 5) signalling severe correlation.

Results

Mammal detections

Camera images generated 15,944 total independent detections of 10 focal species. The most-detected species was white-tailed deer (6,143), followed by snowshoe hare (4,572), red squirrel (2,200), coyote (1,319), moose (696), lynx (526), fisher (262) and grey wolf (226). Caribou, cougars and wolverines had too few detections (115, 37 and 0, respectively) to carry forward into analyses. Coyotes were detected at 172 of 233 sampling sites (74%).

Model Selection

In step1, the wide LF model – which grouped LFs > 5 m in width – was top performing (AICc = 980.4, Δ AICc = 2.04, weight = 0.58; Table 1). The difference in AIC scores between the best-performing model (wide LFs) and second-best performing model (all LFs) was > 2, indicating support for the top model (Burnham and Anderson 2002a, Burnham et al. 2011). Of the three wide LF types, roads had the strongest positive effect on coyote occurrence (β = 0.58612 ± 0.05940, $p < 0.001$), with conventional seismic lines also having a positive – but slightly weaker – influence (β = 0.18439 ± 0.07357, $p = 0.0122$). Transmission lines had a negligible effect on coyote occurrence (β = 0.01404 ± 0.06007, $p = 0.8152$).

In step 2: the global model, which included terms for natural landcover, wide LFs, and prey and competitor species, best predicted coyote occurrence (AICc = 921.9, Δ AICc = 2.09, weight = 0.74; Table 2). The global model with interactions terms was the second-best performing. VIF values for all top model covariates were near 1, indicating little collinearity.

The proportion of wide LFs on the landscape retained a strong positive effect on coyote occurrence ($\beta = 0.49669 \pm 0.06965$, $p < 0.001$), additive to detections of small prey snowshoe hares ($\beta = 0.18827 \pm 0.04769$, $p < 0.001$), and competitors grey wolves ($\beta = 0.18952 \pm 0.05059$, $p < 0.001$) and lynx ($\beta = 0.16876 \pm 0.05007$, $p < 0.001$). The odds of coyote occurrence at a camera site increased by 64% per 1% increase in the proportion of wide LFs (Figure 3, 4). Likewise, the likelihood of coyote occurrence increased by 10% for each snowshoe hare detection; 9% for each grey wolf detection; and 7% for each lynx detection. Total white-tailed deer and red squirrel detections also had a positive relationship with coyote occurrence, but effective size was smaller (white-tailed deer: $\beta = 0.06411 \pm 0.06531$, $p = 0.326270$; red squirrel: $\beta = 0.08085 \pm 0.04686$, $p = 0.084450$). The area of grouped natural landcover was the only covariate to have a clear negative effect on coyote occurrence ($\beta = -0.40375 \pm 0.05459$, $p < 0.001$), with odds of occurrence decreasing by 60% per 1% increase in natural feature coverage. Total moose detections had a slight negative relationship, but again, effect size was small ($\beta = -0.06344 \pm 0.05739$, $p = 0.268944$). Fishers had a negligible influence on coyote occurrence ($\beta = 0.01794 \pm 0.05042$, $p = 0.722021$).

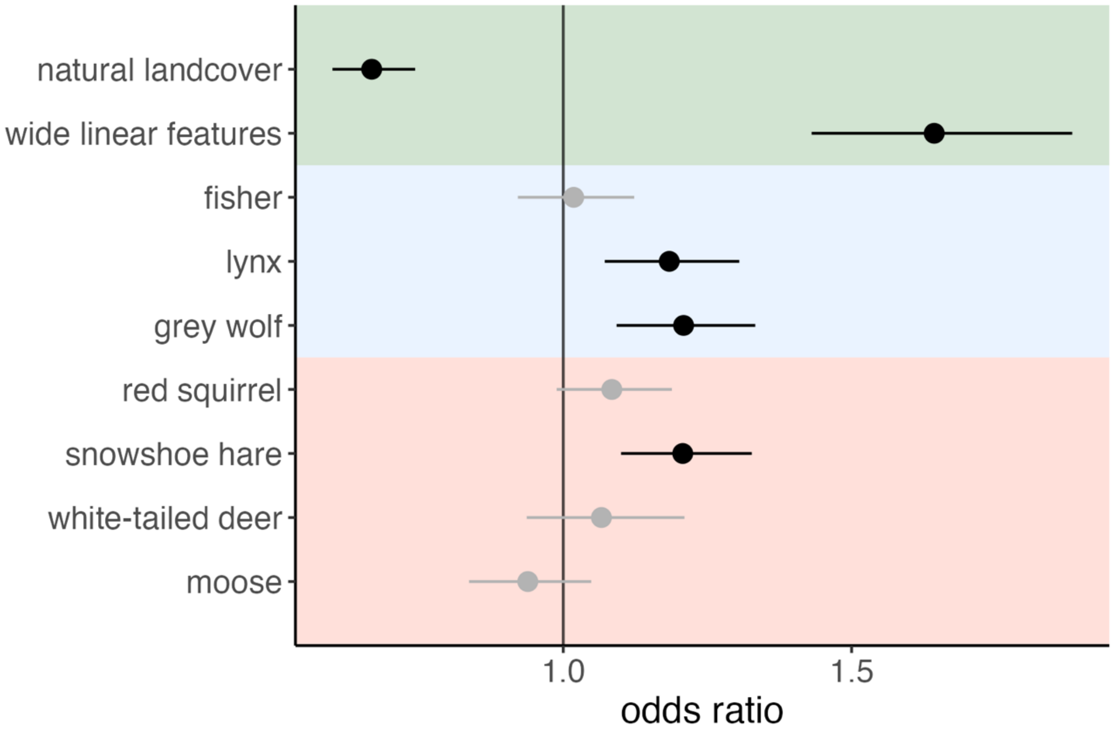

Figure 3. Odds ratio plot for the global model showing the effects of natural landcover and wide linear feature density (green box), and of total competitor (blue box) and prey (red box) species detections, on monthly coyote occurrence. Points represent exponentiated model coefficients; bars represent 97.5% confidence intervals.

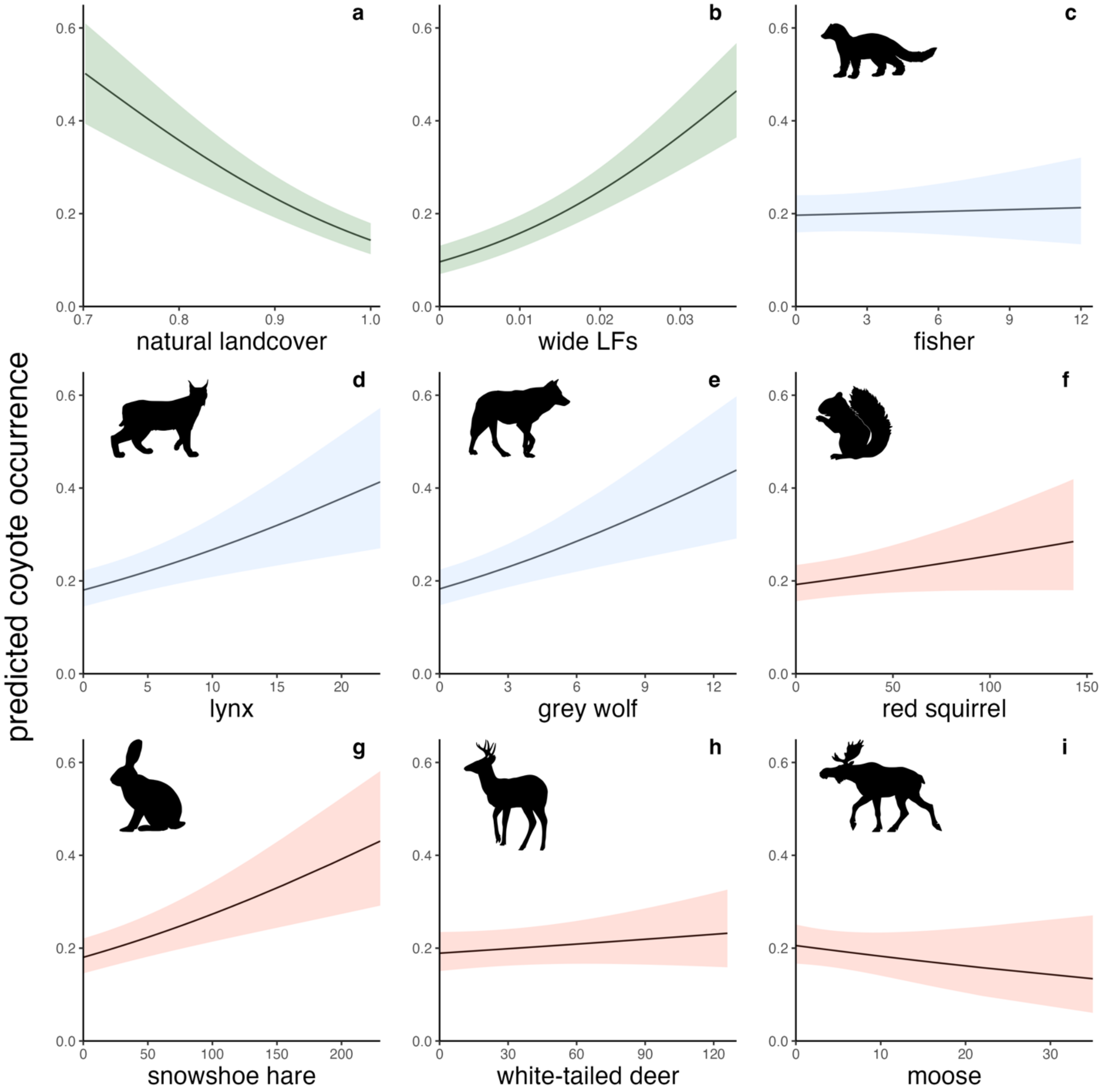

Figure 4. Proportion of natural landcover and wide LFs near camera trap sites, and total detections of prey and competitor species, influence monthly coyote occurrence. Lines represent the predicted relationship between coyote occurrence and covariates ± 95% confidence intervals.

Table 1. Step 1: GLMMs predicting monthly coyote occurrence given LF types. Models are ranked from most-to-least supported. Model statistics include degrees of freedom (df), logistical likelihood (logLik), Akaike information criterion score corrected for small sample size (AICc), difference in AICc score from the best-supported model (Δ AICc) and explanatory value of each model (AICc weight).

model	**covariates**	**df**	**logLik**	**AICc**	**Δ AICc**	**AICc weight**
wide LFs	roads + seismic lines + transmission lines	5	-485.1	980.4	0	0.58
global model	roads + seismic lines + 3D seismic lines + trails + transmission lines	7	-484.0	982.5	2.04	0.21
unvegetated LFs	roads	3	-488.2	982.5	2.05	0.21
vegetated LFs	seismic lines + 3D seismic lines+ trails + transmission lines	6	-527.8	1068.0	87.53	0
narrow LFs	3D seismic lines + trails	4	-533.2	1074.5	94.09	0
pipelines	pipelines	3	-534.3	1074.8	94.34	0
null	---	2	-537.3	1078.6	98.13	0

Table 2. Step 2: GLMMs predicting monthly coyote occurrence given proportion of landcover and wide linear features, and total detections of prey and competitor species. Models are ranked from most-to-least supported. Model statistics include degrees of freedom (df), logistical likelihood (logLik), Akaike information criterion score corrected for small sample size (AICc), difference in AICc score from the best-supported model (Δ AICc) and explanatory value of each model (AICc weight).

model	**covariates**	**df**	**logLik**	**AICc**	**Δ AICc**	**AICc weight**
global	natural landcover + wide LFs + red squirrel + snowshoe hare + white-tailed deer + moose + fisher + lynx + grey wolf	11	-449.3	921.9	0	0.74
global interaction	natural landcover + red squirrel + white-tailed deer + moose + fisher + lynx + wide LFs*snowshoe hare + wide LFs*grey wolf	13	-448.2	924	2.09	0.26
competitor species, natural	natural landcover + wide LFs + fisher + lynx +	7	-461.3	937.1	15.25	0

landcover and wide LFs	grey wolf					
global competitor interaction	natural landcover + fisher + lynx + wide LFs*grey wolf	8	-460.7	938.1	16.2	0
global prey interaction	natural landcover + red squirrel + white-tailed deer + moose + wide LFs*snowshoe hare	9	-461.0	940.8	18.95	0
prey species, natural landcover and wide LFs	natural landcover + wide LFs + red squirrel + snowshoe hare + white-tailed deer + moose	8	-146.2	941	19.12	0
natural landcover and wide LFs	natural landcover + wide LFs	4	-479.0	966.2	44.34	0
prey species and natural landcover	natural landcover + red squirrel + snowshoe hare + white-tailed deer + moose	7	-480.9	976.2	54.33	0
competitor species and natural landcover	natural landcover + fisher + lynx + grey wolf	6	-489.1	990.5	68.62	0
prey species and wide LFs	wide LFs + red squirrel + snowshoe hare + white-tailed deer + moose	7	-489.9	994.3	72.44	0
prey interaction	red squirrel + white-tailed deer + moose + wide LFs*snowshoe hare	8	-489.4	995.5	73.61	0
competitor species and wide LFs	wide LFs + fisher + lynx + grey wolf	6	-492.3	996.9	75.01	0
competitor interaction	fisher + lynx + wide LFs*grey wolf	7	-491.7	997.8	75.91	0
natural landcover	natural landcover	3	-503.7	1013.6	91.69	0
prey species	red squirrel + snowshoe hare + white-tailed deer + moose	6	-512.2	1036.8	114.89	0
competitor species	fisher + lynx + grey wolf	5	-522.6	1055.5	133.63	0
null	---	2	-537.3	1078.6	156.69	0

Discussion

Range-expanding coyotes occur across the Canadian oil sands region of the western boreal forest, and anthropogenic linear features are paving the way. Across multiple landscapes spanning a gradient of disturbance, coyote relative abundance was much higher with high density of wide linear features, and much lower in natural landscapes. Contrary to expectations, coyotes did not avoid competitors, but rather clustered with them in space where prey abundance was high. The prevalence of wide LFs within 4,750 m of a camera site had the strongest positive effect on coyote occurrence, while proportion of natural landcover had the strongest negative effect. Total grey wolf, lynx and snowshoe hare detections had a positive, but smaller, signal. These findings lend support to our hypotheses that coyote occurrence is positively related to LF density and prey species relative abundance, but did not support our hypothesis that coyotes would avoid overlap with competitor species.

Wide LFs – especially roads and seismic lines – had the largest positive effect on coyote occurrence. Coyotes may have selected areas of high wide LF density because these corridors are long, straight and unobstructed, maximizing travel speed, distance covered and line-of-sight for movement and hunting compared to narrow LFs or forest patches (Dickie et al. 2017). Our findings are in line with other studies from the oil sands region linking coyotes and wide LFs (Skatter et al. 2020, Beirne et al. 2021a), and particularly roads (Fisher and Burton 2018, Fisher and Ladle 2022b). Many roads within the oil sands region are low-traffic access routes, with less road-use risk (Van Scoyoc et al. 2024) to weigh against the benefits of roadside hunting and scavenging, and easy movement.

Importantly, the wide LF model (which included roads, seismic lines and transmission lines) outperformed the road-only LF model, indicating seismic lines' importance (the effect of transmission lines was negligible). Roads had the strongest predictive effect on coyote occurrence but seismic lines the second-strongest, suggesting they could provide alternate or additive pathways to roads – which bring wildlife into closer contact with people and increase chances of vehicle strikes (reviewed in Coffin 2007). Coyotes may also exploit seismic lines simply because they are much more pervasive than roads. Within our study LUs and site buffer radius, seismic lines had a mean proportional coverage of 0.7% compared to 0.4% for roads; moreover, seismic lines were represented within-buffer-radius for 99% of camera sites versus

87% for roads. Coyotes may therefore select seismic lines as a “second choice” LF because they are structurally similar (e.g., unobstructed, straight) and abundant.

Coyote occurrence was negatively related to the proportion of natural landcover. The boreal forest is difficult for wildlife to move through, with dense trees, fallen woody debris (Hansson 1992) and bogs. Cleared and compacted LFs increase movement rates for hunting, monitoring, communication and travel through this otherwise challenging landscape (Dickie et al. 2017). Even given the choice between natural (e.g., waterways) and disturbed corridors, canids have been shown to select human-made LFs, especially as anthropogenic LF density increases (Newton et al. 2017). LFs likely represent the least-cost path for coyotes, versus relatively movement-resistant natural landcover (Sawyer et al. 2011).

Contrary to our last hypothesis, coyotes co-occurred with competitor species – particularly grey wolves and lynx. One potential explanation is that coyotes aggregate near competitors to feed on their kills (Paquet 1992, Wilmers et al. 2003). Coyotes are facultative scavengers (Walker et al. 2021) that have been shown to consume more carcasses when wolves are on the landscape (Switalski 2003, Atwood and Gese 2008). The strong predictive signal of wolf detections on coyote occurrence, coupled with the knowledge that LFs may improve predation rates for wolves (Messier and Crête 1985, Fryxell et al. 2007, Dickie et al. 2017), could indicate a higher number of wolf kills and subsequently more scavenging by coyotes.

The outcomes of wolf-coyote competitive interactions also depend on group size. Wolves are considered to be the dominant canid (Levi and Wilmers 2012), with many documented cases of wolves killing coyotes in direct competition (see Mech and Boitani 2019). Wolves can, however, can be overrun or harassed by coyotes when outnumbered (Merkle et al. 2009). In some parts of the oil sands region, coyote density is triple that of wolves (Burgar et al. 2019), and wolf culls for caribou recovery can further reduce wolf population sizes (Hervieux et al. 2014, Grente et al. 2024). Thus, coyotes may be abundant enough in our study area to reduce interference competition with wolves. Coyotes often choose to scavenge on wolf kills, despite the potential risks (Paquet 1992); taken together, our findings could suggest that trade-off is further skewed in the oil sands, where coyotes can outnumber wolves, altering dominance structures and potentially resulting in high rates of scavenging and spatial overlap.

Interacting species must partition time, space or resources to coexist (Schoener 1974). An alternative interpretation of overlapping detections, then, is that coyotes and their competitors partition prey species instead of locking in a "space race" (Muhly et al. 2011). Coyotes and wolves do not typically compete for live prey (Arjo and Pletscher 2000, Arjo et al. 2002): coyotes tend to hunt smaller species (e.g., lagomorphs and rodents; Murray et al. 2015, Hayward et al. 2023) or weaker ungulates (e.g., fawns/calves and adults in poor condition; see Gese and Grothe 1995) while wolves take large ungulates (deer, elk, moose and caribou; Newsome et al. 2016). This could explain why ungulate detections only weakly influence coyote occurrence: coyotes in the oil sands do not seem to predate on ungulates often, instead consuming small mammals and scavenging on wolves' ungulate kills (Todd and Keith 1983).

Snowshoe hares had a clear, positive influence on coyote occurrence, further suggesting that they are in important coyote prey species in the boreal (Todd et al. 1981, O'Donoghue et al. 1998). Lynx and coyote diets could therefore considerably overlap in the oil sands region. To promote spatial overlap, these competitors may consume different proportions of hares (Hinton et al. 2017), or hare density may be high enough to support both species. To the first point: coyotes and lynx can prey on other species (e.g., voles and red squirrels) when snowshoe hare cycles dip (O'Donoghue et al. 1998). To the second point: the hare cycle was likely near its 10-year peak during our sampling period (Skatter et al. 2020). Estimates of peak hare density in the Yukon and Alaska have been as high as 300 to 1,000 hares/km^2 (Ward and Krebs 1985, Slough and Mowat 1996, Krebs et al. 2001a). Lynx eat roughly two snowshoe hares every three days when they are plentiful (Government of Northwest Territories); if hare densities were similar to northern estimates during our camera trap study, competition for food resources may have been minimal.

Still unknown in this system are coyotes' impacts on endangered caribou. Spillover predation, facilitated by hyper-connective LFs (Mumma et al. 2018) and higher coyote populations, has been posited. Indeed, facultative, disturbance mediated coyote-caribou predation is likely in an eastern boreal ecosystem (Boisjoly et al. 2010). Our results do not suggest that ungulates were an important predictor of coyote occurrence during the study period, and by extension that caribou would be a strong predictor. It is, however, possible that coyote diet could shift towards ungulates – including caribou – in low-hare years. Previous analyses have shown that ungulates, including deer and moose, can comprise ¼ to ½ of coyote diet (Boisjoly et al. 2010, Murray et al. 2015, Shi et al. 2021). Further investigation into patterns of coyote predation throughout the hare cycle could elucidate the relationship between coyotes and endangered caribou and clarify management priorities. It is worth noting that too few caribou detections were collected to make direct inferences from our dataset.

Future research could also investigate the nuances of coyote LF use throughout the year. Wolves have been shown to exert seasonal preferences for LF type (Dickie et al. 2017) and weaker selection for LFs during the wintertime (Latham et al. 2011b); similar patterns in coyotes may have been masked by the coarseness of our work. Likewise, overlap with prey species could change seasonally. Other canids tend to consume prey of different sizes during alternating seasons (Latham et al. 2011e), meaning ungulates could be a better predictor of coyote occurrence at finer time scales. Ungulates could better-predict coyote occurrence during ungulate calving, when they are more vulnerable to coyote attacks, as well.

The best-supported buffer size for coyotes in disturbed landscapes resulted in substantial overlap using our sampling design (Chapter 4), which may prompt concerns about pseudoreplication (the treatment of non-independent variables as independent; Whitlock and Schluter 2015). As per Hurlbert (1984), however, independent detections can be influenced by the same predictor variable values without being pseudoreplicated; more important is sound sampling design that accounts for systematic variability (Zuckerberg et al. 2020a). We stratified sampling design at two levels for our study (LU, camera site) to account for natural variability and to parse out the effects of industrial disturbance.

It is possible that the effect of roads was artificially inflated, since most cameras were deployed ~100 m from the nearest road. The topography of Alberta's oil sands region has changed drastically under the compounding pressures of industry. LFs created for forestry and energy extraction have fragmented the boreal forest, creating matrices of treed patches connected by networks of cleared corridors (Pattison et al. 2016). What was previously good habitat for moose, caribou and lynx has given way to landscapes that support generalist, range-expanding species like coyotes and white-tailed deer, fundamentally the changing distribution and relative abundance of mammal populations (Fisher and Burton 2018).

LFs have outsized effects on wildlife ecology (e.g., Trombulak and Frissell 2000, Whittington et al. 2005, Ibisch et al. 2016); in the oil sands, where LF density is high (Komers and Stanojevic 2013, Stern et al. 2018), that effect is even more pronounced, influencing mammals and birds (Lankau et al. 2013, Fisher and Burton 2018, Darling et al. 2019), vegetation community composition and regeneration (van Rensen et al. 2015, Dabros et al. 2017), and interspecific relationships (Heim et al. 2017, Lendrum et al. 2018, Mumma et al. 2019, Chow-Fraser et al. 2022, Fisher and Ladle 2022b, Boczulak et al. 2023). That anthropogenic disturbance is believed to have a bigger role in the spatial distribution of mammals than natural ecological processes (Fisher and Ladle 2022b). With thousands of kilometres of new linear corridors cleared each year (Komers and Stanojevic 2013), a holistic understanding of wildlife LF use is therefore critical for management and conservation (Latham et al. 2011b, Newton et al. 2017, Finnegan et al. 2023, Benoit-Pépin et al. 2024).

Alberta's oil sands are the harbinger of a new hydrocarbon age. Global sources of conventional oil are being depleted (Bentley 2002) and interest retrained on "unconventional" oil sands deposits – resources that sit beneath thousands of square kilometres of forest (Rosa et al. 2017). Regions considering oil sands development should look to Canada's north to better understand how LFs influence wildlife species and interactions and weigh the ecological costs of energy extraction and habitat restoration with economic benefits.

References

Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika **60**:255-265.

Arjo, W. M., and D. H. Pletscher. 2000. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Canadian Journal of Zoology **77**:1919-1927.

Arjo, W. M., D. H. Pletscher, and R. R. Ream. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy **83**:754-766.

Atwood, T. C., and E. M. Gese. 2008. Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. Animal Behaviour **75**:753-762.

Ballard, W. B., L. N. Carbyn, and D. W. Smith. 2003. Wolf interactions with non-prey.

Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J. Paczkowski, and F. E. Stewart. 2024. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Science of the Total Environment **915**:169285.

Bartoń, K. 2024. R package "MuMIn".

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, J. Fox, A. Bauer, P. N. Krivitsky, E. Tanaka, and M. Jagan. 2024. R package "lme4".

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dilligeard, D. Farr, J. T. Fisher, M. Freemark, K. R. Foster, C. Godwin, C. E. Hebert, D. J. Huggard, D. McIssac, T. Narwani, S. E. Nielsen, B. Pauli, S. Prasad, D. R. Roberts, S. Slater, S. J. Song, S. Swanson, P. J. Thomas, J. D. Toms, C. Twitchell, S. R. White, F. Wyatt, and L. Mundy. 2021. Oil Sands Monitoring Program: A Before-After Dose-Response Terrestrial Biological Monitoring Framework for the Oil Sands. (OSM Technical Report Series No. 7). Edmonton, Alberta.

Beirne, C., C. Sun, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2021. Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics. Journal of Applied Ecology **58**:2821-2832.

Benoit-Pépin, A., M. J. Feldman, L. Imbeau, and O. Valeria. 2024. Use of linear features by mammal predators and prey in managed boreal forests. Forest Ecology and Management **561**:121911.

Bentley, R. W. 2002. Global oil & gas depletion: an overview. Energy Policy **30**:189-205.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology **76**:1075-1085.

Boczulak, H., N. P. Boucher, A. Ladle, M. S. Boyce, and J. T. Fisher. 2023. Industrial development alters wolf spatial distribution mediated by prey availability. Ecology and Evolution **13**:e10224.

Boisjoly, D., J. P. OUELLET, and R. Courtois. 2010. Coyote habitat selection and management implications for the Gaspésie caribou. The Journal of Wildlife Management **74**:3-11.

Boutin, S., M. S. Boyce, M. Hebblewhite, D. Hervieux, K. H. Knopff, A. D. M. Latham, M. C. Latham, J. Nagy, D. R. Seip, and R. Serrouya. 2012. Why are caribou declining in the oil sands? Frontiers in Ecology and the Environment **10**:65-67.

Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple interacting species for conservation of species at risk. Conservation Biology **33**:709-715.

Burnham, K., and D. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach 2nd EditionSpringer-Verlag. New York, New York.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology **65**:23-35.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.

Chow-Fraser, G., N. Heim, J. Paczkowski, J. P. Volpe, and J. T. Fisher. 2022. Landscape change shifts competitive dynamics between declining, at-risk wolverines and range-expanding coyotes, compelling a new conservation focus. Biological Conservation **266**.

Coffin, A. W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. Journal of transport Geography **15**:396-406.

Craney, T. A., and J. G. Surles. 2002. Model-dependent variance inflation factor cutoff values. Quality engineering **14**:391-403.

Crawley, M. J. 2012. The R book. John Wiley & Sons.

Dabros, A., H. J. Hammond, J. Pinzon, B. Pinno, and D. Langor. 2017. Edge influence of low-impact seismic lines for oil exploration on upland forest vegetation in northern Alberta (Canada). Forest Ecology and Management **400**:278-288.

Dabros, A., and K. L. Higgins. 2023. Vegetation recovery and edge effects of low impact seismic lines over eight-year period in boreal uplands of northern Alberta. Forest Ecology and Management **532**:120850.

Darling, A. F., L. Leston, and E. M. Bayne. 2019. Small-mammal abundance differs between pipelines, edges, and interior boreal forest habitat. Canadian Journal of Zoology **97**:880-894.

Darlington, S., A. Ladle, A. C. Burton, J. P. Volpe, and J. T. Fisher. 2022. Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. Scientific Reports **12**:1-12.

Dawe, K., E. Bayne, and S. Boutin. 2014. Influence of climate and human land use on the distribution of white-tailed deer (Odocoileus virginianus) in the western boreal forest. Canadian Journal of Zoology **92**:353-363.

DeMars, C. A., and S. Boutin. 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. Journal of Animal Ecology **87**:274-284.

Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. Butchart, and K. M. Chan. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science **366**:eaax3100.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology **54**:253-263.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography **12**:53-64.

Downing, D. J., and W. W. Pettapiece. 2006. Natural Regions and Subregions of Alberta. Government of Alberta, Natural Regions Committee.

Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment **6**:439-447.

Faraway, J. J. 2016. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall/CRC.

Finnegan, L., M. Hebblewhite, and K. E. Pigeon. 2023. Whose line is it anyway? Moose (Alces alces) response to linear features. Ecosphere **14**:e4636.

Finnegan, L., K. E. Pigeon, and D. MacNearney. 2019. Predicting patterns of vegetation recovery on seismic lines: Informing restoration based on understory species composition and growth. Forest Ecology and Management **446**:175-192.

Fisher, J. T., and A. C. Burton. 2018. Wildlife winners and losers in an oil sands landscape. Frontiers in Ecology and the Environment **16**:323-328.

Fisher, J. T., and A. Ladle. 2022. Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. Science of the Total Environment:153432.

Flagel, D. G., G. E. Belovsky, M. J. Cramer, D. E. Beyer Jr, and K. E. Robertson. 2017. Fear and loathing in a Great Lakes forest: cascading effects of competition between wolves and coyotes. Journal of Mammalogy **98**:77-84.

Fox, J., S. Weisberg, B. Price, D. Adler, D. Bates, G. Baud-Bovy, B. Bolker, S. Ellison, D. Firth, M. Friendly, G. Gorjanc, S. Graves, R. Heiberger, P. Krivitsky, R. Laboissiere, M. Maechler, G. Monette, D. Murdoch, H. Nilsson, D. Ogle, B. Ripley, T. Short, W. Venables, S. Walker, D. Winsemius, A. Zeileis, and R-Core. 2019. R package "car".

Fryxell, J. M., A. Mosser, A. R. Sinclair, and C. Packer. 2007. Group formation stabilizes predator–prey dynamics. Nature **449**:1041-1043.

Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist:36-43.

Greenberg, S., and T. Godin. 2012. Timelapse image analysis manual. University of Calgary.

Grente, O., S. Bauduin, N. L. Santostasi, S. Chamaillé-Jammes, C. Duchamp, N. Drouet-Hoguet, and O. Gimenez. 2024. Evaluating the effects of wolf culling on livestock predation when considering wolf population dynamics in an individual-based model. Wildlife Biology **2024**:e01227.

Hansson, L. 1992. Landscape ecology of boreal forests. Trends in Ecology & Evolution **7**:299-302.

Hawkins, B. A., J. A. F. Diniz-Filho, L. Mauricio Bini, P. De Marco, and T. M. Blackburn. 2007. Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography **30**:375-384.

Hayward, M. W., C. D. Mitchell, J. F. Kamler, P. Rippon, D. R. Heit, V. Nams, and R. A. Montgomery. 2023. Diet selection in the Coyote Canis latrans. Journal of Mammalogy **104**:1338-1352.

Heim, N., J. T. Fisher, A. Clevenger, J. Paczkowski, and J. Volpe. 2017. Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (Gulo gulo L.). Ecology and Evolution **7**:8903-8914.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (Canis lupus) to recover threatened woodland caribou (Rangifer tarandus caribou) in Alberta. Canadian Journal of Zoology **92**:1029-1037.

Hinton, J. W., A. K. Ashley, J. A. Dellinger, J. L. Gittleman, F. T. van Manen, and M. J. Chamberlain. 2017. Using diets of Canis breeding pairs to assess resource partitioning between sympatric red wolves and coyotes. Journal of Mammalogy **98**:475-488.

Hody, J. W., and R. Kays. 2018. Mapping the expansion of coyotes (Canis latrans) across North and Central America. ZooKeys:81.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187-211.

Ibisch, P. L., M. T. Hoffmann, S. Kreft, G. Pe'er, V. Kati, L. Biber-Freudenberger, D. A. DellaSala, M. M. Vale, P. R. Hobson, and N. Selva. 2016. A global map of roadless areas and their conservation status. Science **354**:1423-1427.

Institute, A. B. M. 2021. The Human Footprint Inventory (HFI) for Alberta 2021 (version 1.0) : Metadata Documentation.

Institute, A. B. M. 2024. Enhanced Human Footprint Oil Sands Region 2021.

James, A. R., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. The Journal of Wildlife Management:154-159.

Jensen, A. J., C. J. Marneweck, J. C. Kilgo, and D. S. Jachowski. 2022. Coyote diet in North America: geographic and ecological patterns during range expansion. Mammal Review **Early view**.

Jensen, R., J. Ruprecht, E. Orning, T. Levi, D. E. Clark, and T. D. Forrester. 2024. Large-scale overlap and fine-scale avoidance: assessing interactions between coyotes, bobcats, and cougars at multiple scales. Journal of Mammalogy:gyae045.

Jordaan, S. M. 2012. Land and water impacts of oil sands production in Alberta. Environmental Science & Technology **46**:3611-3617.

Kansas, J. L., M. L. Charlebois, and H. G. Skatter. 2015. Vegetation recovery on low impact seismic lines in Alberta's oil sands and visual obstruction of wolves (Canis lupus) and woodland caribou (Rangifer tarandus caribou). Canadian Journal of Wildlife Biology and Management **4**:137-149.

Komers, P., and Z. Stanojevic. 2013. Rates of disturbance vary by data resolution: implications for conservation schedules using the Alberta Boreal Forest as a case study. Global Change Biology **19**:2916-2928.

Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin. 2001a. Estimating snowshoe hare population density from pellet plots: a further evaluation. Canadian Journal of Zoology **79**:1-4.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001b. Ecosystem dynamics of the boreal forest. New York7 The Kluane Project.

Lankau, H. E., E. M. Bayne, and C. S. Machtans. 2013. Ovenbird (Seiurus aurocapilla) territory placement near seismic lines is influenced by forest regeneration and conspecific density. Avian Conservation and Ecology **8**.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications **21**:2854-2865.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011b. The Role of Predation in Woodland Caribou Population Declines in Northeastern Alberta – Coyotes.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011c. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. The Journal of Wildlife Management **75**:204-212.

Lendrum, P. E., J. M. Northrup, C. R. Anderson, G. E. Liston, C. L. Aldridge, K. R. Crooks, and G. Wittemyer. 2018. Predation risk across a dynamic landscape: effects of anthropogenic land use, natural landscape features, and prey distribution. Landscape Ecology **33**:157-170.

Lesmerises, R., J. P. Ouellet, C. Dussault, and M. H. St-Laurent. 2013. The influence of landscape matrix on isolated patch use by wide-ranging animals: conservation lessons for woodland caribou. Ecology and Evolution **3**:2880-2891.

Levi, T., and C. C. Wilmers. 2012. Wolves–coyotes–foxes: a cascade among carnivores. Ecology **93**:921-929.

Lukasik, V. M., and S. M. Alexander. 2012. Spatial and temporal variation of coyote (Canis latrans) diet in Calgary, Alberta. Cities and the Environment (CATE) **4**:8.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248-2255.

Mastro, L. L., D. J. Morin, and E. M. Gese. 2019. Home range and habitat use of West Virginia Canis latrans (Coyote). Northeastern Naturalist **26**:616-628.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface focus **2**:205-216.

Mech, L. D., and L. Boitani. 2019. Wolves: behavior, ecology, and conservation. University of Chicago Press.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology **87**:56-63.

Messier, F., and M. Crête. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia **65**:503-512.

Miller, B. J., H. J. Harlow, T. S. Harlow, D. Biggins, and W. J. Ripple. 2012. Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals. Canadian Journal of Zoology **90**:70-78.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PloS One **6**:e17050.

Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2019. Functional responses to anthropogenic linear features in a complex predator-multi-prey system. Landscape Ecology **34**:2575-2597.

Mumma, M. A., M. P. Gillingham, K. L. Parker, C. J. Johnson, and M. Watters. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. Biological Conservation **228**:215-223.

Murray, D. L., J. Gobin, A. Scully, and D. H. Thornton. 2023. Conventional niche overlap measurements are not effective for assessing interspecific competition. Frontiers in Ecology and Evolution **11**:1281108.

Murray, M., A. Cembrowski, A. Latham, V. Lukasik, S. Pruss, and C. St Clair. 2015. Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict. Ecography **38**:1235-1242.

Nellemann, C., I. Vistnes, P. Jordhøy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation **101**:351-360.

Newsome, T. M., L. Boitani, G. Chapron, P. Ciucci, C. R. Dickman, J. A. Dellinger, J. V. López-Bao, R. O. Peterson, C. R. Shores, and A. J. Wirsing. 2016. Food habits of the world's grey wolves. Mammal Review **46**:255-269.

Newton, E. J., B. R. Patterson, M. L. Anderson, A. R. Rodgers, L. M. Vander Vennen, and J. M. Fryxell. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: implications for caribou conservation. PloS One **12**:e0186525.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera traps in animal ecology: methods and analyses. Springer.

O’Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**:1193-1208.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy **73**:337-343.

Pattison, C. A., M. S. Quinn, P. Dale, and C. P. Catterall. 2016. The landscape impact of linear seismic clearings for oil and gas development in boreal forest. Northwest Science **90**:340-354.

Petroelje, T. R., T. M. Kautz, D. E. Beyer Jr, and J. L. Belant. 2021. Interference competition between wolves and coyotes during variable prey abundance. Ecology and Evolution **11**:1413-1431.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. 2015. The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. Canadian Journal of Forest Research **45**:732-743.

Porter, J., R. Price, and R. McCrossan. 1982. The western Canada sedimentary basin. Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences **305**:169-192.

Prugh, L. R. 2005. Coyote prey selection and community stability during a decline in food supply. Oikos **110**:253-264.

Roberts, D. R., E. M. Bayne, D. Beausoleil, J. Dennett, J. T. Fisher, R. O. Hazewinkel, D. Sayanda, F. Wyatt, and M. G. Dubé. 2022. A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. Integrated Environmental Assessment and Management **18**:388-406.

Rosa, L., K. F. Davis, M. C. Rulli, and P. D'Odorico. 2017. Environmental consequences of oil production from oil sands. Earth's Future **5**:158-170.

Ruggiero, L. F. 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. US Department of Agriculture, Forest Service, Rocky Mountain Forest and ….

Sage, R. F. 2020. Global change biology: a primer. Global Change Biology **26**:3-30.

Sawyer, S. C., C. W. Epps, and J. S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology **48**:668-678.

Schieck, J., P. Sólymos, and D. Huggard. 2014. ABMI science letters: human footprint in Alberta. AMBI, University of Alberta, Edmonton, Alberta, Canada.[online] URL: http ….

Schoener, T. W. 1974. Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. Science **185**:27-39.

Shi, Y., Y. Hoareau, E. M. Reese, and S. K. Wasser. 2021. Prey partitioning between sympatric wild carnivores revealed by DNA metabarcoding: a case study on wolf (Canis lupus) and coyote (Canis latrans) in northeastern Washington. Conservation Genetics **22**:293-305.

Skatter, H. G., J. L. Kansas, M. L. Charlebois, and S. Skatter. 2020. Long-term snow track monitoring to understand factors affecting boreal forest mammal density in an expanding in situ oil sands area. Canadian Wildlife Biology and Management **2**:107-131.

Slough, B. G., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. The Journal of Wildlife Management:946-961.

Steffen, W., R. A. Sanderson, P. D. Tyson, J. Jäger, P. A. Matson, B. Moore III, F. Oldfield, K. Richardson, H.-J. Schellnhuber, and B. L. Turner. 2005. Global Change and the Earth System: a Planet Under Pressure. Springer Science & Business Media.

Stern, E. R., F. Riva, and S. E. Nielsen. 2018. Effects of narrow linear disturbances on light and wind patterns in fragmented boreal forests in northeastern Alberta. Forests **9**:486.

Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Canadian Journal of Zoology **81**:985-993.

Tattersall, E., K. Pigeon, D. MacNearney, and L. Finnegan. 2023. Walking the line: Investigating biophysical characteristics related to wildlife use of linear features. Ecological Solutions and Evidence **4**:e12219.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020. Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape. Ecology and Evolution **10**:1678-1691.

Territories, G. o. N. Lynx-Snowshoe Hare Cycle.

Timoney, K., and P. Lee. 2001. Environmental management in resource-rich Alberta, Canada: first world jurisdiction, third world analogue? Journal of Environmental Management **63**:387-405.

Todd, A. W., and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. The Journal of Wildlife Management:394-404.

Todd, A. W., L. B. Keith, and C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. The Journal of Wildlife Management:629-640.

Toews, M., F. Juanes, and A. C. Burton. 2018. Mammal responses to the human footprint vary across species and stressors. Journal of Environmental Management **217**:690-699.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**:18-30.

van Rensen, C. K., S. E. Nielsen, B. White, T. Vinge, and V. J. Lieffers. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. Biological Conservation **184**:127-135.

Van Scoyoc, A., K. L. Calhoun, and J. S. Brashares. 2024. Using multiple scales of movement to highlight risk–reward strategies of coyotes (Canis latrans) in mixed-use landscapes. Ecosphere **15**:e4977.

Walker, M. A., M. Uribasterra, V. Asher, W. M. Getz, S. J. Ryan, J. M. Ponciano, and J. K. Blackburn. 2021. Factors influencing scavenger guilds and scavenging efficiency in Southwestern Montana. Scientific Reports **11**:4254.

Ward, J. N., J. W. Hinton, K. L. Johannsen, M. L. Karlin, K. V. Miller, and M. J. Chamberlain. 2018. Home range size, vegetation density, and season influences prey use by coyotes (Canis latrans). PloS One **13**:e0203703.

Ward, R. M., and C. J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Canadian Journal of Zoology **63**:2817-2824.

Weir, R. D., A. S. Harestad, and R. C. Wright. 2005. Winter diet of fishers in British Columbia. Northwestern Naturalist **86**:12-19.

Whitlock, M., and D. Schluter. 2015. The analysis of biological data. Roberts Publishers Greenwood Village, Colorado.

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

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf-and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters **6**:996-1003.

Wittische, J., S. Heckbert, P. M. A. James, A. C. Burton, and J. T. Fisher. 2021. Community-level modelling of boreal forest mammal distribution in an oil sands landscape. Science of the Total Environment **755**:142500.

Zuckerberg, B., J. M. Cohen, L. A. Nunes, J. Bernath-Plaisted, J. D. Clare, N. A. Gilbert, S. S. Kozidis, S. B. Maresh Nelson, A. A. Shipley, and K. L. Thompson. 2020. A review of overlapping landscapes: pseudoreplication or a red herring in landscape ecology? Current Landscape Ecology Reports **5**:140-148.

7. WHITE-TAILED DEER ON THE MOVE: A PROPOSED APPROACH TO INVESTIGATE DRIVERS AND IMPACTS OF BOREAL EXPANSION USING STRUCTURAL EQUATION MODELING

Marissa A. Dyck, Andrew F. Barnas, Megan Braun, Jason T. Fisher

OSM Summary

"*Whose problem is it anyway*?" is a question often heard from industry caucus of OSM. One of the principal goals of OSM is to identify which OS features (or other anthropogenic features) are causing negative responses for mammal species, so that restoration or other mitigation actions can be identified. In past works we have shown that multiple features generally contribute to mammals' responses to development (Dickie et al. 2020a, Serrouya et al. 2020, Laurent et al. 2021, Wittische et al. 2021b, Dickie et al. 2022, Fisher and Ladle 2022b, Roberts et al. 2022, Fuller et al. 2023, Barnas et al. 2024c, Carroll et al. 2024). These highlight the complexity of mammal-stressor relationships but cannot fully parse apart relative contributions of different features. Were we proposed an analytical approach – structural equation modelling – to attempt this task. This approach has been used previously in examination of seismic lines (Curveira-Santos et al. 2024) and we show how it can be applied for OSM analysis in a proof-of-concept focussing on a primary indicator of large-scale boreal change: white-tailed deer.

Introduction

Species range dynamics are a fundamental focus of ecology; understanding fluctuations in distribution and abundance of species and the consequences of these changes is also critical for proper management and conservation. Anthropogenic landscape change and climate change are two major drivers of species range dynamics. (Hughes 2000, McCarty 2001, Walther et al. 2002, Thuiller et al. 2008, Dawe and Boutin 2016, Lyn Morelli et al. 2025). More than 75% of ice-free land has undergone human-induced modification, meanwhile, the Earth's climate has warmed 0.38 to 0.68 °C over the last 100 years (Change 1995, Ellis and Ramankutty 2008). Such drastic change has resulted in the range contraction and expansion of many species. Resulting changes to species dynamics are not always easily predicted as effects from climate change and landscape alteration may be conflicting and context dependent. For example, Morelli et al. (2025) found that American red squirrels did not shift their range upslope as would be predicted by climate warming but rather shifted downslope in response to timber harvest-recovered red-spruce forests. The expansion and establishment of species outside their native range (i.e., neonates) can have widespread consequences for native flora and fauna. Prey species in particular, can alter predator-prey dynamics leading to declines in native prey via direct and apparent competition (Serrouya et al. 2015).

In the last century, white-tailed deer (*Odocoileus virginianus)* populations have increased, and they have expanded their range (Veitch 2001, VerCauteren 2003, Dawe and Boutin 2016). White-tailed deer have expanded as far north as Canada's boreal forest where they are indirectly attributed to the decline of Caribou (*Rangifer tarandus*) (Latham et al. 2011d, Hervieux et al. 2013, Latham et al. 2013). Previous research has shown that white-tailed deer expansion and establishment in Canada is largely attributed to climate and landscape change (Dawe 2011, Munro et al. 2012, Dawe and Boutin 2016, Laurent et al. 2021, Dickie et al. 2024a, Felton et al. 2024). However, few studies have investigated the relative importance of individual landscape features (e.g., seismic lines, roads, cutblocks) on white-tailed deer distribution. Management decisions to address and mitigate the effects of neonative white-tailed deer on caribou and other species of concern requires a robust understanding of the direct and indirect impacts that individual disturbance features have on white-tailed deer. We aimed to disentangle the effects of landscape change on white-tailed deer abundance and distribution in part of Canada's western boreal forest, the Athabasca oil sands, using multiple years of camera data and Structural Equation Modeling (SEM).

The Athabasca oil sands is an area where Canada's boreal forest is changing rapidly due to extensive resource extraction. Energy development and exploration in the oil sands has created landscapes without global or historical analogs (Pickell et al. 2015), to the detriment of some species while benefitting others (Fisher and Burton 2018). Previous research shows coyotes (*Canis latrans*) and grey wolves (*Canis lupus*) benefit from linear features which they can use as movement corridors to increase predation opportunities (James and Stuart-Smith 2000b, Latham et al. 2011b, Fisher and Burton 2018, Dickie et al. 2020a). These features simultaneously disadvantage prey species like moose (*Alces alces*) and caribou (James and Stuart-Smith 2000b, Fisher and Burton 2018). Thus, the oil sands represent an ideal system to investigate specific drivers of neonative white-tailed deer distribution and the potential consequences of their expansion into boreal Canada.

Structural equation models (SEMs) are used to test hypothesized causal relations between multiple predictor and response variables by evaluating multiple structured equations in a single causal network (Pearl 2000, Karimi and Meyer 2014), and are particularly useful for quantifying indirect effects as variables can serve as both predictors and responses in the model framework (Lefcheck 2016). SEMs also provide information on the relative importance of variables with standardized coefficient estimates and the total (direct and indirect) effect of individual variables. Current approaches for conducting SEMs, such as piecewise SEM, are highly adaptable and allow for simultaneous implementation of non-normal distributions, random effects, and different correlation structures (Lefcheck 2016). Thus, SEMs work well to address complex ecological questions where underlying causation is of interest and informed by pre-existing knowledge of the system.

Methods

Camera sampling design

This study was part of the joint Canada-Alberta Oil Sands Monitoring program (Roberts et al. 2022) and the design follows the terrestrial Biological Monitoring Program's before-after-dose-response (BADR) design (Bayne et al. 2021a). We employed a constrained stratified sampling design whereby the area was divided into six 1000-2000 km^2 landscape units (LUs) according to degree of development and each LU was further classified as either upland (>50% upland deciduous forest) or lowland (>50% wet coniferous forest) based on the dominant forest type. Within each LU, we divided the area into 2 km^2 hexagonal grid cells using ArcGIS (Version 10.3; ESRI 2014), ensuring that the cells were located within 100 m of accessible roads or trails. We then randomly selected 40-50 cells from within each LU. One remote infrared wildlife camera (Reconyx PC900 Hyperfire™, Holmen, WI, USA) was deployed within each selected cell. To maximize detections. And reduce false absences, cameras were placed along wildlife trails (MacKenzie and Royle 2005)and positioned towards a bait tree which we applied a scent lure to (O'Gorman's™ Long Distance Call, O'Gorman's MT) (Stewart et al. 2019b). Camera deployment locations were at least 100 m from active human-use roads and trails and at least 1 km from other camera locations in adjacent cells. Cameras were deployed from 2021 to

2023 in each of the six LUs and were monitored for approximately 12 months (two LUs from 2021-2022 and four LUs from 2022-2023), however, some monitoring periods were limited due to logistical constraints. Images were identified to the lowest taxonomical classification by trained reviewers using Timelapse Image Analyzer 2.0 (Greenberg et al. 2019a).

From the camera images we calculated the proportion of months white-tailed deer were detected at each camera, controlling for camera failures by omitting months with fewer than 15 operational camera days. Monthly white-tailed deer occurrence was assumed to follow a Bernoulli distribution, whereby each month was considered an independent trial where a species was detected (1) or not detected (0) within a calendar month. We treated 0's as true-absences and not potential false-absences; a non-detection of a white-tailed deer on a wildlife trail, with lure, in an entire month, can confidently be treated as a true absence. We also calculated the total number of independent detections – defined as images of a species taken at least 30 min apart – for six species expected to directly or indirectly influence white-tailed deer relative abundance (moose, grey wolf, coyote, snowshoe hare, black bear, and lynx).

Quantifying natural and anthropogenic landscape features around cameras

We calculated the proportion of anthropogenic and natural landscape features within a 1500-meter buffer around each camera location as this radius was identified as the most informative scale for white-tailed deer in our study are from previous research (Dyck et al., in prep). Anthropogenic disturbance features were derived from the Alberta Biodiversity Monitoring Institute's (ABMI) Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region (Alberta Biodiversity Monitoring 2021) and ecologically similar variables were grouped together (Table S1). Natural landscape features from the ABMI Wall-to-wall Land Cover Map 2010 Version 1.0 (Alberta Biodiversity Monitoring 2010). We assessed multicollinearity among our variables with Pearson's correlation tests and variables with a correlation coefficient (r) greater than 0.6 were not included in the same structured equation (Zuur et al. 2010b).

Model development

To evaluate the relative contributions of different landscape features on the spatial distribution and abundance of white-tailed deer in the oil sands, we used piecewise SEMs. Analysis was conducted in program R version 4.2.1 (R Core Team 2022) using the 'piecewise' package (Lefcheck 2016). Each individual structured equation within our analysis was fit as a generalize linear mixed model (GLMM), with LU as a random effect, using package lme4 (Bates et al. 2015). We modeled white-tailed deer monthly occurrence as an endogenous variable (response variable influenced by other covariates in the model) and landscape covariates as exogenous variables (independent variables not influenced by other covariates in the model) following the formula outlined in equation 1.

Equation 1:

$$\eta_{ij} = \beta_0 + B_1 X_{1ij} + \beta_2 X_{2ij} + \dots \beta_3 X_{nij} + LU_j$$

$$\log(\lambda_{ij}) = \eta_{ij}$$

$$Mammal\ detections_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$LU_j \sim \text{Gaussian}(0, \sigma^2)$$

Where η is the linear predictor, β_0 is the intercept, $\beta_n * X_n$ is a covariate of interest. White-tailed deer occurrence is represented the ith observation at LU_j, where LU is a random intercept with *j*th level *j*= individual landscape unit.

Detections of other mammal species were modeled as both endogenous and exogenous variables (Figure 2) whereby they could represent a covariate X_n of interest as in equation 1 or as a response variable following a Poisson distribution as in equation 2.

Equation 2:

$$\eta_{ij} = \beta_0 + B_1 X_{1ij} + \beta_2 X_{2ij} + \dots \beta_3 X_{nij} + LU_j$$

$$\text{logit}(\theta_{ij}) = \eta_{ij}$$

$$Mammal\ detections \sim \text{Poisson}(\theta_{ij})$$

$$LU_j \sim \text{Gaussian}(0, \sigma^2)$$

Using this framework, we developed an SEM that represented a priori hypothesized causal pathways among species and between species and landscape variables, based on previous research (Figure 2). We evaluated our hypothesized models' fit using Fisher's *C* statistic. The Fisher's C statistic tests the fit of the given model to the data and is compared to a chi-square distribution whereby a non-significant chi-square ($p > 0.05$) means that there is weak support for the sum of the conditional independence claims, and thus indicates the hypothesized relationships are consistent with the data (Lefcheck 2016).

Results and Future Directions

Our initial hypothesized model was a poor fit (C = 508.42, p = 0.00, df = 42), indicting we need to reevaluate the causal paths in our path diagram. We can conduct tests of directed separation, a function built into the 'piecewiseSEM' package to assess independence claims or missing pathways among variables, to look for significant ($p<0.05$) independence claims to optimize our model to the data (Lefcheck 2016, Stenegren et al. 2017). If an independence claim is deemed biologically relevant and improves the model fit (i.e., lowers the Fisher's *C* statistic), we can include it in further iterations of our model and re-evaluate its fit. Once we have fit a model with better explanatory power (non-significant Fisher's C p-value) we can evaluate the relative importance of individual variables on white-tailed deer by comparing the standardized coefficient estimates.

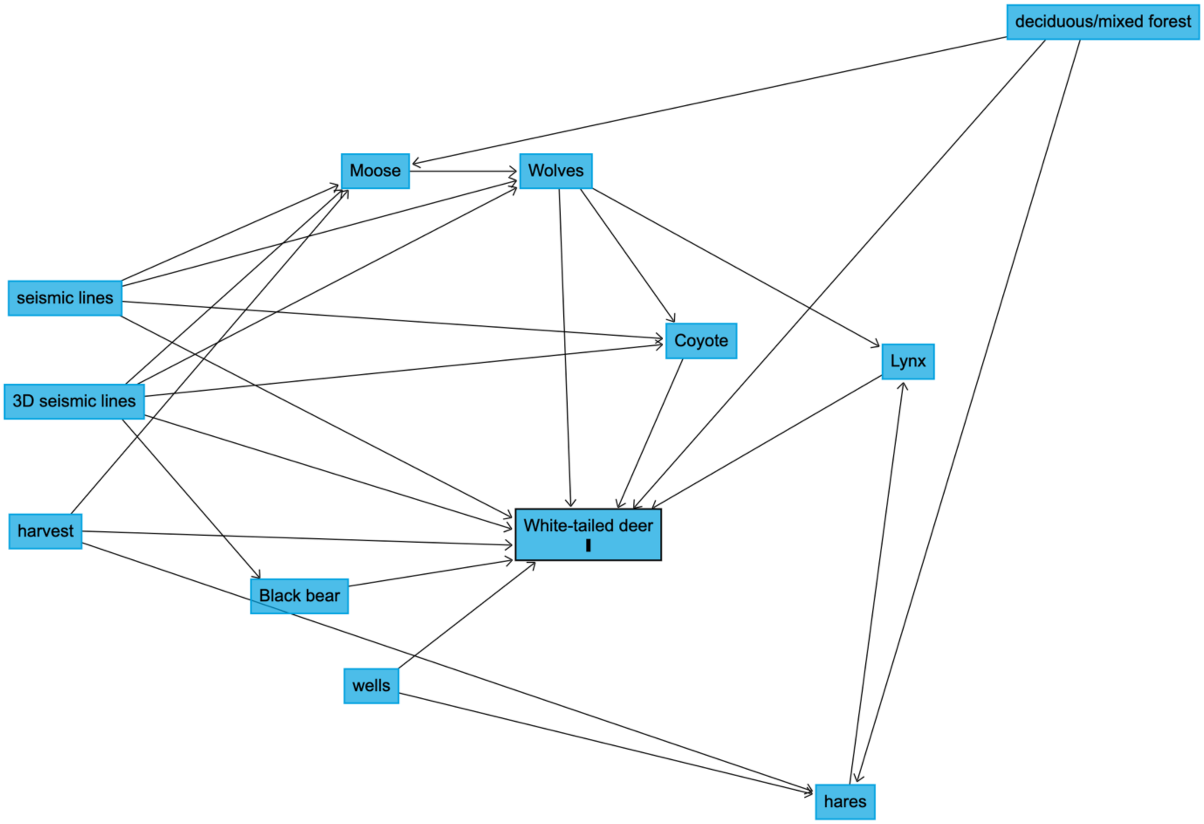

Figure 1: Hypothesized path diagram for landscape and interspecific interactions influencing white-tailed deer distribution and abundance in the oil sands, Alberta, Canada. Boxes represent various covariates and response variables and arrows represent hypothesized causal pathways.

References

Alberta Biodiversity Monitoring, I. 2010. Wall-to-wall Land Cover Inventory.

Alberta Biodiversity Monitoring, I. 2021. Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1-48.

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dillegeard, D. Farr, J. Fisher, M. Freemark, K. Foster, C. Godwin, C. Herbert, D. Huggard, D. McIssac, T. Narwani, S. Nielsen, B. Pauli, S. Prasad, D. Roberts, S. Slater, S. Song, S. Swanson, P. Thomas, J. Toms, C. Twitchell, S. White, F. Wyatt, and L. Mundy. 2021. A Before-After Dose-Response (BADR) Terrestrial Biological Monitoring Framework for the Oil Sands. OSM Technical Report Series 7.

Change, C. 1995. Intergovernmental panel on climate change (IPCC). CC BY **4**:1.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, Odocoileus virginianus, in the boreal forest of northern Alberta, Canada.

Dawe, K. L., and S. Boutin. 2016. Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land use is secondary. Ecology and Evolution **6**:6435-6451.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology **89**:623-634.

Dickie, M., R. Serrouya, M. Becker, C. DeMars, M. J. Noonan, R. Steenweg, S. Boutin, and A. T. Ford. 2024. Habitat alteration or climate: What drives the densities of an invading ungulate? Global Change Biology **30**:e17286.

Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment **6**:439-447.

Felton, A. M., H. K. Wam, Z. Borowski, A. Granhus, L. Juvany, J. Matala, M. Melin, M. Wallgren, and A. Mårell. 2024. Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions. Global Change Biology **30**:e17505.

Fisher, J. T., and A. C. Burton. 2018. Wildlife winners and losers in an oil sands landscape. Frontiers in Ecology and the Environment **16**:323-328.

Greenberg, S., T. Godin, and J. Whittington. 2019. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution **9**:13706-13730.

Hervieux, D., M. Hebblewhite, N. J. DeCesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (Rangifer tarandus caribou) continue in Alberta. Canadian Journal of Zoology **91**:872-882.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution **15**:56-61.

James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of Caribou and Wolves in Relation to Linear Corridors. The Journal of Wildlife Management **64**:154-159.

Karimi, L., and D. Meyer. 2014. Structural Equation Modeling in Psychology: The History, Development and Current Challenges. International Journal of Psychological Studies **6**:p123.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011a. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications **21**:2854-2865.

Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography **36**:1276-1290.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011b. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. The Journal of Wildlife Management **75**:204-212.

Laurent, M., M. Dickie, M. Becker, R. Serrouya, and S. Boutin. 2021. Evaluating the Mechanisms of Landscape Change on White-Tailed Deer Populations. The Journal of Wildlife Management **85**:340-353.

Lefcheck, J. S. 2016. piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution **7**:573-579.

Lyn Morelli, T., M. T. Hallworth, T. Duclos, A. Ells, S. D. Faccio, J. R. Foster, K. P. McFarland, K. Nislow, J. Ralston, M. Ratnaswamy, W. V. Deluca, and A. P. K. Siren. 2025. Does habitat or climate change drive species range shifts? Ecography **n/a**:e07560.

Mackenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105-1114.

McCarty, J. P. 2001. Ecological Consequences of Recent Climate Change. Conservation Biology **15**:320-331.

Munro, K. G., J. Bowman, and L. Fahrig. 2012. Effect of paved road density on abundance of white-tailed deer. Wildlife Research **39**:478.

Pearl, J. 2000. Models, reasoning and inference. Cambridge, UK: CambridgeUniversityPress **19**.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. 2015. The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. Canadian Journal of Forest Research **45**:732-743.

Roberts, D. R., E. M. Bayne, D. Beausoleil, J. Dennett, J. T. Fisher, R. O. Hazewinkel, D. Sayanda, F. Wyatt, and M. G. Dubé. 2022. A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. Integrated Environmental Assessment and Management **18**:388-406.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition. The American Naturalist **185**:665-679.

Stenegren, M., C. Berg, C. C. Padilla, S.-S. David, J. P. Montoya, P. L. Yager, and R. A. Foster. 2017. Piecewise Structural Equation Model (SEM) Disentangles the Environmental Conditions Favoring Diatom Diazotroph Associations (DDAs) in the Western Tropical North Atlantic (WTNA). Frontiers in Microbiology **8**.

Stewart, F. E. C., J. P. Volpe, and J. T. Fisher. 2019. The Debate About Bait: A Red Herring in Wildlife Research. The Journal of Wildlife Management **83**:985-992.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008.

Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics **9**:137-152.

Veitch, A. M. 2001. An unusual record of a white-tailed deer, Odocoileus virginianus, in the Northwest Territories. Canadian Field Naturalist **115**:172-175.

VerCauteren, K. C. 2003. The deer boom: discussins on population growth and range expansion of the white-tailed deer.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. . Methods in Ecology and Evolution **1**:3-14.

8. EVALUATING MODEL SELECTION UNCERTAINTY IN THE CONTEXT OF THE BEFORE-AFTER DOSE-RESPONSE DESIGN USING SIMULATION

Andrew F. Barnas, Marissa Dyck, Jason Fisher

OSM SUMMARY

The OSM TAC, SIKIC, and Oversight Committees are naturally always looking for efficiencies to monitoring. One of the questions that has arisen around the TBM's BADR design (Bayne et al. 2021b) is, "*Do we need to do all of this sampling?*". This question has in part driven the work being done on baselines and triggers, and sensitivity and power analysis. Classic power analysis (Krebs 1989) is designed for parametric statistics and is inappropriate for the information-theoretic approach (Burnham and Anderson 2002a) that underpins all of our analyses. Nonetheless sampling size and extent certainly are expected to influence the accuracy and precision of our model outcomes, and hence our conclusions. Here we use a novel approach based on empirical models and simulations to demonstrate what is gained through the multi-landscape BADR design and how reduced sampling markedly decreases confidence in the model estimates and the subsequent conclusions.

Introduction

Anthropogenic landscape change is a leading cause of biodiversity loss (Butchart et al. 2010), and large mammals are especially at risk (Johnson et al. 2017). Research has shown human disturbance can result in behavioural shifts and altered species interactions (Gaynor et al. 2018, Frey et al. 2020, Boucher et al. 2022), which produce effects that can cascade throughout ecosystems. While much work is being done to mitigate and restore effects of landscape change (Dickie et al. 2023), these problems are inherently complicated due to the complexity of identifying specific drivers of mammalian responses (Barnas et al. 2024a, Dickie et al. 2024a, Dickie et al. 2024b). This complexity necessitates that conservation practitioners rely on robust data collection and subsequent analyses on which to base intervention decisions.

Unfortunately, understanding mammal responses to these disturbances is difficult as ecological processes can change across time and space (Levin 1992). Local environmental conditions, wildlife community structures, and anthropogenic stressors drive changes in these ecological processes (Barnas et al. 2024c), which causes difficulty in generalizing results and recommendations from one study location to another. In some cases mammal populations can even respond to the same stressor in different ways in different sampling regions (Fidino et al. 2021a), which further complicates this problem. Therefore, providing generalizable conservation recommendations for specific species may be limited by constraints on sampling abilities.

To address this problem, there are increasing calls for large-scale synthetic approaches to data collection and analyses, especially with the use of remote camera traps for wildlife surveys (Steenweg et al. 2017a, Kays et al. 2022). These tools are beneficial in that surveys are readily standardized, can easily provide spatial and temporal replication (Burton et al. 2015b), and provide insights on many aspects of wildlife biology including behaviour (Barnas et al. 2022a), population trends (Twining et al. 2024), and demographic information (Goward 2024). Further, by aggregating data across study locations, camera trap surveys should provide an avenue to identify generalizable patterns to better inform conservation practices across broad regions or provide location-specific intervention requirements (Barnas et al. 2024c).

While these collaborative efforts are increasing in popularity, attention needs to be paid to the analytical approaches that are used with these data. A common modeling approach with camera trap data is to use model selection (Tredennick et al. 2021), where the goal is to identify the best predictive model out of a set of proposed candidate models (Bayne et al. 2016, Gaston et al. 2024). However, uncertainty in identifying the “best” model through different analytical choices can mislead researchers directing conservation actions and contribute to the replicability crisis in the sciences (Gould et al. 2023, Yates et al. 2023). Overfitting and sampling variance have been shown to induce uncertainty in model selection results (Arnold 2010, Preacher and Merkle 2012, Yates et al. 2023), and this is potentially problematic for the integration of datasets across multiple landscapes in assessing generalized mammal responses across broad regions. Therefore, assessing the performance of model selection results should be emphasized in synthetic approaches, as this provides insight into the relative confidence of conclusions from a given study design and subsequent inferences.

The goals of this manuscript are to evaluate the effects of sampling variance on model uncertainty and resulting inferences for large mammal responses to anthropogenic oil sands features. To do this we use empirical data from the ongoing Oil Sands Monitoring program to construct models of wildlife occurrence in relation to anthropogenic stressors across multiple landscapes. We then simulate data from these models to evaluate the impact of sampling variance (i.e. effort) across landscapes and evaluate the effect of reducing or increasing sampling effort across landscapes on biological inferences.

Methods

Empirical Data Collection and Study Areas

The ongoing Oil Sands Monitoring program (Roberts et al. 2022) takes place in north-eastern Alberta, Canada and is centered on a Before-After-Dose-Response design (Bayne et al. 2021b). The program is designed to evaluate impacts of oil sands development on the western boreal ecosystem, and the terrestrial mammal monitoring component of this program relies on camera trap surveys of large mammal occurrence. Briefly, 429 cameras across 10 distinct landscapes were selected throughout the region, providing a gradient of landscape disturbance and habitat types. Each landscape was partitioned into grid cells and cells were selected for placement of a single remote camera trap (Reconyx Hyperfire 2, Holmen, Wisconsin, USA). Cameras were programmed to collect images when movement was detected, as well as a single timelapse photo each day to verify that cameras remained operational throughout the year.

Empirical Model Construction

We chose to construct models using two species as case studies, coyote (*Canis latrans*) and moose (*Alces alces*). We chose these species due to their differing life history characteristics and hypothesized contrasting responses, whereby coyotes are small-bodied and known to be anthrophilic towards linear features such as roads, while moose are large-bodied and known to prioritize early seral forage polygonal features and avoid active anthropogenic disturbance such as roads (Ethier et al. 2024b) .

For each camera site, we calculated a proportional binomial response variable of monthly occurrence (1/0 for presence or absence) examining whether each species was detected within a calendar month (Figure 1). To minimize false negatives, we only considered cameras which contained >15 days of camera operability within the month. For explanatory variables, we delineated a 1000m radius buffer around each camera site location and used the Alberta Biodiversity Monitoring Institute's Human Feature Index and the Wall-to-Wall Land Cover Map (ABMI 2018) to extract the proportion landscape composed of broadleaf forest, mixed forest, shrubs, roads, and industrial features (Figure 2). We chose these features due to their differential hypothesized effects on each case study species (i.e. hypothesized negative effect of roads on moose but positive effect on coyotes). However, we remind the reader we are predominately interested in the change in estimated effect for each feature during simulation exercises, rather than constructing a complete causal model of occurrence for each species. We tested for and found no statistically significant Pearson's correlation coefficients between any explanatory variables.

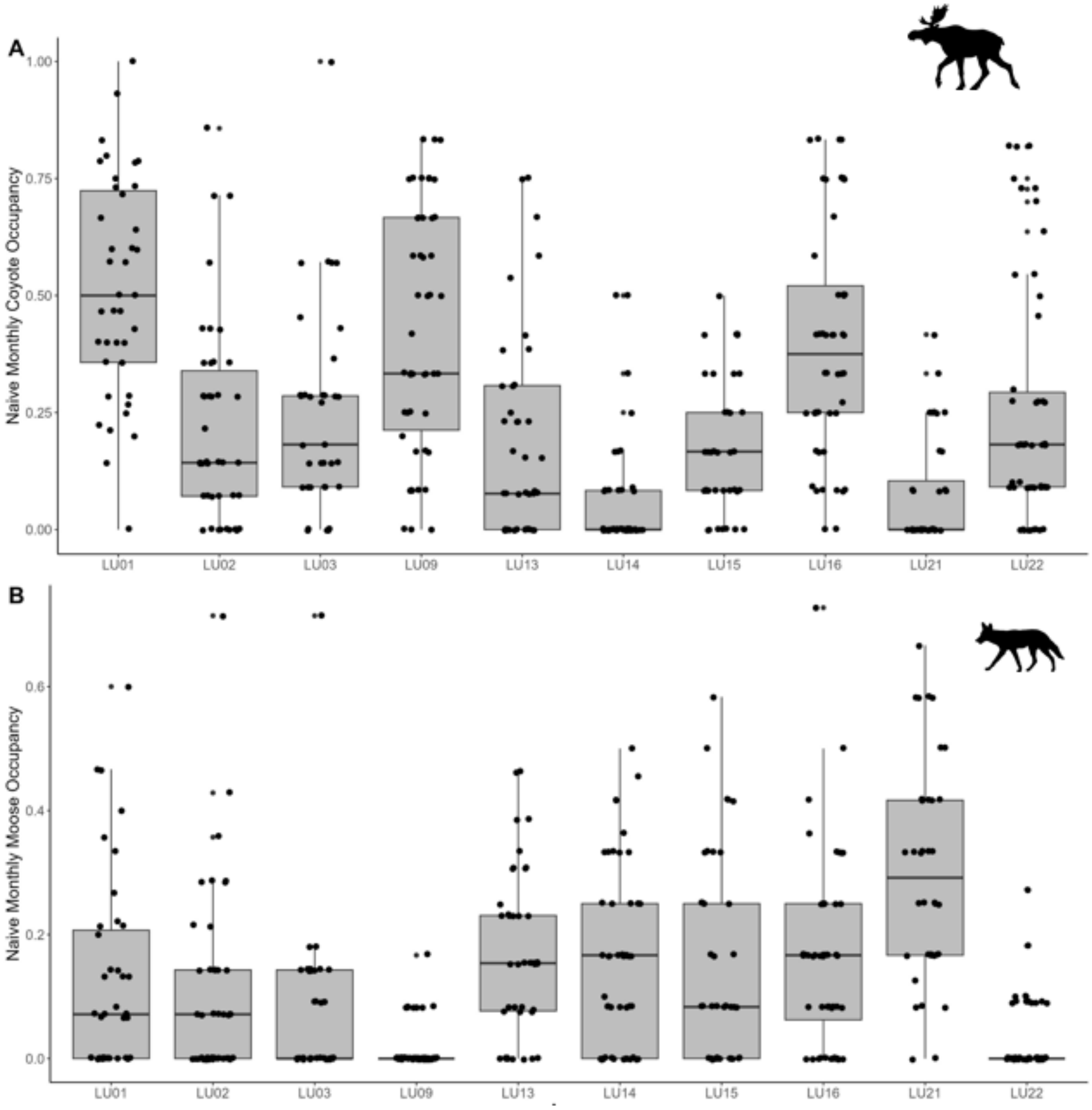

Figure 1. Naïve monthly occurrence of A) coyote and B) moose, calculated as the number of calendar months present divided by the number of months absent on camera traps (n_{total} = 429) within each camera landscape unit (n = 10). Note the number of camera traps varied within each landscape unit.

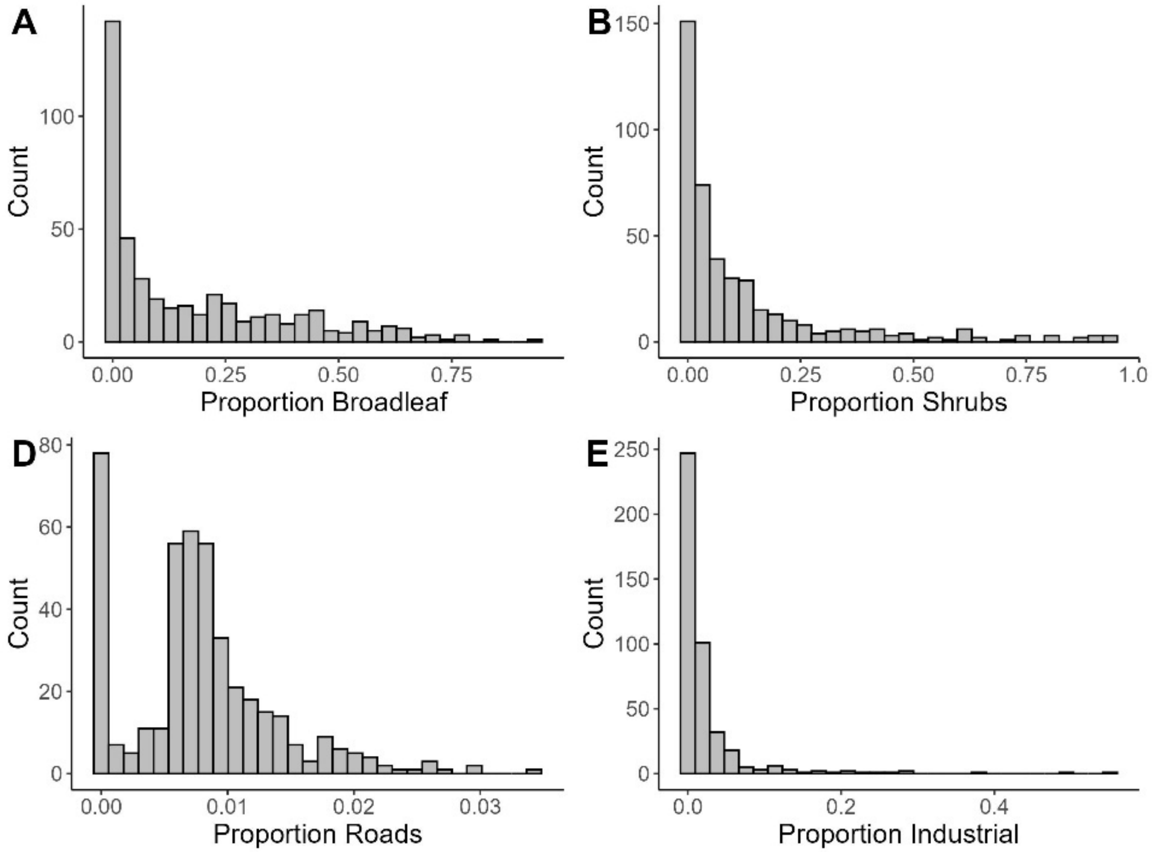

Figure 2. The proportion of landscape within a 1000m radius circular buffer around each camera site (n = 429) composed by A) broadleaf forest, B) shrubs, C) mixed forest, D) road features, and E) industrial features (e.g. mines, borrow pits).

For each species, we constructed a candidate set of generalized linear mixed models based on the fully saturated model provided in Equation 1. We assumed a Bernoulli distribution for each respective response variable represented as the i^{th} observation at LU j, where LU is a random intercept for Landscape Unit with the j^{th} level representing an individual landscape unit. We created a candidate set of models using the *MuMin* package's "dredge" function, to construct a model for every additive combination of fixed effects, keeping the random effect constant in all models. We also included a null model which only included the intercept and random effect. All proportional landscape variables were scaled prior to model fitting to facilitate comparisons between effects sizes. All models were fit with maximum likelihood and ranked based on AICc.

Equation 1:

$$\eta_{ij} = \beta_0 + B_1 Broadleaf_{ij} + \beta_2 Mixed_{ij} + \beta_3 Shrubs_{ij} + \beta_4 Roads_{ij} + \beta_5 Industrial_{ij} + LU_j$$

$$\text{logit}(\theta_{ij}) = \eta_{ij}$$

$$Monthly\ species\ occurrence_{ij} \sim \text{Bernoulli}(\theta_{ij})$$

$$LU_j \sim \text{Gaussian}(0, \sigma^2)$$

Model Simulations

Following model selection from the candidate set of empirical models for each species, we identified the best supported model and simulated new datasets based on parameter estimates from the top model. For simplicity we only considered the single top supported model, recognizing that other models may be competitive (i.e. within Δ2 AICc). However, we are primarily interested in whether simulated datasets from these top models will recover the main top model during repeat model selection, regardless of the empirical uncertainty in the top model. For each species, we simulated the predicted Bernoulli response for number of months present and absent for a total of 12 months based on a Monte Carlo Simulation using the top model's estimated parameters. For each observation, we drew a simulated coefficient estimate based on a random normal draw parameterized by the estimated coefficient mean and standard deviation. We drew a single random effect value for each landscape unit based on the empirical random effect estimate. For each observation we also included a small random observer error effect drawn from a random normal distribution with a mean of zero and standard deviation of 0.05. We simulated fixed effects from a random uniform distribution based off the empirical minimum and maximum values for each variable.

The best supported empirical model for coyote was the model containing broadleaf, shrubs, industrial and roads (Table 1), but for moose was the model containing only broadleaf and industrial (Table 2). In both these cases, not all the variables were present in the top models and mixed forest was not present in either. Therefore, to provide a complete dataset and allow construction of the full candidate model set, we simulated data for missing variables based on a random normal draw with a mean of zero and standard deviation of 0.25. In doing so, we assumed a small, yet non-zero effect for each of the variables not present in the empirical top model.

Table 1 Candidate models examining landscape features on monthly coyote presence/absence.

Model	df	LogLik	AICc	ΔAICc	Weight
broadleaf + industrial + roads + shrubs	**6**	**-989.6**	**1991.3**	**0**	**0.48**
broadleaf + industrial + mixed + roads + shrubs	7	-989.2	1992.8	1.47	0.23
industrial + roads + shrubs	5	-991.7	1993.5	2.18	0.16
industrial + mixed + roads + shrubs	6	-991.1	1994.3	3.04	0.11
industrial + mixed + roads	5	-995.0	2000.2	8.88	0.01
industrial + roads	4	-996.2	2000.4	9.15	0
broadleaf + industrial + roads	5	-995.4	2001.0	9.71	0
broadleaf + industrial + mixed + roads	6	-994.5	2001.1	9.84	0
industrial + shrubs	4	-1005.2	2018.5	27.15	0
broadleaf + industrial + shrubs	5	-1004.4	2018.9	27.65	0
industrial + mixed + shrubs	5	-1004.5	2019.1	27.84	0
broadleaf + industrial + mixed + shrubs	6	-1003.9	2020.0	28.74	0
broadleaf + roads + shrubs	5	-1005.0	2020.2	28.93	0
industrial + mixed	4	-1006.4	2020.9	29.62	0
industrial	3	-1007.5	2021.0	29.72	0
broadleaf + mixed + roads + shrubs	6	-1004.8	2021.8	30.53	0
broadleaf + industrial	4	-1007.2	2022.5	31.25	0
broadleaf + industrial + mixed	5	-1006.3	2022.7	31.38	0
roads + shrubs	4	-1008.5	2025.1	33.78	0
mixed + roads + shrubs	5	-1007.9	2026.0	34.66	0
broadleaf + roads	4	-1013.4	2034.8	43.51	0
broadleaf + mixed + roads	5	-1012.4	2034.9	43.58	0
mixed + roads	4	-1013.5	2035.1	43.77	0
roads	3	-1014.8	2035.6	44.27	0
broadleaf + shrubs	4	-1036.4	2080.9	89.65	0
shrubs	3	-1037.8	2081.7	90.42	0
broadleaf + mixed + shrubs	5	-1036.0	2082.1	90.75	0
mixed + shrubs	4	-1037.1	2082.3	90.95	0
mixed	3	-1039.6	2085.2	93.88	0
null	2	-1040.8	2085.6	94.28	0
broadleaf + mixed	4	-1039.2	2086.4	95.12	0
broadleaf	3	-1040.2	2086.4	95.15	0

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Model	df	LogLik	AICc	ΔAICc	Weight
broadleaf + industrial	**4**	**-688.4**	**1384.9**	**0**	**0.18**
broadleaf + industrial + shrubs	5	-687.4	1384.9	0.05	0.18
broadleaf + industrial + mixed + shrubs	6	-686.7	1385.7	0.77	0.12
broadleaf + industrial + mixed	5	-687.9	1385.9	1.01	0.11
broadleaf + industrial + roads	5	-688.1	1386.3	1.44	0.09
broadleaf + industrial + roads + shrubs	6	-687.3	1386.8	1.89	0.07
broadleaf + industrial + mixed + roads	6	-687.6	1387.3	2.45	0.05
broadleaf + industrial + mixed + roads + shrubs	7	-686.6	1387.5	2.64	0.05
broadleaf + roads	4	-690.2	1388.5	3.65	0.03
broadleaf	3	-691.4	1388.8	3.92	0.03
broadleaf + shrubs	4	-690.6	1389.2	4.36	0.02
broadleaf + mixed + roads	5	-689.7	1389.5	4.66	0.02
broadleaf + roads + shrubs	5	-689.7	1389.6	4.74	0.02
broadleaf + mixed	4	-690.9	1389.9	4.97	0.02
broadleaf + mixed + shrubs	5	-690.0	1390.0	5.16	0.01
broadleaf + mixed + roads + shrubs	6	-689.1	1390.4	5.56	0.01
industrial + roads	4	-701.8	1411.8	26.91	0
industrial	3	-703.0	1412.1	27.18	0
roads	3	-703.2	1412.4	27.49	0
industrial + mixed + roads	5	-701.5	1413.2	28.34	0
industrial + shrubs	4	-702.7	1413.5	28.61	0
industrial + mixed	4	-702.7	1413.5	28.65	0
industrial + roads + shrubs	5	-701.7	1413.6	28.73	0
mixed + roads	4	-702.9	1413.8	28.91	0
roads + shrubs	4	-703.1	1414.3	29.45	0
industrial + mixed + shrubs	5	-702.3	1414.8	29.94	0
null	2	-705.5	1415.0	30.06	0
industrial + mixed + roads + shrubs	6	-701.4	1415.0	30.09	0
mixed + roads + shrubs	5	-702.8	1415.7	30.83	0
mixed	3	-705.2	1416.4	31.53	0
shrubs	3	-705.2	1416.6	31.66	0
mixed + shrubs	4	-704.9	1417.9	33.03	0

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We simulated 100 datasets containing three, six, and twelve landscape units (random effect levels), with 40 camera sites each (n = 120, 240, and 480, respectively), and for each dataset we reconstructed the full candidate set of models as described above. For each dataset and landscape unit sample size, we identified the top model, and calculated the proportion of simulations where each model was identified as top. Next, from the "true" model in each simulation we extracted the fixed and random effect estimates and visualized their distribution with varying landscape unit number compared to the known empirical value. All data manipulation was done in R Studio v4.4.1 (R Core Team 2017) using packages *glmmTMB* for model construction (Magnusson et al. 2017), *dplyr* for general data manipulation (Wickham et al. 2015), *MuMin* for model selection (Barton 2009), and *ggplot2* for data visualization (Wickham 2016).

Results

Model selection uncertainty

The correct top model for coyote was identified in increasing proportion of simulations with increasing number of landscape units: 0.17 for three arrays, 0.42 for six arrays, and 0.51 for twelve arrays (Figure 3). For moose, the correct top model was identified as top in roughly similar proportion of simulations: 0.14 for three arrays, 0.16 for six arrays, and 0.10 for twelve arrays (Figure 4). However, for both species uncertainty in model selection decreased with increasing array number. The number of models selected as top within simulations for coyote was 11 for three arrays, 8 for six arrays, and six for twelve arrays, while for moose was 23 for three arrays, 13 for six arrays, and eight for twelve arrays.

Given that the candidate models were nested in nature, it is also useful to consider the proportion of times the top model contained the fixed effects of interest. For coyotes, models containing all four terms for broadleaf, industrial, mixed, and shrubs were selected correctly in 30% of cases for three arrays, 55% for six arrays, and 74% for twelve arrays. For moose, models containing the two terms broadleaf and industrial were selected in 64% of cases for three arrays, 94% for six arrays, and 100% for twelve arrays.

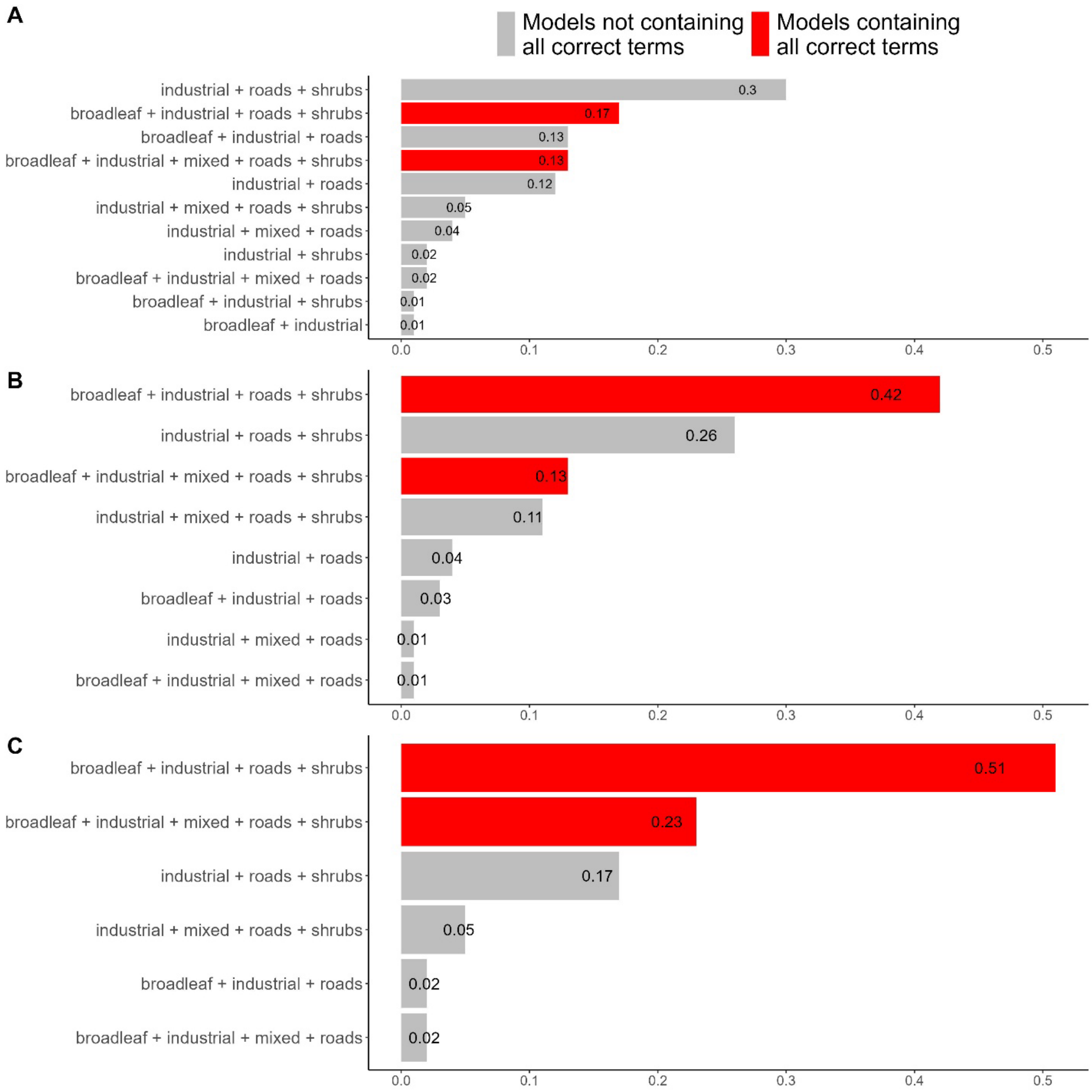

Figure 3. Proportion of simulations (n = 100) for coyotes in which each model was identified as top based on AICc. Data simulated based on the empirically identified top model of broadleaf + industrial + roads + shrubs, with varying number of levels for the array random effect, A) three landscape units, B) six landscape units, and C) twelve landscape units.

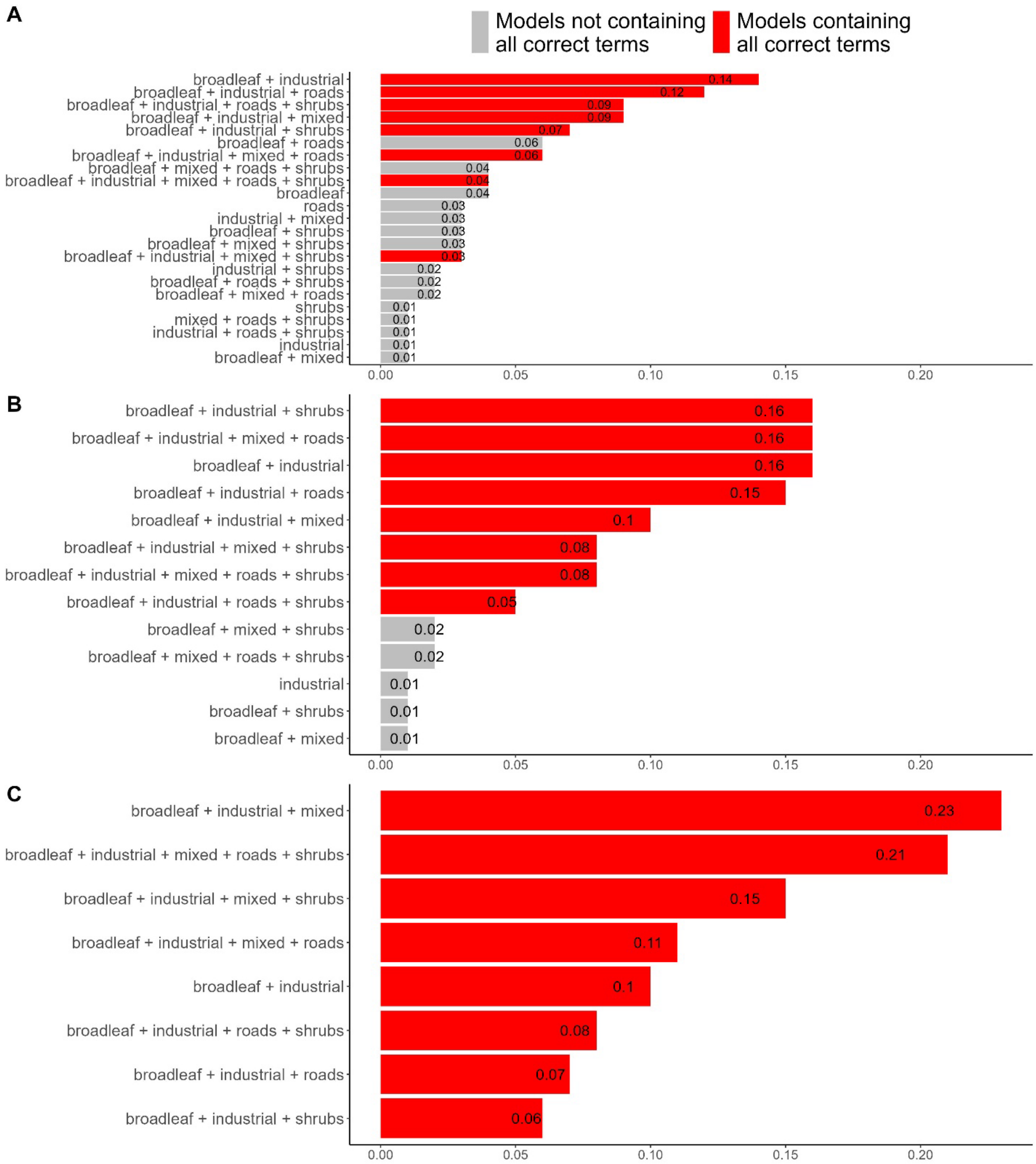

Figure 4. Proportion of simulations (n = 100) for moose in which each model was identified as top based on AICc. Data simulated based on the empirically identified top model of broadleaf + industrial, with varying number of levels for the array random effect, A) three landscape units, B) six landscape units, and C) twelve landscape units.

Model Parameter Estimate Uncertainty

Increasing the number of landscapes led to more precise parameter estimates for both coyote (Figure 5) and moose (Figure 6). In some cases, using only three arrays led to both negative and positive estimates in coyote for broadleaf (Figure 5A) and shrubs (Figure 5D), but increasing the number of arrays removed this negative bias (broadleaf: Figure5 F, K, shrubs Figure 5I, N). For all models we observed a decrease in parameter estimate variance with increasing number of landscapes (Table 3).

Table 3 Variance in fixed and random parameter estimates from the simulated models for moose and coyote

Model Species	Effect Type	Parameter	3 Landscapes	6 Landscapes	12 Landscapes
Moose	Fixed	Broadleaf	0.015	0.007	0.004
	Fixed	Industrial	0.004	0.002	0.0008
	Random	Landscape Unit	0.158	0.101	0.038
Coyote	Fixed	Broadleaf	0.006	0.004	0.002
	Fixed	Industrial	0.001	0.0006	0.0004
	Fixed	Shrubs	0.006	0.002	0.002
	Fixed	Roads	0.006	0.002	0.0008
	Random	Landscape Unit	0.09	0.04	0.01

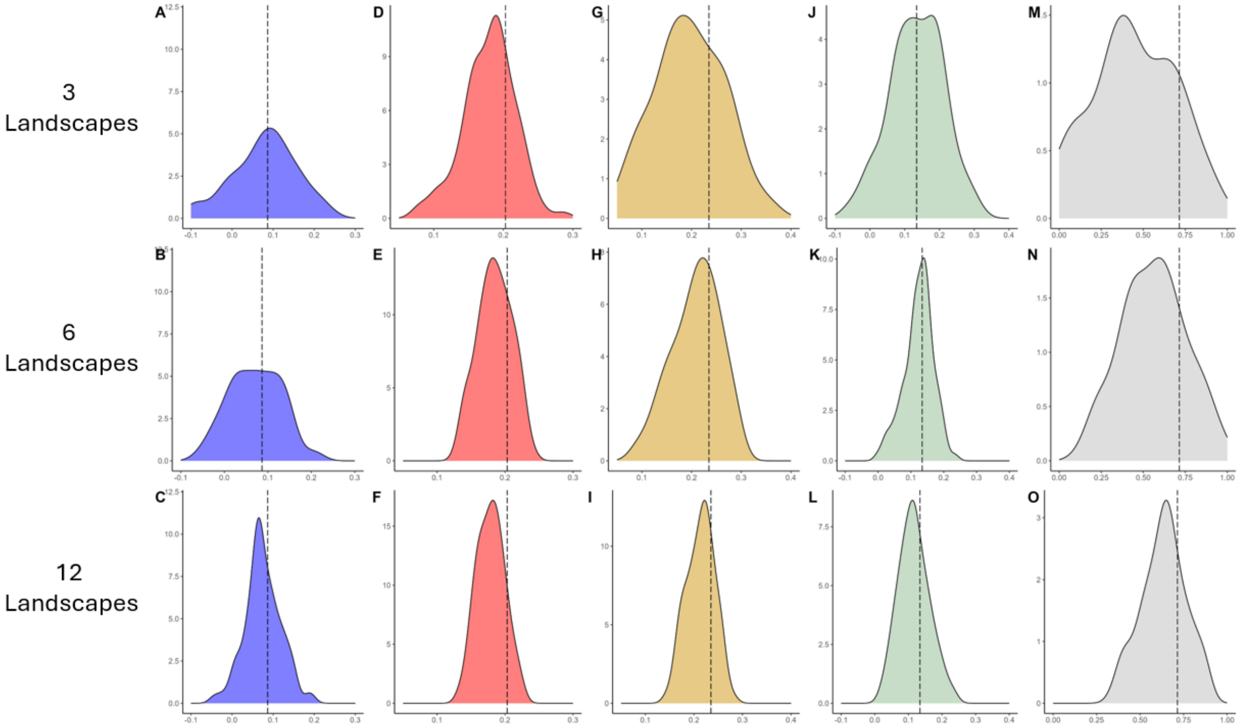

Figure 5 Coyote model parameter estimates from simulations (n = 100) for broadleaf (A, B, C), industrial (D, E, F), roads (G, H, I), shrubs (J, K, L), and the landscape unit random effect (M, N, O). Dashed line in each plot represents the mean estimate from the original empirical top model.

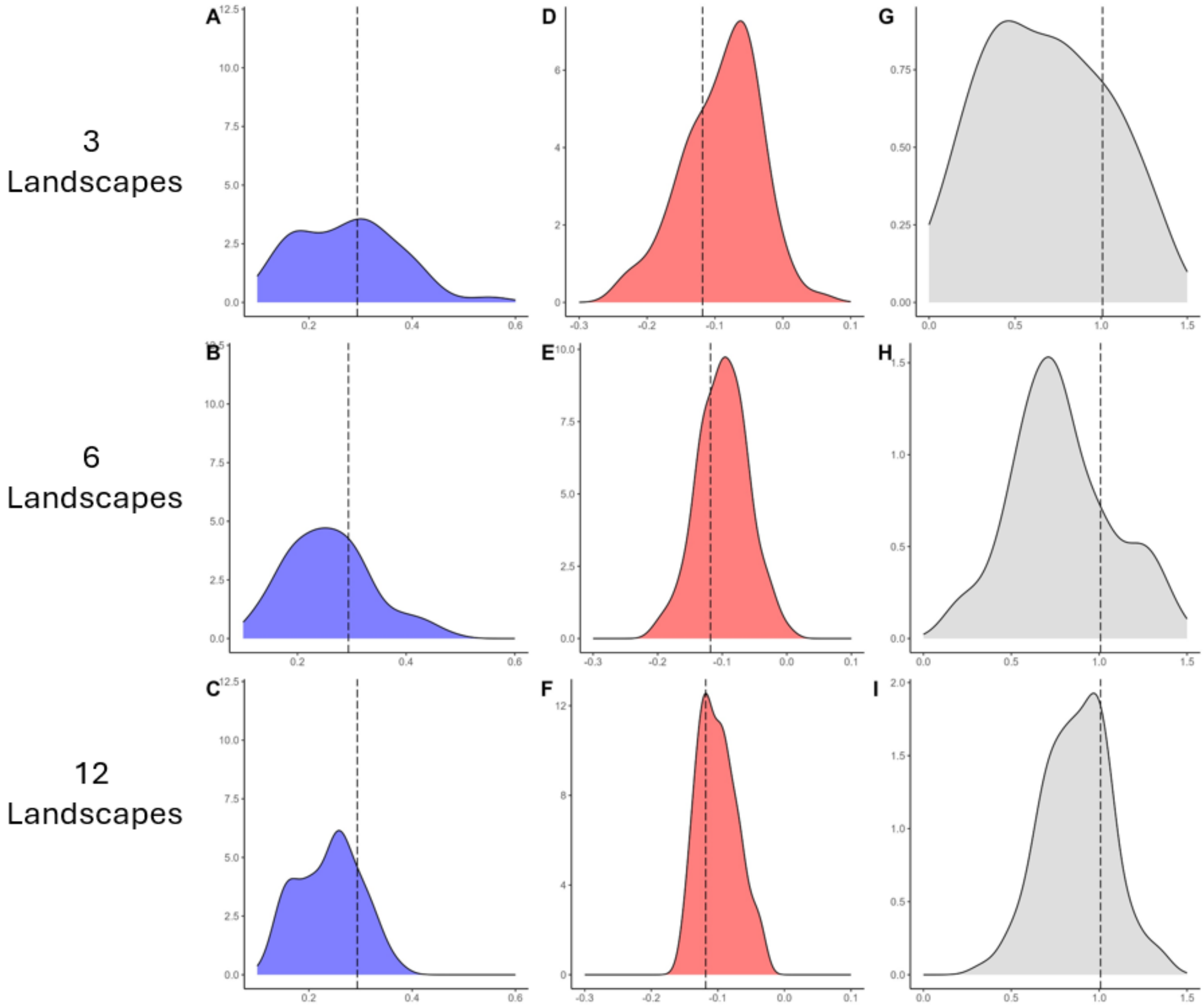

Figure 6 Moose model parameter estimates from simulations (n = 100) for broadleaf (A, B, C) , industrial (D, E, F), and the landscape unit random effect (G, H, I). Dashed line in each plot represents the mean estimate from the original empirical top mode

Discussion

As the popularity of camera traps grows globally (Fisher 2025) the pooling of data across research projects has led to macroecological insights never before possible (Rich et al. 2017, Burton et al. 2024, Devarajan et al. 2025). Expanding the geographic and ecological extent of sampling, as well as sample size, by networking camera arrays has obvious value. However, less well known is the impact on modelling outcomes. We demonstrate the impact of expanding sampling to multiple camera arrays on the outcomes of a commonly used analytical framework, as well as the importance of examining model selection uncertainty with simulation. There were clear reductions in model selection uncertainty by increasing the number of camera arrays ("landscape units") sampled within the oil sands monitoring BADR design. For both moose and coyotes, we show reduced uncertainty in model selection results, and higher precision in estimates for effects of landscape features on monthly occurrence. Importantly, the reduction in uncertainty was not purely a function of sampling variance, but also appeared to be influenced by model complexity. The more complex coyote model, which included four fixed effects (broadleaf, shrubs, industrial, and roads) was selected as the top model even with only three arrays, which likely reflected overfitting where more complex models can spuriously outcompete reduced models in small datasets. By increasing landscape units in the sample, selecting models with the parameters of interest increased. For moose with a simpler top model (two fixed effects: broadleaf and industrial), the true top model was identified less frequently. However, models containing these key parameters were more consistently recovered.

Reducing sampling variance through increasing the number of landscape units had a clear effect of increasing precision of model parameter estimates. This was particularly important for coyotes, where estimates of the broadleaf and shrub parameters included both negative and positive effects with only three landscape units. These biases were reduced with increasing landscape units, which shows the danger of making broad inferences from a few landscapes. While parameter estimates from model selection approaches should be interpreted with caution (Arif and MacNeil 2022), biases in estimates make ecological inferences challenging or potentially nonsensical.

Given the ongoing conservation crisis and the need to properly allocate time and resources to ecological research that informs effective conservation decisions (Martínez-Harms et al. 2024), these simulation results have practical implications for addressing uncertainty in ecological research. Clearly increasing sampling effort reduces uncertainty due to sampling variance and can help increase precision. However, this does not mean smaller scale studies should be overlooked, as landscape-specific insights from individual camera arrays provide valuable local insights (Ethier et al. 2024b, Gaston et al. 2024). These local results provide insights into specific biological relationships, which can then be tested or accounted for in larger synthetic analyses.

One important caveat to this study is the assumption that the original top empirical model represents a valid data-generating structure. We incorporated missing terms for each species so as to not assume a true "zero" effect, recognizing that all candidate models are nothing more than reasonable approximations (Burnham and Anderson 2002b). Concordantly, when the empirical top model already contains uncertainty (e.g. moose, see Table 2), it may be more important to validate model selection and incorporate additional sampling units. However, when initial results are more certain (e.g. coyote, see Table 1), model selection uncertainty will be reduced. While no single dataset will completely eliminate uncertainty, the clear benefits in reducing model selection uncertainty and improved parameter precision with increasing landscape unit number highlight the value of larger, more comprehensive sampling approaches in ecological research.

References

Arif, S., and M. A. MacNeil. 2022. Predictive models aren't for causal inference. Ecology letters **25**:1741-1745.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of wildlife management **74**:1175-1178.

Barnas, A., B. Anholt, A. C. Burton, K. Carroll, S. D. Côté, M. Festa-Bianchet, J. Fryxell, M. H. St-Laurent, and J. T. Fisher. 2024a. The influence of habitat alteration on density of invading white-tailed deer should not be discounted. Global Change Biology **30**:e17498.

Barnas, A. F., B. J. Darby, D. T. Iles, D. N. Koons, R. F. Rockwell, C. A. Semeniuk, and S. N. Ellis-Felege. 2022. Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance. Journal of Avian Biology.

Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J. Paczkowski, F. E. C. Stewart, E. Tattersall, and J. T. Fisher. 2024b. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Science of the total environment **915**:169285.

Barton, K. 2009. MuMIn: multi-model inference. R package version 1. 0. 0. http://r-forge. r-project. org/projects/mumin/.

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dilligeard, D. Farr, J. T. Fisher, M. Freemark, K. R. Foster, C. Godwin, C. E. Hebert, D. J. Huggard, D. McIssac, T. Narwani, S. E. Nielsen, B. Pauli, S. Prasad, D. R. Roberts, S. Slater, S. J. Song, S. Swanson, P. J. Thomas, J. D. Toms, C. Twitchell, S. R. White, F. Wyatt, and L. Mundy. 2021. Oil Sands Monitoring Program: A Before-After Dose-Response Terrestrial Biological Monitoring Framework for the Oil Sands. (OSM Technical Report Series No. 7). Edmonton, Alberta.

Bayne, E., L. Leston, C. L. Mahon, P. Sólymos, C. Machtans, H. Lankau, J. R. Ball, S. L. Van Wilgenburg, S. G. Cumming, and T. Fontaine. 2016. Boreal bird abundance estimates within different energy sector disturbances vary with point count radius. The Condor: Ornithological Applications **118**:376-390.

Boucher, N. P., M. Anderson, A. Ladle, C. Procter, S. Marshall, G. Kuzyk, B. M. Starzomski, and J. T. Fisher. 2022. Cumulative effects of widespread landscape change alter predator–prey dynamics. Scientific Reports **12**:11692.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, USA

Burton, A. C., C. Beirne, K. M. Gaynor, C. Sun, A. Granados, M. L. Allen, J. M. Alston, G. C. Alvarenga, F. S. Á. Calderón, Z. Amir, C. Anhalt-Depies, C. Appel, S. Arroyo-Arce, G. Balme, A. Bar-Massada, D. Barcelos, E. Barr, E. L. Barthelmess, C. Baruzzi, S. M. Basak, N. Beenaerts, J. Belmaker, O. Belova, B. Bezarević, T. Bird, D. A. Bogan, N. Bogdanović, A. Boyce, M. Boyce, L. Brandt, J. F. Brodie, J. Brooke, J. W. Bubnicki, F. Cagnacci, B. S. Carr, J. Carvalho, J. Casaer, R. Černe, R. Chen, E. Chow, M. Churski, C.

Cincotta, D. Ćirović, T. D. Coates, J. Compton, C. Coon, M. V. Cove, A. P. Crupi, S. D. Farra, A. K. Darracq, M. Davis, K. Dawe, V. De Waele, E. Descalzo, T. A. Diserens, J. Drimaj, M. Duľa, S. Ellis-Felege, C. Ellison, A. Ertürk, J. Fantle-Lepczyk, J. Favreau, M. Fennell, P. Ferreras, F. Ferretti, C. Fiderer, L. Finnegan, J. T. Fisher, M. C. Fisher-Reid, E. A. Flaherty, U. Fležar, J. Flousek, J. M. Foca, A. Ford, B. Franzetti, S. Frey, S. Fritts, Š. Frýbová, B. Furnas, B. Gerber, H. M. Geyle, D. G. Giménez, A. J. Giordano, T. Gomercic, M. E. Gompper, D. M. Gräbin, M. Gray, A. Green, R. Hagen, R. Hagen, S. Hammerich, C. Hanekom, C. Hansen, S. Hasstedt, M. Hebblewhite, M. Heurich, T. R. Hofmeester, T. Hubbard, D. Jachowski, P. A. Jansen, K. J. Jaspers, A. Jensen, M. Jordan, M. C. Kaizer, M. J. Kelly, M. T. Kohl, S. Kramer-Schadt, M. Krofel, A. Krug, K. M. Kuhn, D. P. J. Kuijper, E. K. Kuprewicz, J. Kusak, M. Kutal, D. J. R. Lafferty, S. LaRose, M. Lashley, R. Lathrop, T. E. Lee, C. Lepczyk, D. B. Lesmeister, A. Licoppe, M. Linnell, J. Loch, R. Long, R. C. Lonsinger, J. Louvrier, M. S. Luskin, P. MacKay, S. Maher, B. Manet, G. K. H. Mann, A. J. Marshall, D. Mason, Z. McDonald, T. McKay, W. J. McShea, M. Mechler, C. Miaud, J. J. Millspaugh, C. M. Monteza-Moreno, D. Moreira-Arce, K. Mullen, C. Nagy, R. Naidoo, I. Namir, C. Nelson, B. O'Neill, M. T. O'Mara, V. Oberosler, C. Osorio, F. Ossi, P. Palencia, K. Pearson, L. Pedrotti, C. E. Pekins, M. Pendergast, F. F. Pinho, R. Plhal, X. Pocasangre-Orellana, M. Price, M. Procko, M. D. Proctor, E. E. Ramalho, N. Ranc, S. Reljic, K. Remine, M. Rentz, R. Revord, R. Reyna-Hurtado, D. Risch, E. G. Ritchie, A. Romero, C. Rota, F. Rovero, H. Rowe, C. Rutz, M. Salvatori, D. Sandow, C. M. Schalk, J. Scherger, J. Schipper, D. G. Scognamillo, Ç. H. Şekercioğlu, P. Semenzato, J. Sevin, H. Shamon, C. Shier, E. A. Silva-Rodríguez, M. Sindicic, L. K. Smyth, A. Soyumert, T. Sprague, C. C. St. Clair, J. Stenglein, P. A. Stephens, K. M. Stępniak, M. Stevens, C. Stevenson, B. Ternyik, I. Thomson, R. T. Torres, J. Tremblay, T. Urrutia, J.-P. Vacher, D. Visscher, S. L. Webb, J. Weber, K. C. B. Weiss, L. S. Whipple, C. A. Whittier, J. Whittington, I. Wierzbowska, M. Wikelski, J. Williamson, C. C. Wilmers, T. Windle, H. U. Wittmer, Y. Zharikov, A. Zorn, and R. Kays. 2024. Mammal responses to global changes in human activity vary by trophic group and landscape. Nature Ecology & Evolution **8**:924-935.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.

Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, and J. Bruno. 2010. Global biodiversity: indicators of recent declines. Science **328**:1164-1168.

Devarajan, K., M. Fidino, Z. J. Farris, S. A. Adalsteinsson, G. Andrade-Ponce, J. L. Angstmann, W. Anthonysamy, J. Aquino, A. Asefa, B. Avila, L. L. Bailey, L. M. de Sousa Barbosa, M. de Frias Barreto, O. Barton, C. E. Bates, M. G. Beltrão, T. Bird, E. G. Biro, F. Bisi, D. Bohórquez, M. Boyce, J. S. Brashares, G. Bullington, P. Burns, J. Burr, A. R. Butler, K. L. Calhoun, T. T. Cao, N. Casado, J. C. Cepeda-Duque, J. D. Cepek, A. G. Chiarello, M. Collins, P. Cordeiro-Estrela, S. Costa, G. Cremonesi, B. Cristescu, P. Cruz, A. C. F. de Albuquerque, C. De Angelo, C. B. de Campos, L. M. M. de Sena, M. Di Bitetti, D. de Matos Dias, D. Diefenbach, T. S. Doherty, T. P. dos Santos, G. T. Duarte, T. M. Eppley, J. Erb, C. F. Esteves, B. Evans, M. L. M. Falcão, H. Fernandes-Ferreira, J. R. Fieberg, L. C. F. de Souza Filho, J. Fisher, M.-J. Fortin, G. A. Gale, T. Gallo, L. S. Ganoe, R. Garcia-Anleu, K. M. Gaynor, T. A. Gelmi-Candusso, P. N. Gichuru, Q. Gomez, A. M. Green, L. N. Guimarães, J. D. Haight, L. R. Harris, Z. D. Hawn, J. Heiman, H. Q. Hoang, S. Huebner, F. Iannarilli, M. E. Iezzi, J. S. Ivan, K. J. Jaspers, M. J. Jordan, J. Kamilar, M. Kane, M. H. Karimi, M. Kelly, M. T. Kohl, W. P. Kuvlesky, A. Ladle, R. N. Larson, Q. T. Le, D. Le, V. S. Le, E. W. Lehrer, P. E. Lendrum, J. Lewis, A. Link, D. J. Lizcano, J. V. Lombardi, R. Long, E. López-Tello, C. Lugarini, D. Lugo, P. MacKay, M. Madadi, R. A. Magalhães, S. B. Magle, L. H. R. D. Maia, S. Mandujano, T. Marchenkova, P. H. Marinho, L. Marker, J. M. Pardo, A. Martinoli, R. L. Massara, J. Masseloux, D. Matiukhina, A. Mayer, L. Mazariegos, M. R. McClung, A. McInturff, D. McPhail, A. Mertl, C. R. Middaugh, D. Miller, D. Mills, D. Miquelle, V. Miritis, R. J. Moll, P. Molnár, R. A. Montgomery, T. L. Morelli, A. Mortelliti, R. I. Mueller, A. S. Mukhacheva, K. Mullen, A. Murphy, V. Nepomuceno, D. Ngoprasert, A. Nguyen, T. Van Nguyen, V. T. Nguyen, H. A. N. Quang, R. Nipko, A. C. C. Nobre, J. Northrup, M. A. Owen, A. P. Paglia, M. S. Palmer, G. Palomo-Munoz, L. E. Pardo, C. Parks, A. M. de Oliveira Paschoal, B. Patterson, A. Paviolo, L. Pejchar, M. E. Pendergast, H. L. Perotto-

Baldivieso, T. Petrov, M. K. P. Poisson, D. J. Polli, M. Pourmirzai, A. Reebin, K. R. Remine, L. Rich, C. S. Richardson, F. Robino, D. G. Rocha, F. L. Rocha, F. H. G. Rodrigues, A. T. Rohnke, T. J. Ryan, C. M. Salsbury, H. A. Sander, N. M. da Cruz Santos-Cavalcante, C. H. Sekercioglu, I. Seryodkin, D. H. Setiawan, S. Shadloo, M. Shahhosseini, G. Shannon, C. J. Shier, G. B. Smith, T. Snyder, R. Sollmann, K. L. Sparks, K. Sribuarod, C. C. St. Clair, T. Stankowich, R. Steinmetz, C. J. Stevenson, T. D. Surasinghe, S. V. Sutyrina, R. R. Swaisgood, A. Taktehrani, K. Thapa, M. Thorton, A. Tilker, M. W. Tobler, V. B. Tran, J. Tucker, R. C. Van Horn, J. S. Vargas-Soto, K. L. Velásquez-C, J. Venter, E. M. Venticinque, S. Verschueren, E. Wampole, D. J. Watchorn, O. R. Wearn, K. C. B. Weiss, A. Welschen, F. A. Widodo, J. Williamson, A. Wilting, G. Wittemyer, A. Zavaleta, A. J. Zellmer, and B. D. Gerber. 2025. When the wild things are: Defining mammalian diel activity and plasticity. Science Advances **11**:eado3843.

Dickie, M., R. Serrouya, M. Becker, C. DeMars, M. J. Noonan, R. Steenweg, S. Boutin, and A. T. Ford. 2024a. Habitat alteration or climate: What drives the densities of an invading ungulate? Global Change Biology **30**:e17286.

Dickie, M., R. Serrouya, M. Becker, C. DeMars, M. J. Noonan, R. Steenweg, S. Boutin, and A. T. Ford. 2024b. The influence of habitat alteration is widespread, but the impact of climate cannot continue to be discounted. Global Change Biology **30**:e17497.

Dickie, M., G. G. Sherman, G. D. Sutherland, R. S. McNay, and M. Cody. 2023. Evaluating the impact of caribou habitat restoration on predator and prey movement. Conservation Biology **37**:e14004.

Ethier, C. A., A. F. Barnas, N. P. Boucher, K. Baillie-David, and J. T. Fisher. 2024. Lethal wolf control elicits change in moose habitat selection in unexpected ways. The Journal of wildlife management **88**:e22620.

Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. Kay, H. A. Sander, B. MacDougall, C. M. Salsbury, T. J. Ryan, and J. L. Angstmann. 2021. Landscape-scale differences among cities alter common species' responses to urbanization. Ecological Applications **31**:e02253.

Fisher, J. T. 2025. Ecological Insights From Camera Trapping Span Biological Taxa, and the Globe. Ecology and Evolution **15**:e70947.

Frey, S., J. Volpe, N. Heim, J. Paczkowski, and J. Fisher. 2020. Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. Oikos **129**:1128-1140.

Gaston, M. V., A. F. Barnas, R. M. Smith, S. Murray, and J. T. Fisher. 2024. Native prey, not landscape change or novel prey, drive cougar (Puma concolor) distribution at a boreal forest range edge. Ecology and Evolution **14**:e11146.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Gould, E., H. S. Fraser, T. H. Parker, S. Nakagawa, S. C. Griffith, P. A. Vesk, F. Fidler, D. G. Hamilton, R. N. Abbey-Lee, and J. K. Abbott. 2023. Same data, different analysts: variation in effect sizes due to analytical decisions in ecology and evolutionary biology.

Goward, S. L. 2024. Using remote camera traps to monitor population demographics and community ecology of divii (Dall's sheep): Part of a community-based monitoring program in the Northern Richardson Mountains, NT.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science **356**:270-275.

Kays, R., M. V. Cove, J. Diaz, K. Todd, C. Bresnan, M. Snider, T. E. Lee Jr, J. G. Jasper, B. Douglas, and A. P. Crupi. 2022. SNAPSHOT USA 2020: A second coordinated national camera trap survey of the United States during the COVID-19 pandemic. Wiley Online Library.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology **73**:1943-1967.

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. 2017. Package 'glmmtmb'. R Package Version 0.2. 0.

Martínez-Harms, M. J., R. A. Estévez, and E. Álvarez-Miranda. 2024. Conservation triage in action: Planning, governance and knowledge co-production for biodiversity protection. Journal of Applied Ecology **61**:2328-2334.

Preacher, K. J., and E. C. Merkle. 2012. The problem of model selection uncertainty in structural equation modeling. Psychological methods **17**:1.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing; Available at https://www.r-project.org/.

Rich, L. N., C. L. Davis, Z. J. Farris, D. A. Miller, J. M. Tucker, S. Hamel, M. S. Farhadinia, R. Steenweg, M. S. Di Bitetti, and K. Thapa. 2017. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. Global Ecology and Biogeography **26**:918-929.

Roberts, D. R., E. M. Bayne, D. Beausoleil, J. Dennett, J. T. Fisher, R. O. Hazewinkel, D. Sayanda, F. Wyatt, and M. G. Dubé. 2022. A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. Integrated Environmental Assessment and Management **18**:388-406.

Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. T. Fisher, C. Burton, S. E. Townsend, C. Carbone, J. M. Rowcliffe, and J. Whittington. 2017. Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**:26-34.

Tredennick, A. T., G. Hooker, S. P. Ellner, and P. B. Adler. 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology **102**:e03336.

Twining, J. P., D. Kramer, K. A. Perkins, and A. K. Fuller. 2024. Landscape-scale population trends in the occurrence and abundance of wildlife populations using long term camera-trapping data. Biological Conservation **290**:110398.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer.

Wickham, H., R. Francois, L. Henry, and K. Müller. 2015. dplyr: A grammar of data manipulation. R package version 0.4 **3**.

Yates, L. A., Z. Aandahl, S. A. Richards, and B. W. Brook. 2023. Cross validation for model selection: a review with examples from ecology. Ecological monographs **93**:e1557.

9. MAIN REPORT REFERENCES

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos:340-346.

Akaike, H. 1973. Maximum likelihood identification of Gaussian autoregressive moving average models. Biometrika **60**:255-265.

Akaike, H. 1998. Information Theory and an Extension of the Maximum Likelihood Principle. Pages 199-213 *in* E. Parzen, K. Tanabe, and G. Kitagawa, editors. Selected Papers of Hirotugu Akaike. Springer, New York, NY.

Alberta Biodiversity Monitoring, I. 2010. Wall-to-wall Land Cover Inventory.

Alberta Biodiversity Monitoring, I. 2021. Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region.

Alberta Biodiversity Monitoring Institute. 2010. Wall-to-wall Land Cover Map.

Alberta Biodiversity Monitoring Institute. 2019. Wall-to-Wall Human Footprint Inventory, Enhanced for Oil Sands Monitoring Region.

Alberta Government. 2016. Management plan for black bears in Alberta. Alberta Environment and Parks., Edmonton, Alberta.

Alberta Government. 2023. About oil sands.

Alberta Government. 2024. Hunter harvest report : black bear.

Allen, T. F., and T. W. Hoekstra. 2015. Toward a unified ecology. Columbia University Press.

Allen, T. F. H., and T. Hoekstra. 1992. Toward a unified ecology New York (NY) Columbia University Press.

Arif, S., and M. A. MacNeil. 2022. Predictive models aren't for causal inference. Ecology letters **25**:1741-1745.

Arjo, W. M., and D. H. Pletscher. 2000. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Canadian Journal of Zoology **77**:1919-1927.

Arjo, W. M., D. H. Pletscher, and R. R. Ream. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. Journal of Mammalogy **83**:754-766.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. The Journal of Wildlife Management **74**:1175-1178.

Atwood, T. C., and E. M. Gese. 2008. Coyotes and recolonizing wolves: social rank mediates risk-conditional behaviour at ungulate carcasses. Animal Behaviour **75**:753-762.

Aubertin-Young, M. 2022. Industrial landscape changes alter fine-scale mammal diversity and mammalian predator–prey dynamics in the northwest Nearctic. University of Victoria, Victoria, British Columbia.

Ballard, W. B., L. N. Carbyn, and D. W. Smith. 2003. Wolf interactions with non-prey.

Barnas, A., B. Anholt, A. C. Burton, K. Carroll, S. D. Côté, M. Festa-Bianchet, J. Fryxell, M. H. St-Laurent, and J. T. Fisher. 2024a. The influence of habitat alteration on density of invading white-tailed deer should not be discounted. Global Change Biology **30**:e17498.

Barnas, A. F., B. J. Darby, D. T. Iles, D. N. Koons, R. F. Rockwell, C. A. Semeniuk, and S. N. Ellis-Felege. 2022a. Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance. Journal of Avian Biology.

Barnas, A. F., B. J. Darby, D. T. Iles, D. N. Koons, R. F. Rockwell, C. A. D. Semeniuk, and S. N. Ellis-Felege. 2022b. Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance. Journal of Avian Biology **2022**:e02840.

Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J. Paczkowski, and F. E. Stewart. 2024b. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Science of the Total Environment **915**:169285.

Barnas, A. F., A. Ladle, J. M. Burgar, A. C. Burton, M. S. Boyce, L. Eliuk, F. Grey, N. Heim, J. Paczkowski, F. E. C. Stewart, E. Tattersall, and J. T. Fisher. 2024c. How landscape traits affect boreal mammal responses to anthropogenic disturbance. Science of the Total Environment **915**:169285.

Barton, K. 2009. MuMIn: multi-model inference. R package version 1. 0. 0. http://r-forge. r-project. org/projects/mumin/.

Bartoń, K. 2020. MuMIn: Multi-Model Inference.

Bartoń, K. 2024. R package “MuMIn”.

Bastille-Rousseau, G., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2011. Foraging strategies by omnivores: are black bears actively searching for ungulate neonates or are they simply opportunistic predators? Ecography (Copenhagen) **34**:588-596.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1-48.

Bates, D., M. Maechler, B. Bolker, S. Walker, R. H. B. Christensen, H. Singmann, B. Dai, F. Scheipl, G. Grothendieck, P. Green, J. Fox, A. Bauer, P. N. Krivitsky, E. Tanaka, and M. Jagan. 2024. R package "lme4".

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dillegeard, D. Farr, J. Fisher, M. Freemark, K. Foster, C. Godwin, C. Herbert, D. Huggard, D. McIssac, T. Narwani, S. Nielsen, B. Pauli, S. Prasad, D. Roberts, S. Slater, S. Song, S. Swanson, P. Thomas, J. Toms, C. Twitchell, S. White, F. Wyatt, and L. Mundy. 2021a. A Before-After Dose-Response (BADR) Terrestrial Biological Monitoring Framework for the Oil Sands. OSM Technical Report Series 7.

Bayne, E., J. Dennett, J. Dooley, M. Kohler, J. Ball, M. Bidwell, A. Braid, J. Chetelat, E. Dilligeard, D. Farr, J. T. Fisher, M. Freemark, K. R. Foster, C. Godwin, C. E. Hebert, D. J. Huggard, D. McIssac, T. Narwani, S. E. Nielsen, B. Pauli, S. Prasad, D. R. Roberts, S. Slater, S. J. Song, S. Swanson, P. J. Thomas, J. D. Toms, C. Twitchell, S. R. White, F. Wyatt, and L. Mundy. 2021b. Oil Sands Monitoring Program: A Before-After Dose-Response Terrestrial Biological Monitoring Framework for the Oil Sands. (OSM Technical Report Series No. 7). Edmonton, Alberta.

Bayne, E., Dennett, J., Kohler, M., Ball, J., Bidwell, M., Braid, A., Chetelat, J., Dillegeard, E., Farr, D., Fisher, J., Freemark, M., Foster, K., Godwin, C., Hebert, C., Huggard, D., McIssac, D., Narwani, T., Nielsen, S., Pauli, B., Prasad, S., Roberts, D., Slater, S., Song, S., Swanson, S., Thomas, P., Toms, J., Twichell, C., White, S., Wyatt, F., Mundy, L. 2021. Oil Sands Monitoring Program: A before-after dose-response (BADR) terrestrial biological monitoring framework for the oil sands.

Bayne, E., Lankau, H., Tigner, J. 2011. Ecologically-based criteria to assess the impact and recovery of seismic lines: The importance of width, regeneration, and seismic density. Edmonton, AB.

Bayne, E., L. Leston, C. L. Mahon, P. Sólymos, C. Machtans, H. Lankau, J. R. Ball, S. L. Van Wilgenburg, S. G. Cumming, and T. Fontaine. 2016. Boreal bird abundance estimates within different energy sector disturbances vary with point count radius. The Condor: Ornithological Applications **118**:376-390.

Beirne, C., C. Sun, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2021a. Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics. Journal of Applied Ecology **58**:2821-2832.

Beirne, C., C. Sun, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2021b. Multispecies modelling reveals potential for habitat restoration to re-establish boreal vertebrate community dynamics. Journal of Applied Ecology **58**:2821-2832.

Ben-David, M., K. Titus, and L. R. Beier. 2004. Consumption of Salmon by Alaskan Brown Bears: A Trade-off between Nutritional Requirements and the Risk of Infanticide? Oecologia **138**:465-474.

Benoit-Pépin, A., M. J. Feldman, L. Imbeau, and O. Valeria. 2024. Use of linear features by mammal predators and prey in managed boreal forests. Forest Ecology and Management **561**:121911.

Bentley, R. W. 2002. Global oil & gas depletion: an overview. Energy Policy **30**:189-205.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology letters (2005) **3**:620-623.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology **76**:1075-1085.

Boczulak, H., N. P. Boucher, A. Ladle, M. S. Boyce, and J. T. Fisher. 2023. Industrial development alters wolf spatial distribution mediated by prey availability. Ecology and Evolution **13**:e10224.

Boisjoly, D., J. P. OUELLET, and R. Courtois. 2010. Coyote habitat selection and management implications for the Gaspésie caribou. The Journal of Wildlife Management **74**:3-11.

Boucher, N. P., M. Anderson, A. Ladle, C. Procter, S. Marshall, G. Kuzyk, B. M. Starzomski, and J. T. Fisher. 2022. Cumulative effects of widespread landscape change alter predator–prey dynamics. Scientific Reports **12**:11692.

Boutin, S., M. S. Boyce, M. Hebblewhite, D. Hervieux, K. H. Knopff, A. D. M. Latham, M. C. Latham, J. Nagy, D. R. Seip, and R. Serrouya. 2012. Why are caribou declining in the oil sands? Frontiers in Ecology and the Environment **10**:65-67.

Brodeur, V., J.-P. Ouellet, R. Courtois, and D. Fortin. 2008. Habitat selection by black bears in an intensively logged boreal forest. Canadian journal of zoology **86**:1307-1316.

Brooks, M. E., K. Kristensen, K. J. v. Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal **9**:378.

Burgar, J. M., A. C. Burton, and J. T. Fisher. 2019. The importance of considering multiple interacting species for conservation of species at risk. Conservation Biology **33**:709-715.

Burgar, J. M., F. E. Stewart, J. P. Volpe, J. T. Fisher, and A. C. Burton. 2018. Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models. Global Ecology and Conservation **15**:e00411.

Burnham, K., and D. Anderson. 2002a. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach 2nd EditionSpringer-Verlag. New York, New York.

Burnham, K. P., and D. R. Anderson. 2002b. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York, USA

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology **65**:23-35.

Burton, A. C., C. Beirne, K. M. Gaynor, C. Sun, A. Granados, M. L. Allen, J. M. Alston, G. C. Alvarenga, F. S. Á. Calderón, Z. Amir, C. Anhalt-Depies, C. Appel, S. Arroyo-Arce, G. Balme, A. Bar-Massada, D. Barcelos, E. Barr, E. L. Barthelmess, C. Baruzzi, S. M. Basak, N. Beenaerts, J. Belmaker, O. Belova, B. Bezarević, T. Bird, D. A. Bogan, N. Bogdanović, A. Boyce, M. Boyce, L. Brandt, J. F. Brodie, J. Brooke, J. W. Bubnicki, F. Cagnacci, B. S. Carr, J. Carvalho, J. Casaer, R. Černe, R. Chen, E. Chow, M. Churski, C. Cincotta, D. Ćirović, T. D. Coates, J. Compton, C. Coon, M. V. Cove, A. P. Crupi, S. D. Farra, A. K. Darracq, M. Davis, K. Dawe, V. De Waele, E. Descalzo, T. A. Diserens, J. Drimaj, M. Duľa, S. Ellis-Felege, C. Ellison, A. Ertürk, J. Fantle-Lepczyk, J. Favreau, M. Fennell, P. Ferreras, F. Ferretti, C. Fiderer, L. Finnegan, J. T. Fisher, M. C. Fisher-Reid, E. A. Flaherty, U. Fležar, J. Flousek, J. M. Foca, A. Ford, B. Franzetti, S. Frey, S. Fritts, Š. Frýbová, B. Furnas, B. Gerber, H. M. Geyle, D. G. Giménez, A. J. Giordano, T. Gomercic, M. E. Gompper, D. M. Gräbin, M. Gray, A. Green, R. Hagen, R. Hagen, S. Hammerich, C. Hanekom, C. Hansen, S. Hasstedt, M. Hebblewhite, M. Heurich, T. R. Hofmeester, T. Hubbard, D. Jachowski, P. A. Jansen, K. J. Jaspers, A. Jensen, M. Jordan,

M. C. Kaizer, M. J. Kelly, M. T. Kohl, S. Kramer-Schadt, M. Krofel, A. Krug, K. M. Kuhn, D. P. J. Kuijper, E. K. Kuprewicz, J. Kusak, M. Kutal, D. J. R. Lafferty, S. LaRose, M. Lashley, R. Lathrop, T. E. Lee, C. Lepczyk, D. B. Lesmeister, A. Licoppe, M. Linnell, J. Loch, R. Long, R. C. Lonsinger, J. Louvrier, M. S. Luskin, P. MacKay, S. Maher, B. Manet, G. K. H. Mann, A. J. Marshall, D. Mason, Z. McDonald, T. McKay, W. J. McShea, M. Mechler, C. Miaud, J. J. Millspaugh, C. M. Monteza-Moreno, D. Moreira-Arce, K. Mullen, C. Nagy, R. Naidoo, I. Namir, C. Nelson, B. O'Neill, M. T. O'Mara, V. Oberosler, C. Osorio, F. Ossi, P. Palencia, K. Pearson, L. Pedrotti, C. E. Pekins, M. Pendergast, F. F. Pinho, R. Plhal, X. Pocasangre-Orellana, M. Price, M. Procko, M. D. Proctor, E. E. Ramalho, N. Ranc, S. Reljic, K. Remine, M. Rentz, R. Revord, R. Reyna-Hurtado, D. Risch, E. G. Ritchie, A. Romero, C. Rota, F. Rovero, H. Rowe, C. Rutz, M. Salvatori, D. Sandow, C. M. Schalk, J. Scherger, J. Schipper, D. G. Scognamillo, Ç. H. Şekercioğlu, P. Semenzato, J. Sevin, H. Shamon, C. Shier, E. A. Silva-Rodríguez, M. Sindicic, L. K. Smyth, A. Soyumert, T. Sprague, C. C. St. Clair, J. Stenglein, P. A. Stephens, K. M. Stępniak, M. Stevens, C. Stevenson, B. Ternyik, I. Thomson, R. T. Torres, J. Tremblay, T. Urrutia, J.-P. Vacher, D. Visscher, S. L. Webb, J. Weber, K. C. B. Weiss, L. S. Whipple, C. A. Whittier, J. Whittington, I. Wierzbowska, M. Wikelski, J. Williamson, C. C. Wilmers, T. Windle, H. U. Wittmer, Y. Zharikov, A. Zorn, and R. Kays. 2024. Mammal responses to global changes in human activity vary by trophic group and landscape. Nature Ecology & Evolution **8**:924-935.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015a. REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne, and S. Boutin. 2015b. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology **52**:675-685.

Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, J. E. Baillie, B. Bomhard, C. Brown, and J. Bruno. 2010. Global biodiversity: indicators of recent declines. Science **328**:1164-1168.

Caravaggi, A., P. B. Banks, A. C. Burton, C. M. V. Finlay, P. M. Haswell, M. W. Hayward, M. J. Rowcliffe, and M. D. Wood. 2017. A review of camera trapping for conservation behaviour research. Remote Sensing in Ecology and Conservation **3**:109-122.

Carroll, K., F. Grey, N. Anderson, N. Anderson, and J. Fisher. 2024. Indigenous-led analysis of important subsistence species response to resource extraction. Authorea, Inc.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances **1**:e1400253.

Ceballos, G., P. R. Ehrlich, and R. Dirzo. 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences **114**:E6089-E6096.

Change, C. 1995. Intergovernmental panel on climate change (IPCC). CC BY **4**:1.

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology Letters **16**:4-16.

Chow-Fraser, G., N. Heim, J. Paczkowski, J. P. Volpe, and J. T. Fisher. 2022. Landscape change shifts competitive dynamics between declining, at-risk wolverines and range-expanding coyotes, compelling a new conservation focus. Biological Conservation **266**.

Coffin, A. W. 2007. From roadkill to road ecology: A review of the ecological effects of roads. Journal of transport Geography **15**:396-406.

Cove, M. V., R. Kays, H. Bontrager, C. Bresnan, M. Lasky, T. Frerichs, R. Klann, T. E. Lee Jr, S. C. Crockett, A. P. Crupi, K. C. B. Weiss, H. Rowe, T. Sprague, J. Schipper, C. Tellez, C. A. Lepczyk, J. E. Fantle-Lepczyk, S. LaPoint, J. Williamson, M. C. Fisher-Reid, S. M. King, A. J. Bebko, P. Chrysafis, A. J. Jensen, D. S. Jachowski, J. Sands, K. A. MacCombie, D. J. Herrera, M. van der Merwe, T. W. Knowles, R. V. Horan Iii, M. S. Rentz, L. S. E. Brandt, C. Nagy, B. T. Barton, W. C. Thompson, S. P. Maher, A. K. Darracq, G. Hess, A. W. Parsons, B. Wells, G. W. Roemer, C. J. Hernandez, M. E. Gompper, S. L. Webb, J. P. Vanek, D. J. R. Lafferty, A. M. Bergquist, T. Hubbard, T. Forrester, D. Clark, C. Cincotta, J. Favreau, A. N. Facka, M. Halbur, S. Hammerich, M. Gray, C. C. Rega-Brodsky, C. Durbin, E. A. Flaherty, J. M. Brooke, S. S. Coster, R. G. Lathrop, K. Russell, D. A. Bogan, R. Cliché, H. Shamon, M. T. R. Hawkins, S. B. Marks, R. C. Lonsinger, M. T. O'Mara, J. A. Compton, M. Fowler, E. L. Barthelmess, K. E.

Andy, J. L. Belant, D. E. Beyer Jr, T. M. Kautz, D. G. Scognamillo, C. M. Schalk, M. S. Leslie, S. L. Nasrallah, C. N. Ellison, C. Ruthven, S. Fritts, J. Tleimat, M. Gay, C. A. Whittier, S. A. Neiswenter, R. Pelletier, B. A. DeGregorio, E. K. Kuprewicz, M. L. Davis, A. Dykstra, D. S. Mason, C. Baruzzi, M. A. Lashley, D. R. Risch, M. R. Price, M. L. Allen, L. S. Whipple, J. H. Sperry, R. H. Hagen, A. Mortelliti, B. E. Evans, C. E. Studds, A. P. K. Sirén, J. Kilborn, C. Sutherland, P. Warren, T. Fuller, N. C. Harris, N. H. Carter, E. Trout, M. Zimova, S. T. Giery, F. Iannarilli, S. D. Higdon, R. S. Revord, C. P. Hansen, J. J. Millspaugh, A. Zorn, J. F. Benson, N. H. Wehr, J. N. Solberg, B. D. Gerber, J. C. Burr, J. Sevin, A. M. Green, Ç. H. Şekercioğlu, M. Pendergast, K. A. Barnick, A. J. Edelman, J. R. Wasdin, A. Romero, B. J. O'Neill, N. Schmitz, J. M. Alston, K. M. Kuhn, D. B. Lesmeister, M. A. Linnell, C. L. Appel, C. Rota, J. L. Stenglein, C. Anhalt-Depies, C. Nelson, R. A. Long, K. Jo Jaspers, K. R. Remine, M. J. Jordan, D. Davis, H. Hernández-Yáñez, J. Y. Zhao, and W. J. McShea. 2021. SNAPSHOT USA 2019: a coordinated national camera trap survey of the United States. Ecology **102**:e03353.

Craney, T. A., and J. G. Surles. 2002. Model-dependent variance inflation factor cutoff values. Quality engineering **14**:391-403.

Crawley, M. J. 2012. The R book. John Wiley & Sons.

Curveira-Santos, G., S. Marion, C. Sutherland, C. Beirne, E. J. Herdman, E. R. Tattersall, J. M. Burgar, J. T. Fisher, and A. C. Burton. 2024. Disturbance-mediated changes to boreal mammal spatial networks in industrializing landscapes. Ecological Applications **34**:e3004.

Cuveira-Santos, G., Marion, S., Sutherland, C., Beirne, C., Herdman, E., Tattersall, E., Burgar, J., Fisher, J., Burton, C. 2024. Disturbance-mediatd changes to boreal mammal spatial networks in industrializing landscapes [DRAFT]. Ecological Applications.

Czetwertynski, S. 2008. Effects of hunting on the demographics, movement, and habitat selection of american black bears.

Dabros, A., H. J. Hammond, J. Pinzon, B. Pinno, and D. Langor. 2017. Edge influence of low-impact seismic lines for oil exploration on upland forest vegetation in northern Alberta (Canada). Forest Ecology and Management **400**:278-288.

Dabros, A., and K. L. Higgins. 2023. Vegetation recovery and edge effects of low impact seismic lines over eight-year period in boreal uplands of northern Alberta. Forest Ecology and Management **532**:120850.

Dabros, A., M. Pyper, and G. Castilla. 2018. Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. Environmental Reviews **26**:214-229.

Dalerum, F., S. Boutin, and J. S. Dunford. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Canadian Journal of Zoology **85**:26-32.

Darling, A. F., L. Leston, and E. M. Bayne. 2019. Small-mammal abundance differs between pipelines, edges, and interior boreal forest habitat. Canadian Journal of Zoology **97**:880-894.

Darlington, S., A. Ladle, A. C. Burton, J. P. Volpe, and J. T. Fisher. 2022. Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. Scientific Reports **12**:1-12.

Dawe, C. A., A. T. Filicetti, and S. E. Nielsen. 2017. Effects of Linear Disturbances and Fire Severity on Velvet Leaf Blueberry Abundance, Vigor, and Berry Production in Recently Burned Jack Pine Forests. Forests **8**:398.

Dawe, K., E. Bayne, and S. Boutin. 2014. Influence of climate and human land use on the distribution of white-tailed deer (Odocoileus virginianus) in the western boreal forest. Canadian Journal of Zoology **92**:353-363.

Dawe, K. L. 2011. Factors driving range expansion of white-tailed deer, Odocoileus virginianus, in the boreal forest of northern Alberta, Canada.

Dawe, K. L., and S. Boutin. 2016. Climate change is the primary driver of white-tailed deer (Odocoileus virginianus) range expansion at the northern extent of its range; land use is secondary. Ecology and Evolution **6**:6435-6451.

Demars, C. A., and S. Boutin. 2018. Nowhere to hide: Effects of linear features on predator–prey dynamics in a large mammal system. Journal of Animal Ecology **87**:274-284.

Devarajan, K., M. Fidino, Z. J. Farris, S. A. Adalsteinsson, G. Andrade-Ponce, J. L. Angstmann, W. Anthonysamy, J. Aquino, A. Asefa, B. Avila, L. L. Bailey, L. M. de Sousa Barbosa, M. de Frias Barreto, O. Barton, C. E. Bates, M. G. Beltrão, T. Bird, E. G. Biro, F. Bisi, D. Bohórquez, M. Boyce, J. S. Brashares, G. Bullington, P. Burns, J. Burr, A. R. Butler, K.

L. Calhoun, T. T. Cao, N. Casado, J. C. Cepeda-Duque, J. D. Cepek, A. G. Chiarello, M. Collins, P. Cordeiro-Estrela, S. Costa, G. Cremonesi, B. Cristescu, P. Cruz, A. C. F. de Albuquerque, C. De Angelo, C. B. de Campos, L. M. M. de Sena, M. Di Bitetti, D. de Matos Dias, D. Diefenbach, T. S. Doherty, T. P. dos Santos, G. T. Duarte, T. M. Eppley, J. Erb, C. F. Esteves, B. Evans, M. L. M. Falcão, H. Fernandes-Ferreira, J. R. Fieberg, L. C. F. de Souza Filho, J. Fisher, M.-J. Fortin, G. A. Gale, T. Gallo, L. S. Ganoe, R. Garcia-Anleu, K. M. Gaynor, T. A. Gelmi-Candusso, P. N. Gichuru, Q. Gomez, A. M. Green, L. N. Guimarães, J. D. Haight, L. R. Harris, Z. D. Hawn, J. Heiman, H. Q. Hoang, S. Huebner, F. Iannarilli, M. E. Iezzi, J. S. Ivan, K. J. Jaspers, M. J. Jordan, J. Kamilar, M. Kane, M. H. Karimi, M. Kelly, M. T. Kohl, W. P. Kuvlesky, A. Ladle, R. N. Larson, Q. T. Le, D. Le, V. S. Le, E. W. Lehrer, P. E. Lendrum, J. Lewis, A. Link, D. J. Lizcano, J. V. Lombardi, R. Long, E. López-Tello, C. Lugarini, D. Lugo, P. MacKay, M. Madadi, R. A. Magalhães, S. B. Magle, L. H. R. D. Maia, S. Mandujano, T. Marchenkova, P. H. Marinho, L. Marker, J. M. Pardo, A. Martinoli, R. L. Massara, J. Masseloux, D. Matiukhina, A. Mayer, L. Mazariegos, M. R. McClung, A. McInturff, D. McPhail, A. Mertl, C. R. Middaugh, D. Miller, D. Mills, D. Miquelle, V. Miritis, R. J. Moll, P. Molnár, R. A. Montgomery, T. L. Morelli, A. Mortelliti, R. I. Mueller, A. S. Mukhacheva, K. Mullen, A. Murphy, V. Nepomuceno, D. Ngoprasert, A. Nguyen, T. Van Nguyen, V. T. Nguyen, H. A. N. Quang, R. Nipko, A. C. C. Nobre, J. Northrup, M. A. Owen, A. P. Paglia, M. S. Palmer, G. Palomo-Munoz, L. E. Pardo, C. Parks, A. M. de Oliveira Paschoal, B. Patterson, A. Paviolo, L. Pejchar, M. E. Pendergast, H. L. Perotto-Baldivieso, T. Petrov, M. K. P. Poisson, D. J. Polli, M. Pourmirzai, A. Reebin, K. R. Remine, L. Rich, C. S. Richardson, F. Robino, D. G. Rocha, F. L. Rocha, F. H. G. Rodrigues, A. T. Rohnke, T. J. Ryan, C. M. Salsbury, H. A. Sander, N. M. da Cruz Santos-Cavalcante, C. H. Sekercioglu, I. Seryodkin, D. H. Setiawan, S. Shadloo, M. Shahhosseini, G. Shannon, C. J. Shier, G. B. Smith, T. Snyder, R. Sollmann, K. L. Sparks, K. Sribuarod, C. C. St. Clair, T. Stankowich, R. Steinmetz, C. J. Stevenson, T. D. Surasinghe, S. V. Sutyrina, R. R. Swaisgood, A. Taktehrani, K. Thapa, M. Thorton, A. Tilker, M. W. Tobler, V. B. Tran, J. Tucker, R. C. Van Horn, J. S. Vargas-Soto, K. L. Velásquez-C, J. Venter, E. M. Venticinque, S. Verschueren, E. Wampole, D. J. Watchorn, O. R. Wearn, K. C. B. Weiss, A. Welschen, F. A. Widodo, J. Williamson, A.

Wilting, G. Wittemyer, A. Zavaleta, A. J. Zellmer, and B. D. Gerber. 2025. When the wild things are: Defining mammalian diel activity and plasticity. Science Advances **11**:eado3843.

Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. Butchart, and K. M. Chan. 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. Science **366**:eaax3100.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, and T. Avgar. 2020a. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. Journal of Animal Ecology **89**:623-634.

Dickie, M., S. R. McNay, G. D. Sutherland, M. Cody, T. Avgar, and A. Loison. 2020b. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. The Journal of animal ecology **89**:623-634.

Dickie, M., R. Serrouya, M. Becker, C. DeMars, M. J. Noonan, R. Steenweg, S. Boutin, and A. T. Ford. 2024a. Habitat alteration or climate: What drives the densities of an invading ungulate? Global Change Biology **30**:e17286.

Dickie, M., R. Serrouya, M. Becker, C. DeMars, M. J. Noonan, R. Steenweg, S. Boutin, and A. T. Ford. 2024b. The influence of habitat alteration is widespread, but the impact of climate cannot continue to be discounted. Global Change Biology **30**:e17497.

Dickie, M., R. Serrouya, R. S. McNay, and S. Boutin. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. Journal of Applied Ecology **54**:253-263.

Dickie, M., G. G. Sherman, G. D. Sutherland, R. S. McNay, and M. Cody. 2022. Evaluating the impact of caribou habitat restoration on predator and prey movement. Conservation Biology **37**:e14004.

Dickie, M., G. G. Sherman, G. D. Sutherland, R. S. McNay, and M. Cody. 2023. Evaluating the impact of caribou habitat restoration on predator and prey movement. Conservation Biology **37**:e14004.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography **12**:53-64.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the Anthropocene. Science **345**:401-406.

Downing, D. J., and W. W. Pettapiece. 2006. Natural Regions and Subregions of Alberta. Government of Alberta, Natural Regions Committee.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos:169-175.

Dyck, M. A., R. Iosif, B. Promberger–Fürpass, and V. D. Popescu. 2022. Dracula's ménagerie: A multispecies occupancy analysis of lynx, wildcat, and wolf in the Romanian Carpathians. Ecology and Evolution **12**:e8921.

Ellis, E. C., and N. Ramankutty. 2008. Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment **6**:439-447.

ESRI. 2014. ArcGIS Desktop.

Ethier, C. A., A. F. Barnas, N. P. Boucher, K. Baillie-David, and J. T. Fisher. 2024a. Lethal wolf control elicits change in moose habitat selection in unexpected ways. The Journal of Wildlife Management **88**:e22620.

Ethier, C. A., A. F. Barnas, N. P. Boucher, K. Baillie-David, and J. T. Fisher. 2024b. Lethal wolf control elicits change in moose habitat selection in unexpected ways. The Journal of wildlife management **88**:e22620.

Faraway, J. J. 2016. Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models. Chapman and Hall/CRC.

Felton, A. M., H. K. Wam, Z. Borowski, A. Granhus, L. Juvany, J. Matala, M. Melin, M. Wallgren, and A. Mårell. 2024. Climate change and deer in boreal and temperate regions: From physiology to population dynamics and species distributions. Global Change Biology **30**:e17505.

Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. Kay, H. A. Sander, B. MacDougall, C. M. Salsbury, T. J. Ryan, and J. L. Angstmann. 2021a. Landscape-scale differences among cities alter common species' responses to urbanization. Ecological Applications **31**:e02253.

Fidino, M., T. Gallo, E. W. Lehrer, M. H. Murray, C. A. M. Kay, H. A. Sander, B. Macdougall, C. M. Salsbury, T. J. Ryan, J. L. Angstmann, J. Amy Belaire, B. Dugelby, C. J. Schell, T. Stankowich, M. Amaya, D. Drake, S. H. Hursh, A. A. Ahlers, J. Williamson, L. M. Hartley, A. J. Zellmer, K. Simon, and S. B. Magle. 2021b. Landscape-scale differences among cities alter common species' responses to urbanization. Ecological Applications **31**.

Finnegan, L., M. Hebblewhite, and K. E. Pigeon. 2023. Whose line is it anyway? Moose (Alces alces) response to linear features. Ecosphere **14**:e4636.

Finnegan, L., K. E. Pigeon, and D. MacNearney. 2019. Predicting patterns of vegetation recovery on seismic lines: Informing restoration based on understory species composition and growth. Forest Ecology and Management **446**:175-192.

Fisher, J., J. Burgar, M. Dickie, C. Burton, and R. Serrouya. 2021a. Density Estimates of Unmarked Large Mammals at Camera Traps Vary among Models, Species, and Years, Signalling Importance of Model Assumptions.

Fisher, J., A. Burton, M. Hiltz, L. Nolan, and L. Roy. 2016. White-tailed Deer Distribution, Density, and Habitat Selection in the Northeast Boreal Forest: The Alberta Boreal Deer Project Final Report. Alberta Innovates-Technology Futures Vegreville, Alberta, Canada.

Fisher, J. T. 2025. Ecological Insights From Camera Trapping Span Biological Taxa, and the Globe. Ecology and Evolution **15**:e70947.

Fisher, J. T., B. Anholt, and J. P. Volpe. 2011. Body mass explains characteristic scales of habitat selection in terrestrial mammals. Ecology and Evolution **1**:517-528.

Fisher, J. T., and A. C. Burton. 2018. Wildlife winners and losers in an oil sands landscape. Frontiers in Ecology and the Environment **16**:323-328.

Fisher, J. T., and A. C. Burton. 2020. Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. Ecology and Evolution **n/a**.

Fisher, J. T., and A. C. Burton. 2021. Spatial structure of reproductive success infers mechanisms of ungulate invasion in Nearctic boreal landscapes. Ecology and Evolution **11**:900-911.

Fisher, J. T., A. C. Burton, L. Nolan, and L. Roy. 2020. Influences of landscape change and winter severity on invasive ungulate persistence in the Nearctic boreal forest. Scientific Reports **10**:1-11.

Fisher, J. T., F. Grey, N. Anderson, J. Sawan, N. Anderson, S.-L. Chai, L. Nolan, A. Underwood, J. Amerongen Maddison, H. W. Fuller, and S. Frey. 2021b. Indigenous-led camera-trap research on traditional territories informs conservation decisions for resource extraction. FACETS **6**:1266-1284.

Fisher, J. T., F. Grey, N. Anderson, J. Sawan, N. Anderson, S.-L. Chai, L. Nolan, A. Underwood, J. A. Maddison, H. W. Fuller, S. Frey, and M. Mallory. 2021c. Indigenous-led camera-trap research on traditional territories informs conservation decisions for resource extraction. FACETS **6**:1266-1284.

Fisher, J. T., and A. Ladle. 2022a. Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. Science of The Total Environment **822**:153432.

Fisher, J. T., and A. Ladle. 2022b. Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. Science of the Total Environment:153432.

Fisher, J. T., and A. Ladle. 2022c. Syntopic species interact with large boreal mammals' response to anthropogenic landscape change. The Science of the total environment **822**:153432-153432.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire and timber harvest in the North American boreal forest. Mammal review **35**:51-81.

Flagel, D. G., G. E. Belovsky, M. J. Cramer, D. E. Beyer Jr, and K. E. Robertson. 2017. Fear and loathing in a Great Lakes forest: cascading effects of competition between wolves and coyotes. Journal of Mammalogy **98**:77-84.

Fox, J., S. Weisberg, B. Price, D. Adler, D. Bates, G. Baud-Bovy, B. Bolker, S. Ellison, D. Firth, M. Friendly, G. Gorjanc, S. Graves, R. Heiberger, P. Krivitsky, R. Laboissiere, M. Maechler, G. Monette, D. Murdoch, H. Nilsson, D. Ogle, B. Ripley, T. Short, W. Venables, S. Walker, D. Winsemius, A. Zeileis, and R-Core. 2019. R package “car”.

Frey, S., D. Tejero, K. Baillie-David, A. C. Burton, and J. T. Fisher. 2022. Predator control alters wolf interactions with prey and competitor species over the diel cycle. Oikos:e08821.

Frey, S., J. Volpe, N. Heim, J. Paczkowski, and J. Fisher. 2020. Move to nocturnality not a universal trend in carnivore species on disturbed landscapes. Oikos **129**:1128-1140.

Fryxell, J. M., A. Mosser, A. R. Sinclair, and C. Packer. 2007. Group formation stabilizes predator–prey dynamics. Nature **449**:1041-1043.

Fuller, H. W., S. Frey, and J. T. Fisher. 2022. Integration of aerial surveys and resource selection analysis indicates human land-use supports boreal deer expansion. Ecological Applications **e2722**.

Fuller, H. W., S. Frey, and J. T. Fisher. 2023. Integration of aerial surveys and resource selection analysis indicates human land use supports boreal deer expansion. Ecological Applications **33**:e2722.

Gantchoff, M. G., D. Beyer, and J. L. Belant. 2019. Reproductive class influences risk tolerance during denning and spring for American black bears (Ursus americanus). Ecosphere (Washington, D.C) **10**:e02705-n/a.

Garneau, D. E., E. Post, T. Boudreau, M. Keech, and P. Valkenburg. 2007. Spatio-temporal Patterns of Predation among Three Sympatric Predators in a single-prey System. Wildlife Biology **13**:186-194.

Gaston, M. V., A. F. Barnas, R. M. Smith, S. Murray, and J. T. Fisher. 2024. Native prey, not landscape change or novel prey, drive cougar (Puma concolor) distribution at a boreal forest range edge. Ecology and Evolution **14**:e11146.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science **360**:1232-1235.

Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. American Midland Naturalist:36-43.

Gilbert, N. A., J. D. Clare, J. L. Stenglein, and B. Zuckerberg. 2020. Abundance estimation methods for unmarked animals with camera traps. Conservation Biology.

Gould, E., H. S. Fraser, T. H. Parker, S. Nakagawa, S. C. Griffith, P. A. Vesk, F. Fidler, D. G. Hamilton, R. N. Abbey-Lee, and J. K. Abbott. 2023. Same data, different analysts: variation in effect sizes due to analytical decisions in ecology and evolutionary biology.

Goward, S. L. 2024. Using remote camera traps to monitor population demographics and community ecology of divii (Dall's sheep): Part of a community-based monitoring program in the Northern Richardson Mountains, NT.

Greenberg, S., and T. Godin. 2012. Timelapse image analysis manual. University of Calgary.

Greenberg, S., T. Godin, and J. Whittington. 2019a. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution **9**:13706-13730.

Greenberg, S., T. Godin, and J. Whittington. 2019b. Design patterns for wildlife-related camera trap image analysis. Ecology and Evolution **9**:13706-13730.

Grente, O., S. Bauduin, N. L. Santostasi, S. Chamaillé-Jammes, C. Duchamp, N. Drouet-Hoguet, and O. Gimenez. 2024. Evaluating the effects of wolf culling on livestock predation when considering wolf population dynamics in an individual-based model. Wildlife Biology **2024**:e01227.

Hansson, L. 1992. Landscape ecology of boreal forests. Trends in Ecology & Evolution **7**:299-302.

Hawkins, B. A., J. A. F. Diniz-Filho, L. Mauricio Bini, P. De Marco, and T. M. Blackburn. 2007. Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography **30**:375-384.

Hayward, M. W., C. D. Mitchell, J. F. Kamler, P. Rippon, D. R. Heit, V. Nams, and R. A. Montgomery. 2023. Diet selection in the Coyote Canis latrans. Journal of Mammalogy **104**:1338-1352.

Heim, N., J. T. Fisher, A. Clevenger, J. Paczkowski, and J. Volpe. 2017. Cumulative effects of climate and landscape change drive spatial distribution of Rocky Mountain wolverine (Gulo gulo L.). Ecology and Evolution **7**:8903-8914.

Hervieux, D., M. Hebblewhite, N. J. DeCesare, M. Russell, K. Smith, S. Robertson, and S. Boutin. 2013. Widespread declines in woodland caribou (Rangifer tarandus caribou) continue in Alberta. Canadian Journal of Zoology **91**:872-882.

Hervieux, D., M. Hebblewhite, D. Stepnisky, M. Bacon, and S. Boutin. 2014. Managing wolves (Canis lupus) to recover threatened woodland caribou (Rangifer tarandus caribou) in Alberta. Canadian Journal of Zoology **92**:1029-1037.

Hinton, J. W., A. K. Ashley, J. A. Dellinger, J. L. Gittleman, F. T. van Manen, and M. J. Chamberlain. 2017. Using diets of Canis breeding pairs to assess resource partitioning between sympatric red wolves and coyotes. Journal of Mammalogy **98**:475-488.

Hody, J. W., and R. Kays. 2018. Mapping the expansion of coyotes (Canis latrans) across North and Central America. ZooKeys:81.

Holbrook, S. J., and R. J. Schmitt. 1988a. The Combined Effects of Predation Risk and Food Reward on Patch Selection. Ecology **69**:125-134.

Holbrook, S. J., and R. J. Schmitt. 1988b. Combined Effects of Predation Risk and Food Reward on Patch Selection. Ecology (Durham) **69**:125-134.

Holland, J. D., D. G. Bert, and L. Fahrig. 2004. Determining the spatial scale of species' response to habitat. BioScience **54**:227-233.

Holland, J. D., L. Fahrig, and N. Cappuccino. 2005. Body size affects the spatial scale of habitat–beetle interactions. Oikos **110**:101-108.

Holland, J. D., and S. Yang. 2016. Multi-scale studies and the ecological neighborhood. Current Landscape Ecology Reports **1**:135-145.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution **15**:56-61.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187-211.

Ibisch, P. L., M. T. Hoffmann, S. Kreft, G. Pe'er, V. Kati, L. Biber-Freudenberger, D. A. DellaSala, M. M. Vale, P. R. Hobson, and N. Selva. 2016. A global map of roadless areas and their conservation status. Science **354**:1423-1427.

Institute, A. B. M. 2024. Enhanced Human Footprint Oil Sands Region 2021.

Iosif, R., V. D. Popescu, L. Ungureanu, C. Șerban, M. A. Dyck, and B. Promberger-Fürpass. 2022. Eurasian lynx density and habitat use in one of Europe's strongholds, the Romanian Carpathians. Journal of Mammalogy **103**:gyab157.

Jacques, C. N., R. W. Klaver, T. C. Swearingen, E. D. Davis, C. R. Anderson, J. A. Jenks, C. S. Deperno, and R. D. Bluett. 2019. Estimating density and detection of bobcats in fragmented midwestern landscapes using spatial capture–recapture data from camera traps. Wildlife Society Bulletin **43**:256-264.

James, A. R., and A. K. Stuart-Smith. 2000a. Distribution of caribou and wolves in relation to linear corridors. The Journal of Wildlife Management:154-159.

James, A. R. C., and A. K. Stuart-Smith. 2000b. Distribution of Caribou and Wolves in Relation to Linear Corridors. The Journal of Wildlife Management **64**:154-159.

Jensen, A. J., C. J. Marneweck, J. C. Kilgo, and D. S. Jachowski. 2022. Coyote diet in North America: geographic and ecological patterns during range expansion. Mammal Review **Early view**.

Jensen, R., J. Ruprecht, E. Orning, T. Levi, D. E. Clark, and T. D. Forrester. 2024. Large-scale overlap and fine-scale avoidance: assessing interactions between coyotes, bobcats, and cougars at multiple scales. Journal of Mammalogy:gyae045.

Johnson, C. J., and R. V. Rea. 2023. Response of moose to forest harvest and management: a literature review. Canadian Journal of Forest Research **54**:366-388.

Johnson, C. N., A. Balmford, B. W. Brook, J. C. Buettel, M. Galetti, L. Guangchun, and J. M. Wilmshurst. 2017. Biodiversity losses and conservation responses in the Anthropocene. Science **356**:270-275.

Jordaan, S. M. 2012. Land and water impacts of oil sands production in Alberta. Environmental Science & Technology **46**:3611-3617.

Kansas, J. L., M. L. Charlebois, and H. G. Skatter. 2015. Vegetation recovery on low impact seismic lines in Alberta's oil sands and visual obstruction of wolves (Canis lupus) and woodland caribou (Rangifer tarandus caribou). Canadian Journal of Wildlife Biology and Management **4**:137-149.

Karimi, L., and D. Meyer. 2014. Structural Equation Modeling in Psychology: The History, Development and Current Challenges. International Journal of Psychological Studies **6**:p123.

Kays, R., M. V. Cove, J. Diaz, K. Todd, C. Bresnan, M. Snider, T. E. Lee Jr, J. G. Jasper, B. Douglas, and A. P. Crupi. 2022. SNAPSHOT USA 2020: A second coordinated national camera trap survey of the United States during the COVID-19 pandemic. Wiley Online Library.

Kelly, M. J., J. Betsch, C. Wultsch, B. Mesa, and L. S. Mills. 2012. Noninvasive sampling for carnivores. Carnivore ecology and conservation: a handbook of techniques:47-69.

Kelt, D. A., and D. H. Van Vuren. 2001. The ecology and macroecology of mammalian home range area. The American Naturalist **157**:637-645.

Khan, P., L. Eliuk, S. Frey, C. Bone, and J. T. Fisher. 2023. Shifts in diel activity of Rocky Mountain mammal communities in response to anthropogenic disturbance and sympatric invasive white-tailed deer. Global Ecology and Conservation **41**:e02355.

Komers, P., and Z. Stanojevic. 2013. Rates of disturbance vary by data resolution: implications for conservation schedules using the Alberta Boreal Forest as a case study. Global Change Biology **19**:2916-2928.

Krebs, C. J. 1989. Ecological methodology. Harper & Row New York.

Krebs, C. J., R. Boonstra, V. Nams, M. O'Donoghue, K. E. Hodges, and S. Boutin. 2001a. Estimating snowshoe hare population density from pellet plots: a further evaluation. Canadian Journal of Zoology **79**:1-4.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001b. Ecosystem dynamics of the boreal forest. New York7 The Kluane Project.

Lankau, H. E., E. M. Bayne, and C. S. Machtans. 2013. Ovenbird (Seiurus aurocapilla) territory placement near seismic lines is influenced by forest regeneration and conspecific density. Avian Conservation and Ecology **8**.

Latham, A. D. M., M. C. Latham, and M. S. Boyce. 2011a. Habitat selection and spatial relationships of black bears (Ursus americanus) with woodland caribou (Rangifer tarandus caribou) in northeastern Alberta. Canadian journal of zoology **89**:267-277.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011b. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. Ecological Applications **21**:2854-2865.

Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011c. The Role of Predation in Woodland Caribou Population Declines in Northeastern Alberta – Coyotes.

Latham, A. D. M., M. C. Latham, K. H. Knopff, M. Hebblewhite, and S. Boutin. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. Ecography **36**:1276-1290.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011d. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. The Journal of Wildlife Management **75**:204-212.

Latham, A. D. M., M. C. Latham, N. A. McCutchen, and S. Boutin. 2011e. Invading white-tailed deer change wolf–caribou dynamics in northeastern Alberta. The Journal of Wildlife Management **75**:204-212.

Laurent, M., M. Dickie, M. Becker, R. Serrouya, and S. Boutin. 2021. Evaluating the Mechanisms of Landscape Change on White-Tailed Deer Populations. The Journal of Wildlife Management **85**:340-353.

Lawler, J. J., and C. E. Torgersen. 2020. Assessing the Relative Importance of Factors at Multiple Spatial Scales Affecting Terrestrial and Aquatic Wildlife. Current Landscape Ecology Reports **5**:12-24.

Lawton, J. H. 1999. Are there general laws in ecology? Oikos:177-192.

Lefcheck, J. S. 2016. piecewiseSEM : Piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution **7**:573-579.

Lendrum, P. E., J. M. Northrup, C. R. Anderson, G. E. Liston, C. L. Aldridge, K. R. Crooks, and G. Wittemyer. 2018. Predation risk across a dynamic landscape: effects of anthropogenic land use, natural landscape features, and prey distribution. Landscape Ecology **33**:157-170.

Lesmerises, R., J. P. Ouellet, C. Dussault, and M. H. St-Laurent. 2013. The influence of landscape matrix on isolated patch use by wide-ranging animals: conservation lessons for woodland caribou. Ecology and Evolution **3**:2880-2891.

Lesmerises, R., L. Rebouillat, C. Dussault, and M.-H. St-Laurent. 2015. Linking GPS Telemetry Surveys and Scat Analyses Helps Explain Variability in Black Bear Foraging Strategies. PLOS ONE **10**:e0129857-e0129857.

Levi, T., and C. C. Wilmers. 2012. Wolves–coyotes–foxes: a cascade among carnivores. Ecology **93**:921-929.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. Ecology **73**:1943-1967.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian journal of zoology **68**:619-640.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time, and body size in mammals. Ecology **67**:413-418.

Lukasik, V. M., and S. M. Alexander. 2012. Spatial and temporal variation of coyote (Canis latrans) diet in Calgary, Alberta. Cities and the Environment (CATE) **4**:8.

Lyn Morelli, T., M. T. Hallworth, T. Duclos, A. Ells, S. D. Faccio, J. R. Foster, K. P. McFarland, K. Nislow, J. Ralston, M. Ratnaswamy, W. V. Deluca, and A. P. K. Siren. 2025. Does habitat or climate change drive species range shifts? Ecography **n/a**:e07560.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences **51**:1207-1210.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**:2200-2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology **83**:2248-2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017a. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2017b. Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence. Elsevier.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: general advice and allocating survey effort. Journal of Applied Ecology **42**:1105-1114.

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. 2017. Package 'glmmtmb'. R Package Version 0.2. 0.

Mahon, C. L., G. Holloway, P. Sólymos, S. G. Cumming, E. M. Bayne, F. K. Schmiegelow, and S. J. Song. 2016. Community structure and niche characteristics of upland and lowland western boreal birds at multiple spatial scales. Forest Ecology and Management **361**:99-116.

Mahon, C. L., G. L. Holloway, E. M. Bayne, and J. D. Toms. 2019. Additive and interactive cumulative effects on boreal landbirds: winners and losers in a multi-stressor landscape. Ecological Applications **29**:e01895.

Martínez-Harms, M. J., R. A. Estévez, and E. Álvarez-Miranda. 2024. Conservation triage in action: Planning, governance and knowledge co-production for biodiversity protection. Journal of Applied Ecology **61**:2328-2334.

Mastro, L. L., D. J. Morin, and E. M. Gese. 2019. Home range and habitat use of West Virginia Canis latrans (Coyote). Northeastern Naturalist **26**:616-628.

Mazziotta, A., A. Lindén, K. Eyvindson, S. Bianchi, A. Kangas, M. Melin, L. Ruha, and J. T. Forsman. 2024. Unraveling the characteristic spatial scale of habitat selection for forest grouse species in the boreal landscape. Forest Ecology and Management **563**:122008.

McCarty, J. P. 2001. Ecological Consequences of Recent Climate Change. Conservation Biology **15**:320-331.

McKay, T. L., and L. A. Finnegan. 2022. Predator–prey co-occurrence in harvest blocks: Implications for caribou and forestry. Conservation Science and Practice **4**:e12847.

McKenzie, H. W., E. H. Merrill, R. J. Spiteri, and M. A. Lewis. 2012. How linear features alter predator movement and the functional response. Interface focus **2**:205-216.

Mech, L. D., and L. Boitani. 2019. Wolves: behavior, ecology, and conservation. University of Chicago Press.

Meek, P. D., G.-A. Ballard, P. J. S. Fleming, M. Schaefer, W. Williams, and G. Falzon. 2014. Camera Traps Can Be Heard and Seen by Animals. PLOS ONE **9**:e110832.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology **87**:56-63.

Messier, F., and M. Crête. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia **65**:503-512.

Metthé, L., C. Dussault, and S. Hamel. 2025. Linking spatial variations in life-history traits to environmental conditions across American black bear populations. Ecological monographs **95**.

Miller, B. J., H. J. Harlow, T. S. Harlow, D. Biggins, and W. J. Ripple. 2012. Trophic cascades linking wolves (Canis lupus), coyotes (Canis latrans), and small mammals. Canadian Journal of Zoology **90**:70-78.

Moore, S. A., T. M. Wolf, W. J. Severud, E. J. Isaac, and Y. M. Chenaux-Ibrahim. 2024. Spring black bear harvest and predation pressure on moose calves in a multi-predator system. The Journal of Wildlife Management **88**:n/a.

Mosnier, A., J.-P. Ouellet, and R. Courtois. 2008. Black bear adaptation to low productivity in the boreal forest. Écoscience **15**:485-497.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PloS One **6**:e17050.

Mumma, M. A., M. P. Gillingham, C. J. Johnson, and K. L. Parker. 2019. Functional responses to anthropogenic linear features in a complex predator-multi-prey system. Landscape Ecology **34**:2575-2597.

Mumma, M. A., M. P. Gillingham, K. L. Parker, C. J. Johnson, and M. Watters. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: Evidence of wolf spatial responses independent of apparent competition. Biological Conservation **228**:215-223.

Munro, K. G., J. Bowman, and L. Fahrig. 2012. Effect of paved road density on abundance of white-tailed deer. Wildlife Research **39**:478.

Murray, D. L., J. Gobin, A. Scully, and D. H. Thornton. 2023. Conventional niche overlap measurements are not effective for assessing interspecific competition. Frontiers in Ecology and Evolution **11**:1281108.

Murray, M., A. Cembrowski, A. Latham, V. Lukasik, S. Pruss, and C. St Clair. 2015. Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict. Ecography **38**:1235-1242.

Nakashima, Y., K. Fukasawa, and H. Samejima. 2018. Estimating animal density without individual recognition using information derivable exclusively from camera traps. Journal of Applied Ecology **55**:735-744.

Nakashima, Y., S. Hongo, and E. F. Akomo-Okoue. 2020. Landscape-scale estimation of forest ungulate density and biomass using camera traps: Applying the REST model. Biological Conservation **241**:108381.

Nams, V. O., G. Mowat, and M. A. Panian. 2006. Determining the spatial scale for conservation purposes–an example with grizzly bears. Biological Conservation **128**:109-119.

Nellemann, C., I. Vistnes, P. Jordhøy, and O. Strand. 2001. Winter distribution of wild reindeer in relation to power lines, roads and resorts. Biological Conservation **101**:351-360.

Newsome, T. M., L. Boitani, G. Chapron, P. Ciucci, C. R. Dickman, J. A. Dellinger, J. V. López-Bao, R. O. Peterson, C. R. Shores, and A. J. Wirsing. 2016. Food habits of the world's grey wolves. Mammal Review **46**:255-269.

Newton, E. J., B. R. Patterson, M. L. Anderson, A. R. Rodgers, L. M. Vander Vennen, and J. M. Fryxell. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: implications for caribou conservation. PloS One **12**:e0186525.

Nielsen, S. E., J. M. Dennett, and C. W. Bater. 2020. Predicting Occurrence, Abundance, and Fruiting of a Cultural Keystone Species to Inform Landscape Values and Priority Sites for Habitat Enhancements. Forests **11**:783.

O'Connell, A. F., J. D. Nichols, and K. U. Karanth. 2011. Camera traps in animal ecology: methods and analyses. Springer.

O’Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**:1193-1208.

Ordiz, A., O.-G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological conservation **152**:21-28.

Paquet, P. C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Journal of Mammalogy **73**:337-343.

Pattison, C. A., M. S. Quinn, P. Dale, and C. P. Catterall. 2016. The landscape impact of linear seismic clearings for oil and gas development in boreal forest. Northwest Science **90**:340-354.

Pearl, J. 2000. Models, reasoning and inference. Cambridge, UK: CambridgeUniversityPress **19**.

Pelchat, B. O., and R. L. Ruff. 1986. Habitat and Spatial Relationships of Black Bears in Boreal Mixedwood Forest of Alberta. Bears: Their Biology and Management **6**:81.

Petroelje, T. R., T. M. Kautz, D. E. Beyer Jr, and J. L. Belant. 2021. Interference competition between wolves and coyotes during variable prey abundance. Ecology and Evolution **11**:1413-1431.

Pickell, P. D., D. W. Andison, and N. C. Coops. 2013. Characterizations of anthropogenic disturbance patterns in the mixedwood boreal forest of Alberta, Canada. Forest ecology and management **304**:243-253.

Pickell, P. D., D. W. Andison, N. C. Coops, S. E. Gergel, and P. L. Marshall. 2015. The spatial patterns of anthropogenic disturbance in the western Canadian boreal forest following oil and gas development. Canadian Journal of Forest Research **45**:732-743.

Pickell, P. D., N. C. Coops, S. E. Gergel, D. W. Andison, and P. L. Marshall. 2016a. Evolution of Canada's Boreal Forest Spatial Patterns as Seen from Space. PLOS ONE **11**:e0157736-e0157736.

Pickell, P. D., N. C. Coops, S. E. Gergel, D. W. Andison, and P. L. Marshall. 2016b. Evolution of Canada's boreal forest spatial patterns as seen from space. PLOS ONE **11**:e0157736.

Pickell, P. D., S. E. Gergel, N. C. Coops, and D. W. Andison. 2014. Monitoring forest change in landscapes under-going rapid energy development: challenges and new perspectives. Land **3**:617-638.

Porter, J., R. Price, and R. McCrossan. 1982. The western Canada sedimentary basin. Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences **305**:169-192.

Poulin, M.-P., S. G. Cherry, and J. A. Merkle. 2023. Dynamic balancing of risks and rewards in a large herbivore: Further extending predator-prey concepts to road ecology. The Journal of animal ecology **92**:1954-1965.

Preacher, K. J., and E. C. Merkle. 2012. The problem of model selection uncertainty in structural equation modeling. Psychological methods **17**:1.

Price, L. E., B. P. Skelly, E. E. Morrison, C. P. Carpenter, C. W. Ryan, and C. T. Rota. 2024. TWS Journals. Wildlife Society Bulletin **48**.

Prugh, L. R. 2005. Coyote prey selection and community stability during a decline in food supply. Oikos **110**:253-264.

Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. The American Naturalist **137**:S50-S66.

Pyke, G. H. 1984. Optimal foraging theory: a critical review. Annual review of ecology and systematics **15**:523-575.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing; Available at https://www.r-project.org/.

R Core Team. 2024a. R: A language and environment for statistical computing.

R Core Team. 2024b. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raine, R. M., and J. L. Kansas. 1990. Black Bear Seasonal Food Habits and Distribution by Elevation in Banff National Park, Alberta. Bears, their biology and management **8**:297-304.

Rich, L. N., C. L. Davis, Z. J. Farris, D. A. Miller, J. M. Tucker, S. Hamel, M. S. Farhadinia, R. Steenweg, M. S. Di Bitetti, and K. Thapa. 2017. Assessing global patterns in mammalian carnivore occupancy and richness by integrating local camera trap surveys. Global Ecology and Biogeography **26**:918-929.

Roberts, D. R., E. M. Bayne, D. Beausoleil, J. Dennett, J. T. Fisher, R. O. Hazewinkel, D. Sayanda, F. Wyatt, and M. G. Dubé. 2022. A synthetic review of terrestrial biological research from the Alberta oil sands region: 10 years of published literature. Integrated Environmental Assessment and Management **18**:388-406.

Romain, D. A., M. E. Obbard, and J. L. Atkinson. 2013. Temporal variation in food habits of the American Black Bear (Ursus americanus) in the boreal forest of northern Ontario. Canadian field-naturalist **127**:118-130.

Rosa, L., K. F. Davis, M. C. Rulli, and P. D'Odorico. 2017. Environmental consequences of oil production from oil sands. Earth's Future **5**:158-170.

Routh, M. R., and S. E. Nielsen. 2021. Dynamic patterns in winter ungulate browse succession in the Boreal Plains of Alberta. Forest Ecology and Management **492**:119242.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2014. Spatial capture-recapture. Academic Press.

Ruggiero, L. F. 1994. The scientific basis for conserving forest carnivores: American marten, fisher, lynx, and wolverine in the western United States. US Department of Agriculture, Forest Service, Rocky Mountain Forest and ….

Sage, R. F. 2020. Global change biology: a primer. Global Change Biology **26**:3-30.

Sarkar, S. 1984. Hierarchy: Perspectives for Ecological Complexity. JSTOR.

Sawyer, S. C., C. W. Epps, and J. S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology **48**:668-678.

Schieck, J., P. Sólymos, and D. Huggard. 2014. ABMI science letters: human footprint in Alberta. AMBI, University of Alberta, Edmonton, Alberta, Canada.[online] URL: http ….

Schoener, T. W. 1974. Resource Partitioning in Ecological Communities: Research on how similar species divide resources helps reveal the natural regulation of species diversity. Science **185**:27-39.

Serrouya, R., M. Dickie, C. DeMars, M. Wittmann, and S. Boutin. 2020. Predicting the effects of restoring linear features on woodland caribou populations. Ecological Modelling **416**:108891.

Serrouya, R., M. J. Wittmann, B. N. McLellan, H. U. Wittmer, and S. Boutin. 2015. Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition. The American Naturalist **185**:665-679.

Shi, Y., Y. Hoareau, E. M. Reese, and S. K. Wasser. 2021. Prey partitioning between sympatric wild carnivores revealed by DNA metabarcoding: a case study on wolf (Canis lupus) and coyote (Canis latrans) in northeastern Washington. Conservation Genetics **22**:293-305.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters **5**:785-791.

Skatter, H. G., J. L. Kansas, M. L. Charlebois, and S. Skatter. 2020. Long-term snow track monitoring to understand factors affecting boreal forest mammal density in an expanding in situ oil sands area. Canadian Wildlife Biology and Management **2**:107-131.

Slough, B. G., and G. Mowat. 1996. Lynx population dynamics in an untrapped refugium. The Journal of Wildlife Management:946-961.

Smith, R. 2018. Evaluating the impacts of anthropogenic development on large mammals across protected and industrialized landscapes in Western Canada. University of Victoria.

Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. T. Fisher, C. Burton, S. E. Townsend, C. Carbone, J. M. Rowcliffe, and J. Whittington. 2017a. Scaling-up camera traps: Monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**:26-34.

Steenweg, R., M. Hebblewhite, R. Kays, J. Ahumada, J. T. Fisher, C. Burton, S. E. Townsend, C. Carbone, J. M. Rowcliffe, J. Whittington, J. Brodie, J. A. Royle, A. Switalski, A. P. Clevenger, N. Heim, and L. N. Rich. 2017b. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Frontiers in Ecology and the Environment **15**:26-34.

Steffen, W., R. A. Sanderson, P. D. Tyson, J. Jäger, P. A. Matson, B. Moore III, F. Oldfield, K. Richardson, H.-J. Schellnhuber, and B. L. Turner. 2005. Global Change and the Earth System: a Planet Under Pressure. Springer Science & Business Media.

Stenegren, M., C. Berg, C. C. Padilla, S.-S. David, J. P. Montoya, P. L. Yager, and R. A. Foster. 2017. Piecewise Structural Equation Model (SEM) Disentangles the Environmental Conditions Favoring Diatom Diazotroph Associations (DDAs) in the Western Tropical North Atlantic (WTNA). Frontiers in Microbiology **8**.

Stern, E. R., F. Riva, and S. E. Nielsen. 2018. Effects of narrow linear disturbances on light and wind patterns in fragmented boreal forests in northeastern Alberta. Forests **9**:486.

Stewart, F. E., J. P. Volpe, and J. T. Fisher. 2019a. The Debate About Bait: A Red Herring in Wildlife Research. The Journal of Wildlife Management **83**:985-992.

Stewart, F. E. C., J. P. Volpe, and J. T. Fisher. 2019b. The Debate About Bait: A Red Herring in Wildlife Research. The Journal of Wildlife Management **83**:985-992.

Stillfried, M., J. L. Belant, N. J. Svoboda, D. E. Beyer, and S. Kramer-Schadt. 2015. When top predators become prey: Black bears alter movement behaviour in response to hunting pressure. Behavioural processes **120**:30-39.

Stuber, E. F., and J. J. Fontaine. 2019. How characteristic is the species characteristic selection scale? Global Ecology and Biogeography **28**:1839-1854.

Sun, C., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2022. A cautionary tale comparing spatial count and partial identity models for estimating densities of threatened and unmarked populations. Global Ecology and Conservation **38**:e02268.

Sun, C. C., A. K. Fuller, and J. A. Royle. 2014. Trap configuration and spacing influences parameter estimates in spatial capture-recapture models. PloS One **9**:e88025.

Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. Canadian Journal of Zoology **81**:985-993.

Tattersall, E., K. Pigeon, D. MacNearney, and L. Finnegan. 2023a. Walking the line: Investigating biophysical characteristics related to wildlife use of linear features. Ecological Solutions and Evidence **4**:e12219.

Tattersall, E., K. Pigeon, D. MacNearney, and L. Finnegan. 2023b. Walking the line: Investigating biophysical characteristics related to wildlife use of linear features. Ecological solutions and evidence **4**:n/a.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020a. Boreal predator co-occurrences reveal shared use of seismic lines in a working landscape. Ecology and Evolution **10**:1678-1691.

Tattersall, E. R., J. M. Burgar, J. T. Fisher, and A. C. Burton. 2020b. Mammal seismic line use varies with restoration: Applying habitat restoration to species at risk conservation in a working landscape. Biological Conservation **241**:108295.

Territories, G. o. N. Lynx-Snowshoe Hare Cycle.

Thuiller, W., C. Albert, M. B. Araújo, P. M. Berry, M. Cabeza, A. Guisan, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes, and N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics **9**:137-152.

Tigner, J., E. M. Bayne, and S. Boutin. 2014. Black bear use of seismic lines in Northern Canada. The Journal of Wildlife Management **78**:282-292.

Timoney, K., and P. Lee. 2001. Environmental management in resource-rich Alberta, Canada: first world jurisdiction, third world analogue? Journal of Environmental Management **63**:387-405.

Todd, A. W., and L. B. Keith. 1983. Coyote demography during a snowshoe hare decline in Alberta. The Journal of Wildlife Management:394-404.

Todd, A. W., L. B. Keith, and C. A. Fischer. 1981. Population ecology of coyotes during a fluctuation of snowshoe hares. The Journal of Wildlife Management:629-640.

Toews, M., F. Juanes, and A. C. Burton. 2018. Mammal responses to the human footprint vary across species and stressors. Journal of Environmental Management **217**:690-699.

Tredennick, A. T., G. Hooker, S. P. Ellner, and P. B. Adler. 2021. A practical guide to selecting models for exploration, inference, and prediction in ecology. Ecology **102**:e03336.

Trenberth, K. E. 2018. Climate change caused by human activities is happening and it already has major consequences. Journal of Energy & Natural Resources Law **36**:463-481.

Trolliet, F., C. Vermeulen, M.-C. Huynen, and A. Hambuckers. 2014. Use of camera traps for wildlife studies: a review. Biotechnologie, Agronomie, Société et Environnement **18**.

Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**:18-30.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual review of ecology and systematics:171-197.

Twining, J. P., D. Kramer, K. A. Perkins, and A. K. Fuller. 2024. Landscape-scale population trends in the occurrence and abundance of wildlife populations using long term camera-trapping data. Biological Conservation **290**:110398.

Urban, D. 2014. On Scale and Pattern. The Bulletin of the Ecological Society of America **95**:124-125.

van Rensen, C. K., S. E. Nielsen, B. White, T. Vinge, and V. J. Lieffers. 2015. Natural regeneration of forest vegetation on legacy seismic lines in boreal habitats in Alberta's oil sands region. Biological Conservation **184**:127-135.

Van Scoyoc, A., K. L. Calhoun, and J. S. Brashares. 2024. Using multiple scales of movement to highlight risk–reward strategies of coyotes (Canis latrans) in mixed-use landscapes. Ecosphere **15**:e4977.

Veitch, A. M. 2001. An unusual record of a white-tailed deer, Odocoileus virginianus, in the Northwest Territories. Canadian Field Naturalist **115**:172-175.

VerCauteren, K. C. 2003. The deer boom: discussins on population growth and range expansion of the white-tailed deer.

Walker, M. A., M. Uribasterra, V. Asher, W. M. Getz, S. J. Ryan, J. M. Ponciano, and J. K. Blackburn. 2021. Factors influencing scavenger guilds and scavenging efficiency in Southwestern Montana. Scientific Reports **11**:4254.

Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature **416**:389-395.

Ward, J. N., J. W. Hinton, K. L. Johannsen, M. L. Karlin, K. V. Miller, and M. J. Chamberlain. 2018. Home range size, vegetation density, and season influences prey use by coyotes (Canis latrans). PloS One **13**:e0203703.

Ward, R. M., and C. J. Krebs. 1985. Behavioural responses of lynx to declining snowshoe hare abundance. Canadian Journal of Zoology **63**:2817-2824.

Weir, R. D., A. S. Harestad, and R. C. Wright. 2005. Winter diet of fishers in British Columbia. Northwestern Naturalist **86**:12-19.

Whitlock, M., and D. Schluter. 2015. The analysis of biological data. Roberts Publishers Greenwood Village, Colorado.

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

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. Springer.

Wickham, H., R. Francois, L. Henry, and K. Müller. 2015. dplyr: A grammar of data manipulation. R package version 0.4 **3**.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385-397.

Wiens, J. A., and B. T. Milne. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology **3**:87-96.

Wiewel, A. S., W. R. Clark, and M. A. Sovada. 2007. Assessing Small Mammal Abundance with Track-Tube Indices and Mark–Recapture Population Estimates. Journal of Mammalogy **88**:250-260.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and W. M. Getz. 2003. Resource dispersion and consumer dominance: scavenging at wolf-and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters **6**:996-1003.

Wittische, J., S. Heckbert, P. M. A. James, A. C. Burton, and J. T. Fisher. 2021a. Community-level modelling of boreal forest mammal distribution in an oil sands landscape. The Science of the total environment **755**:142500-142500.

Wittische, J., S. Heckbert, P. M. A. James, A. C. Burton, and J. T. Fisher. 2021b. Community-level modelling of boreal forest mammal distribution in an oil sands landscape. Science of the Total Environment **755**:142500.

Yates, L. A., Z. Aandahl, S. A. Richards, and B. W. Brook. 2023. Cross validation for model selection: a review with examples from ecology. Ecological monographs **93**:e1557.

Young, B. F., and R. L. Ruff. 1982. Population Dynamics and Movements of Black Bears in East Central Alberta. The Journal of Wildlife Management **46**:845.

Zager, P., and J. Beecham. 2006. The role of American black bears and brown bears as predators on ungulates in North America. Ursus (International Association for Bear Research and Management) **17**:95-108.

Zuckerberg, B., J. M. Cohen, L. A. Nunes, J. Bernath-Plaisted, J. D. Clare, N. A. Gilbert, S. S. Kozidis, S. B. Maresh Nelson, A. A. Shipley, and K. L. Thompson. 2020a. A review of overlapping landscapes: pseudoreplication or a red herring in landscape ecology? Current Landscape Ecology Reports **5**:140-148.

Zuckerberg, B., J. M. Cohen, L. A. Nunes, J. Bernath-Plaisted, J. D. J. Clare, N. A. Gilbert, S. S. Kozidis, S. B. Maresh Nelson, A. A. Shipley, K. L. Thompson, and A. Desrochers. 2020b. A Review of Overlapping Landscapes: Pseudoreplication or a Red Herring in Landscape Ecology? Current landscape ecology reports **5**:140-148.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010a. A protocol for data exploration to avoid common statistical problems. Methods in ecology and evolution **1**:3-14.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010b. A protocol for data exploration to avoid common statistical problems: Data exploration. . Methods in Ecology and Evolution **1**:3-14.