Investigating the impacts of anthropogenic disturbance in Canada's Oil Sands Region on large mammals, with a focus on black bears (*Ursus americanus*) and moose (*Alces alces*)

by

Megan Braun
B.Sc. (Honours), University of Guelph, 2023

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We acknowledge and respect the Ləkʷəŋən (Songhees and Xʷsepsəm/ Esquimalt) Peoples on whose territory the university stands, and the Ləkʷəŋən and W̱SÁNEĆ Peoples whose historical relationships with the land continue to this day.

Supervisory Committee

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Abstract

Rapid and expansive anthropogenic landscape change is transforming wildlife habitat and driving global biodiversity loss. In this thesis, I used wildlife camera traps to investigate how the spatial distributions of two culturally and ecologically important species, black bear and moose, are affected by industrial development in the Oil Sands Region (OSR) of western Canada. In both cases, I applied novel analytical approaches to address key ecological knowledge gaps and better understand species' responses to shifting risk-reward trade-offs associated with landscape change. In Chapter 2, I addressed the lack of clarity surrounding black bear responses to industrial disturbance by incorporating seasonal and demographic considerations into the analysis. This finer-scale approach revealed that spatial associations with disturbances features were shaped by both season and demographic group. Notably, solitary adults exhibited seasonal variation in road associations, potentially linked to changes in hunter activity. These findings highlight the importance of considering ecological and social context when evaluating species' responses to landscape change, with direct implications for wildlife management and conservation. In Chapter 3, I used structural equation modelling (SEM) to investigate potential drivers of moose population declines in the OSR, assessing both direct and indirect effects of natural habitat, industrial disturbance, and predator occurrence. I found a strong negative direct effect of roads on moose, which outweighed positive associations with forage-subsiding features, suggesting an overall net-negative impact of industrial disturbance. However, due to the limited capacity of camera traps to capture fine-scale predator-prey dynamics, I was unable to evaluate potential indirect effects mediated by predators. This study demonstrates the value of SEM as a mechanism-oriented alternative to traditional predictive models and provides a transferable framework for understanding complex ecological relationships in other disturbed systems.

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Chapter 1: Introduction

1.1 Anthropogenic landscape modification is driving global biodiversity loss

It is widely acknowledged that we are living in the Anthropocene, a geological epoch in which human activity is a dominant force shaping Earth's systems, with profound implications for ecosystem function and our relationship with the natural world (Malhi 2017). One of the most pervasive outcomes of human activity on ecosystems is anthropogenic landscape modification, with approximately 75% of the Earth's ice-free land now affected (Ellis and Navin 2008). Loss and alteration of natural landcover for purposes including agriculture, urban development, transportation, resource extraction, and energy production are driven by a growing human population and increasing global demand for natural resources (Maxwell et al. 2016). These processes have intensified in recent decades and are projected to continue accelerating (Theobald et al. 2020). The loss of natural habitat affects wildlife by altering species distributions, diversity, abundances, and interspecific interactions (Malhi 2017), and is a major driver of the current biodiversity crisis (Maxwell et al. 2016).

1.2 Mammal species sensitivity to landscape change varies

Species do not respond uniformly to anthropogenic landscape change. Among mammals, body size and ecological specialization are two key traits influencing sensitivity (Keinath et al. 2017). Large-bodied, specialist species that require extensive, specific habitats are generally more vulnerable to habitat loss and fragmentation than smaller-bodied or generalist species, which are capable of using a broader range of resources and habitats (Crooks et al. 2017, Keinath et al. 2017).

Generalist species, by definition, exhibit greater ecological flexibility and may even benefit from disturbance when it increases the availability of useable resources (Fisher and Burton 2018). However, this flexibility has limits. The success of generalist populations likely depends on how anthropogenic disturbance reshapes the spatial distribution and relative availability of risks and rewards on the landscape.

For instance, disturbances that remove mature forest can promote early seral vegetation, increasing forage availability for herbivores. Conversely, these same disturbances may also reduce cover or facilitate predator movement via linear features, thereby increasing predation risk. When such risks outweigh rewards, even generalist species may be unable to adapt effectively. Therefore, explicitly considering how landscape change alters the balance of ecological costs and benefits is essential for predicting species' responses to anthropogenic disturbance.

1.3 Industrial disturbances affect black bears and moose in Canada's Oil Sands Region

In the Oil Sands Region (OSR) of western Canada, largescale landscape change related to petroleum extraction and processing has substantially transformed boreal habitats (Pickell et al. 2013). Two culturally and ecologically significant species that inhabit this region and are directly affected by such disturbances are black bears and moose. These species share many similarities: both are iconic and charismatic Canadian wildlife, and culturally important subsistence species for First Nation communities (Clark 2020, Carroll et al. 2024). Ecologically, they are large-bodied generalists, capable of adapting to a variety of habitat conditions and altering their spatial behaviour in response to fluctuating resource availability (Stewart et al. 2010, Alberta Government 2016). Both species also fulfill important ecological roles in boreal systems. Moose are key browsers and a primary prey species for large carnivores (Connor et al. 2000), while black bears are the region's only large omnivore and contribute to ecological processes including seed dispersal, carcass scavenging, soil aeration, and regulation of prey populations (Harrer and Levi 2018).

However, despite their shared generalist strategies, black bears and moose appear to be experiencing differential success in the OSR. While black bear populations seem stable, both government data and traditional knowledge from First Nations suggest that moose populations are declining (Parlee et al. 2012, Lamy and Finnegan 2019). Understanding the mechanisms behind these declines requires investigating moose-habitat relationships within this transformed landscape, while considering how industrial development may be shifting the spatial distribution of risks and rewards.

Although numerous studies have investigated black bear associations with anthropogenic disturbance features, findings remain mixed, with both positive and negative relationships reported (Mosnier et al. 2008, Tigner et al. 2014, Fisher and Burton 2018, Beirne et al. 2021). This inconsistency makes it difficult to predict how black bears will respond to future landscape changes, including feature creation or restoration. It also challenges our ability to understand the effects of their spatial distribution on other species. Notably, black bears are predators of woodland caribou calves, and increased spatial overlap due to industrial disturbance could have negative implications for endangered caribou populations (Latham et al. 2011b). As generalists, black bears likely respond to landscape change through temporally dynamic trade-offs between access to different resources and risk exposure. A finer-scale investigation is needed to detect these more nuanced patterns of response.

1.4 Thesis objectives

In this thesis, I explore how anthropogenic landscape change is influencing the spatial distributions of black bears and moose in the OSR, addressing key knowledge gaps in how these generalist species respond to industrial disturbances. Using data collected from wildlife camera traps deployed across ten, 1500 km^2 study landscapes throughout the OSR, I apply novel analytical approaches to gain deeper insights into habitat associations within the framework of risk-reward trade-offs.

In Chapter Two, I examine black bear associations with anthropogenic disturbance features and investigate how these relationships vary by season and demographic group. This finer-scale analysis aims to reveal patterns of habitat use that have been obscured in previous studies, helping to clarify how black bears navigate dynamic risk-reward trade-offs in modified landscapes.

In Chapter Three, I evaluate moose responses to landscape change using a causal statistical methodology, which simultaneously assesses multiple drivers of moose distribution within a single framework. This is one of the first applications of causal methodologies in this ecosystem and allows for the identification of not only direct impacts of disturbance, but also indirect effects mediated through predator presence.

The overarching goal of both chapters is to develop a more nuanced understanding of how industrial development is reshaping habitat use and species interactions in the OSR, with the broader aim of informing wildlife management and conservation efforts in disturbed boreal ecosystems.

Chapter 2: Seasonal and demographic variation in black bear (*Ursus americanus*) responses to industrial landscape change

2.1 Abstract

Habitat selection by wildlife often reflects trade-offs between the spatiotemporal distribution of perceived risks and rewards, which may be altered by anthropogenic disturbance. In the Canadian Oil Sands Region, landscape changes associated with resource extraction have substantially modified habitat availability for mammals. Black bear (*Ursus americanus*) habitat selection in response to these disturbances remains poorly understood, with inconsistent findings across studies- possibly because most have pooled data across seasons and demographic groups to overcome low sample sizes. Such pooling may mask spatiotemporal variation in responses, wherein contrasting behaviours among seasons or age-sex classes are effectively cancelled out. We hypothesized that black bear use of disturbance features reflects seasonal trade-offs between benefits and risks, and that solitary adults and females with young differ in risk tolerance, producing distinct habitat associations. Using data from 233 camera traps deployed across six western boreal forest landscapes for one year each, we constructed a candidate set of generalized linear mixed models with predictors hypothesized to influence black bear occurrence frequency. Consistent with our hypotheses, black bear occurrence frequency varied seasonally and demographically in relation to disturbance features. Linear disturbances, particularly roads, generally had strong negative effects. However, solitary adult occurrence frequency did not decline with increasing road proportion in the summer non-hunting season, suggesting a trade-off between foraging opportunities and fluctuating mortality risk. In contrast, female with young occurrence frequency consistently declined with road proportion across seasons. This pattern suggests lower risk tolerance to human disturbance and does not support the hypothesis that

these bears use roads as “human shields” from infanticidal adult bears during hunting periods, despite being legally protected from hunting. Solitary adult occurrence frequency also increased with higher ungulate relative abundance in spring, likely reflecting neonate predation. These findings provide insight into how demographic and seasonal variation in risk–reward trade-offs shape wildlife responses to landscape change and highlight the importance of considering these dynamics in management and conservation planning.

2.2 Introduction

Habitat selection by wildlife often reflects a trade-off between the spatial distribution of risks and rewards across a landscape, where if high reward (ex., food-rich) habitats also have high mortality risk, then lower reward habitats with less risk may be preferred (Holbrook and Schmitt 1988, Frid and Dill 2002). Further, risk-reward trade-offs are dynamic and can 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 diel cycles of predator activity (Lima and Dill 1990), or forage availability fluctuating seasonally. Risk tolerance can also shift though time based on life history stage; according to parental investment theory (Trivers, 1972), individuals with dependent offspring may prioritize risk avoidance to increase offspring survival (Ben-David et al. 2004).

Animal trade-off decisions are further complicated by human disturbance, which can reshape the spatiotemporal distribution of risks and rewards. Disturbances can provide new benefits, such as food subsidies from waste disposal near human settlements (Lunn and Stirling 1985), but also introduce risks like vehicle collisions (Poulin et al. 2023). How animals perceive these risks, whether or not they are truly lethal, shapes their behavioural responses (Frid and Dill 2002). The spatial patterning of these perceived risks is often referred to as the "landscape of fear" (Laundre et al. 2010). Humans can be perceived as potential predators, and thus wildlife may respond to human activity similar as they would predation risk (Gill et al. 1996), for example through spatial segregation. The behavioural response to human disturbance is influenced by eco-evolutionary history (Bro-Jørgensen et al. 2019), resulting in interspecific variation in risk perception. For example, reindeer (*Rangifer tarandus tarandus*) have shown strong avoidance of powerlines, in contrast to other ungulate species like elk (*Cervus* *canadensis*) and white-tailed deer (*Odocoileus virginianus*) that frequently use these areas for foraging (Gundula et al. 2014).

For prey species, differences in how they and their predators perceive risk can sometimes give rise to a benefit known as the "human shield effect." Here, if predator species perceive human activity as high risk and avoid such areas, while prey species perceive the same disturbance as less risky relative to predator presence, prey may aggregate near human infrastructure to "buffer" themselves from predators (Berger 2007), though with highly variable expression (Granados et al. 2023). For instance, a study found wolves (*Canis lupus*) were less abundant on walking trails with high human activity, while elk were more abundant on these trails than those with low human activity (Muhly et al. 2011). Use of the "human shield" can also differ within species by demographic group when predation risk varies by demographic. For example, pregnant moose (*Alces alces*) shifted closer to roads during calving, which are areas avoided by brown bears (*Ursus arctos*), a major predator of calves (Berger 2007). This behaviour was not observed in non-pregnant females – which as adults are unlikely to be predated by bears – or in areas without bears, indicating a strategic use of human infrastructure to reduce calf predation risk (Berger 2007). As anthropogenic landscape change alters resources and risks for species around the world (Maxwell et al. 2016), understanding species' response to these changes is vital to conservation efforts.

In western Canada, the Oil Sands Region (OSR) represents a prime example of extensive human-induced landscape change. Largescale disturbance has occurred in the wake of petroleum extraction, timber harvest, and transportation, influencing mammal abundance and spatial distribution (Pickell et al. 2013, Roberts et al. 2022, Barnas et al. 2024). Landscape disturbances in the OSR are typically categorized as polygonal features (e.g., oil well sites) and linear features (e.g., geo-survey "seismic" lines), which affect mammal species in different ways (Roberts et al. 2022). Depending on species-specific resource requirements, these novel features create "winner" species that generally benefit from disturbances, and "losers" which are negatively impacted (Fisher and Burton 2018). Numerous studies have investigated the responses of individual species, and mammal communities, to OSR disturbances, ultimately to inform industrial activities and restoration efforts (Fisher and Burton 2018, Beirne et al. 2021, Wittische et al. 2021). Although clear and consistent patterns have emerged for some species, such as the use of linear features by canids (Dickie et al. 2017, Clarke et al. 2025), there is still uncertainty regarding the responses of other community members, especially the large, omnivorous black bear (*Ursus americanus*).

Current knowledge of black bear habitat selection in relation to linear and polygonal disturbances in the OSR is inconsistent. Studies have reported positive (Mosnier et al. 2008, Bayne 2011, Latham et al. 2011b, Tigner et al. 2014, Demars and Boutin 2018, Dickie et al. 2020), negative (Fisher and Burton 2018, Fisher and Ladle 2022, Curveira-Santos et al. 2024), and negligible (Beirne et al. 2021) associations between black bears and disturbance features. Ultimately, this lack of consensus signifies that overall, black bear preference and use of these features is uncertain, making it difficult to draw informative conclusions for management actions. Studies on black bear habitat selection in the OSR have largely considered feature response over the entire active season (i.e., the non-hibernation period) and without demographic discernment (with the exception of select telemetry work, e.g. Latham et al. (2011b)). 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 response could have been previously overlooked, warranting a finer scale investigation into potential mechanisms (i.e., risks and rewards) that dictate both feature attraction and avoidance.

Several factors may mediate black bear attraction to linear and polygonal features. First, both feature types provide forage subsidies throughout the active season. Black bears are opportunistic omnivores that primarily consume vegetation and select the most nutrient-rich foods available (Pelchat and Ruff 1986). In the western boreal, the plant component of their diet follows a seasonal progression- from green vegetation after hibernation, to early-ripening berries by mid-July, and late-ripening berries by mid-August until denning (Pelchat and Ruff 1986). Similar patterns have been reported across the boreal forest (Raine and Kansas 1990, Mosnier et al. 2008, Romain et al. 2013, Lesmerises et al. 2015). Many of these plant species are abundant in early seral communities typical of linear and polygonal features (Fisher and Wilkinson 2005, Dabros et al. 2018, Sutheimer and Nielsen 2025). These features often green-up earlier in spring than surrounding forest due to greater solar exposure, offering early-season nutritional advantages (Mosnier et al. 2008). Berry-producing species also tend to thrive on these disturbances, showing greater vigor and fruit production on seismic lines and in open canopies than in mature forest (Dawe et al. 2017, Nielsen et al. 2020).

Second, linear features can provide movement subsidies for black bears. Seismic lines facilitate travel between vegetation patches and can enhance prey search efficiency (Bastille-Rousseau et al. 2011, Dickie et al. 2020, Tattersall et al. 2023) for species such as snowshoe hare (*Lepus americanus*) and neonates of ungulates including white-tailed deer, caribou (*Rangifer tarandus caribou*), and moose (Latham et al. 2011b, Lesmerises et al. 2015). These movement benefits may be especially important in spring when there are newborn fawns and calves, and vegetation is scarce and nutrient-poor, necessitating greater movement between patches (Young and Ruff 1982).

Although disturbance features offer forage and movement subsidies throughout the active season, black bear use of these features may be mediated by trade-offs with associated risks. One risk is human hunting activity, which is the primary source of black bear mortality in the OSR (Alberta Government 2016). During the spring and fall hunting seasons, black bears may avoid linear features that are used as hunter access routes (Dabros et al. 2018) and polygonal features where they are more visible. Empirical evidence supports this behavioural shift in response to hunting pressure. Stillfried et al. (2015) found that black bears increased avoidance of non-paved roads – commonly used by hunters – during the hunting season relative to the non-hunting season. Similarly, Ordiz et al. (2012) observed that bears altered their behaviour and movement patterns during hunting seasons, providing evidence that they are aware of hunting risk.

Risk associated with disturbance features may also vary among demographic groups and drive behavioural differences. For females with dependent young, another risk influencing habitat selection is infanticide by other adult black bears. Infanticide can be a major source of cub mortality in bear populations, and females with young may select suboptimal habitats to minimize encounters with other bears (Ben-David et al. 2004, Gantchoff et al. 2019). If solitary adult bears use disturbance features for foraging and travel, females with young may avoid these areas despite their benefits. If this pattern exists, it is also possible that it reverses temporally if solitary adult bears avoid disturbance features during the spring and fall hunting seasons. 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 largely unaffected during hunting seasons, in contrast to solitary adult bears. In addition, Stillfried et al. (2015) reported that female black bears selected habitat much closer to unpaved roads during the hunting season compared to males. This pattern was interpreted as a potential use of hunter activity as a "human shield" against infanticide risk (Stillfried et al. 2015). A similar phenomenon may occur with disturbance features in the OSR.

Our objective was to evaluate competing hypotheses about black bear habitat selection in relation to OSR disturbance features, and to determine the relative importance of disturbance features in driving habitat selection compared to other ecological factors, such as prey abundance and natural landcover. We hypothesized that (1) black bear use of disturbance features varies seasonally with changing resource and risk dynamics, and (2) use differs between demographic groups due to distinct primary risks – hunting for solitary adults and infanticide for females with young. We predicted that solitary adults would avoid both linear and polygonal disturbance features during the spring and fall hunting seasons but would increase use in summer to exploit forage and movement benefits. Conversely, we predicted that females with young would exhibit the opposite pattern – being attracted to linear and polygonal features during the hunting seasons to benefit from subsidies and the "shield" against infanticide risk but avoiding features in summer due to increased presence of solitary adult bears.

2.3 Methods

2.3.1 Study area

Our study was situated in the boreal forest of northeastern Alberta, Canada. This region is characterized by a mosaic of upland forests dominated by jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*), interspersed with lowland muskegs of larch (*Larix laricina*) and black spruce (*Picea mariana*) (Pickell et al. 2013). The boreal landscape is naturally dynamic, presenting as a patchwork of stands at varying successional stages driven by recurring disturbances such as wildfire and insect outbreaks (Pickell et al. 2013). Beneath this landscape lies one of the world's largest hydrocarbon deposits, which led to the development of the OSR (Alberta Government 2023). The OSR encompasses approximately 142,200 km^2 (Alberta Government 2023) and has undergone extensive industrial development resulting in widespread landscape change without global or historic analogues (Pickell et al. 2016). Surface mining of bitumen occurs over roughly 3.4% of the OSR (Alberta Government 2023), while in situ extraction predominates elsewhere, creating dense networks of anthropogenic disturbance features such as roads, seismic lines, pipelines, and well pads (Bayne 2021).

2.3.2 Camera trap arrays

We investigated black bear-habitat relationships using detection data from remote camera traps (O'Connell et al. 2011, Burton et al. 2015). Cameras were deployed across six study landscapes ("landscape units," LUs) within the OSR (Figure 1) as part of the Oil Sands Monitoring Program (Bayne 2021). LUs were delineated using watershed boundaries and selected by stratifying watersheds according to disturbance magnitude, followed by random selection from each stratum (Bayne 2021). The sampled LUs each encompassed approximately 1500 km^2 and spanned a gradient of anthropogenic disturbance intensity (Bayne 2021).

Camera deployment locations (i.e., "sites") were selected using a stratified random design. Within each LU, dominant forest classes (>50% composition: conifer, deciduous, or mixed-wood) were used as strata to account for natural variation in sampling locations. A 2-km^2 hexagonal grid was overlaid in ArcGIS Desktop (ESRI 2014), with grid cell size selected to ensure adequate spacing between cameras for spatial independence (Zuckerberg et al. 2020). Thirty grid cells were randomly chosen from each forest class, yielding 60 potential sampling sites per LU. To facilitate site access, grid cells were constrained to within 100 m of accessible roads, when possible, except in LU21 where all sites were accessed by helicopter (Figure 1).

Between 40 and 50 Reconyx PC900 Hyperfire infrared remote digital cameras (Holmen, WI) were deployed per LU, one per grid cell. These cameras were heat-in-motion triggered and have previously shown to provide high detection probabilities for bears (Fisher et al. 2014). Cameras were positioned approximately 1 m above ground, ≥100 m from active roads, and ≥1 km from other cameras. To enhance detection probability, cameras were placed along active game trails (Fisher and Burton 2018), and scent lure (O'Gorman's™ Long Distance Call, Broadus, MT, USA) was applied to a tree 4-7 m in front of each unit (Fisher and Bradbury 2014). Cameras were set to high sensitivity, capturing a single image per trigger with no delay, and took one daily 'timelapse' image to confirm functionality.

A total of 233 cameras were deployed across the six LUs sampled between 2021 and 2023. In 2021, 78 cameras were deployed across LU2 and LU3 in July and retrieved in either February or September 2022 due to logistical constraints (Figure 15). In 2022, 155 cameras were deployed across LU13, LU21, LU15, and LU1 in September-October, and retrieved in

September-October 2023 (Figure 15). Once collected, images were manually classified by trained reviewers using *Timelapse Image Analyzer 2.0* (Greenberg et al. 2019) to identify species and demographic characteristics.

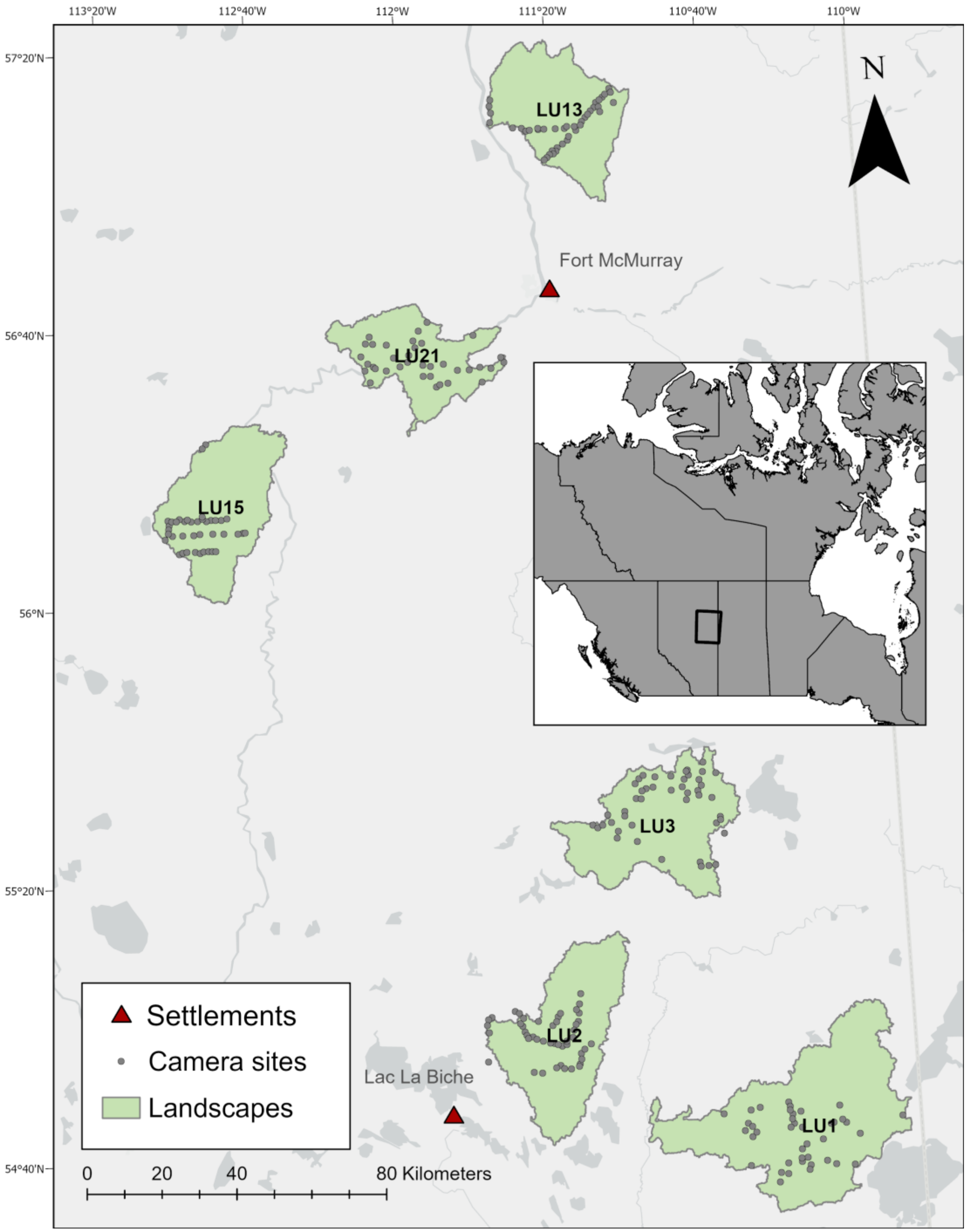

Figure 1. The six landscape units (LUs) surveyed (green polygons) and camera site locations (grey dots). The inset map indicates the extent of the Oil Sands Region in Alberta, Canada. Number of camera sites per LU were: LU13: n = 41, LU21: n = 36, LU15: n = 39, LU3: n = 36, LU2: n = 42, LU1: n = 39.

2.3.3 Black bear demographic data

We analyzed relationships between black bears and anthropogenic features separately for two demographic groups – (1) females with young and (2) solitary adults – within three seasons of the active period. We used the raw Timelapse images to identify independent detection events, defined as black bear detections separated by >30 min. For each event, we recorded demographic information as young-of-year (Figure 2A), yearling (Figure 2B) or adult (Figure 2C).

We sought to avoid false cub absences due to our image classifying process, which could arise if demographic labels were assigned based on a single image or 'episode' (i.e., images captured <1 min apart) within the 30-min window defining independent detections. For instance, a female may be photographed alone initially and misclassified as a solitary adult, even if cubs appear in subsequent images within the same detection period. To address this, we determined the maximum 'group count' for each age class within an independent detection event and used these values to define demographic groupings. Events in which cubs or dependent yearlings were present were classified as "females with young," while events containing at least one adult but no cubs or yearlings were classified as "solitary adults." With this protocol we assumed detection histories reflected true zeros, rather than potential false absences as assumed in occupancy models (MacKenzie et al. 2002), as our focus was on occurrence frequency through time rather than simple presence-absence.

We then constructed a proportional binomial response variable, occurrence frequency, representing the proportion of 15-day sampling intervals ("occasion periods") during which a demographic group was detected. In other words, within each season, we summed the number of occasion periods with at least one detection (1) and divided by the total number of valid occasion periods (those with ≥ 6 active camera days, ~50 % of the interval). This yielded a continuous measure from 0 to 1 describing how frequently each group was detected within a season, rather than a binary measure of occurrence. Seasons were defined approximately according to hunting periods: spring (1 Apr – 14 Jun), summer (15 Jun – 28 Aug), and fall (29 Aug – 11 Nov). These divisions also align with major changes in food resource availability, such as berry phenology.

Due to variability in deployment schedules, not all cameras operated across every season (besides fall), resulting in a different number of useable sites: spring = 188 sites, summer = 231, fall = 233 (Figure 15). Winter was excluded because black bears hibernate during this period.

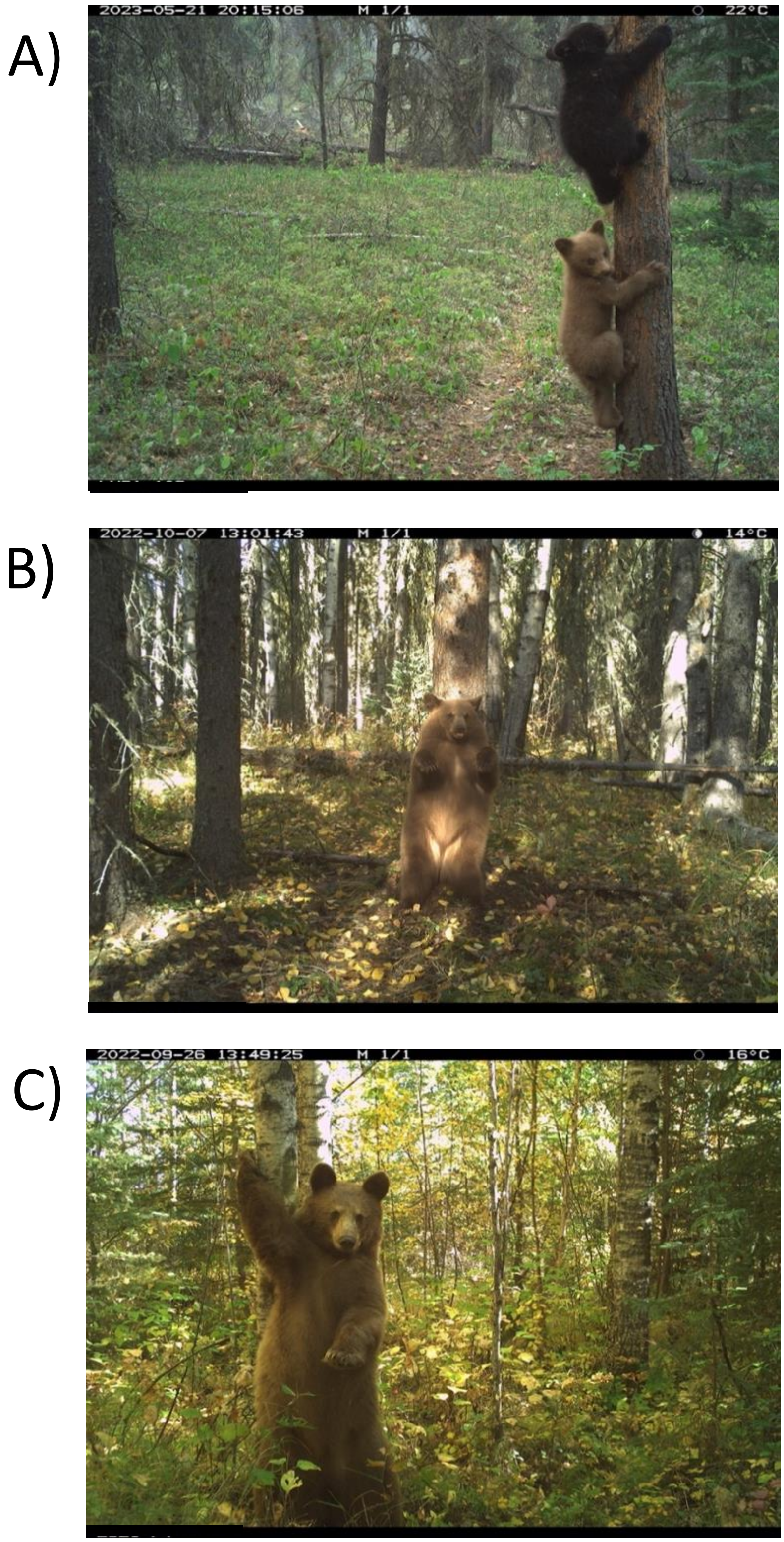

Figure 2. Camera images of different black bear demographics in the Oil Sands Region of western Canada. A) Cubs, B) Yearling, C) Adult.

2.3.4 Predictor variables

We examined four categories of predictors hypothesized to influence black bear habitat selection: 1) relative abundance of prey species, 2) proportion of polygonal disturbance features, 3) proportion of linear disturbance features, and 4) proportion of natural landcover (Table 1).

Prey relative abundance was estimated as the total number of independent detections for three species – snowshoe hare, moose, and white-tailed deer – at each site per season. We did not consider other potential prey species (ex. caribou) due to insufficient detections.

Anthropogenic landcover data were obtained from the Alberta Biodiversity Monitoring Institute's (ABMI) *Human Footprint Inventory* (Alberta Biodiversity Monitoring Institute 2021). For linear features, we included roads (combining paved and unpaved roads into a single variable), conventional seismic lines, 3D seismic lines, pipelines, transmission lines, and trails; for polygonal features we considered well pads and forest cutblocks. Natural landcover data on the distribution of shrubland, grassland, deciduous forest, coniferous forest, and mixed-wood forest were extracted from ABMI's *Wall-to-Wall Land Cover Map* (Alberta Biodiversity Monitoring Institute 2010). To account for scale dependence in habitat selection (Holland et al. 2004, Holland and Yang 2016), we calculated the proportion of each disturbance feature and landcover type within concentric circular buffers (250 m – 5,000 m radii, increasing by 250 m) around each camera, following Fisher et al. (2011).

Table 1. Descriptions of predictor variables used in the generalized linear mixed models (GLMMs) to predict black bear occurrence in the Oil Sands Region of western Canada. Landscape variables were grouped into three categories: anthropogenic linear features, anthropogenic polygonal features, and natural landcover types. Descriptions were derived from the metadata of their respective sources. Animal species occurrence data were collected using camera traps deployed in the study area.

Category	**Variable**	**Description**	**Source**
Anthropogenic linear features	Roads	Non-vegetated, impermeable surfaces used for motorized vehicle or aircraft transportation or access	ABMI Wall-to-Wall Human Footprint Inventory (2021)
	Conventional seismic lines	Cleared corridors created during hydrocarbon exploration 6 m wide	
	3D seismic lines	Cleared corridors created during hydrocarbon exploration 3 m wide	
	Pipelines	A line of underground and overground pipes, of substantial length and capacity, used to convey petrochemicals. The physical clearing contains underground and above-ground high-pressure pipelines	
	Transmission lines	Cleared corridors designated for the location of power transmission line infrastructure	
	Trails	Cleared corridors created during hydrocarbon exploration 4 m wide	
Anthropogenic polygonal features	Wells	Ground cleared for an oil/gas well pad (active/inactive)	ABMI Wall-to-Wall Human Footprint Inventory (2021)
	Cutblocks	Areas where forestry operations have occurred (clear-cut, selective harvest, salvage logging, etc.)	
Natural landcover	Deciduous forest	Treed areas with at least a 10% crown closure of trees, where broadleaf trees are 75% or more of the crown closure	ABMI Wall-to-Wall Landcover Map (2010)
	Conifer forest	Treed areas with at least a 10% crown closure of trees, where conifer trees are 75% or more of the crown closure	
	Mixed-wood forest	Treed areas with at least a 10% crown closure of trees, where neither conifer nor broadleaf trees account for >75% of the crown closure	
	Grassland	Predominately native grasses and other herbaceous vegetation with a minimum of 20% ground cover	

	Shrubland	At least 20% ground cover which is at least one-third shrub, with no or little presence of trees (<10% crown closure)	
Prey species	Moose White-tailed deer Snowshoe hare	Detections from deployed cameras	Camera arrays

2.3.5 Assessing correlation of predictors

At each spatial scale, we assessed collinearity using Pearson's correlation coefficient (Figure 16) and ensured that all pairwise combinations had $|r| < 0.7$ (Zuur et al. 2010). Correlations between roads and well pads exceeded this threshold beyond the 1500 m scale, so we limited analyses to the six smallest scales (≤ 1500 m) as both variables were key to our study objectives and could not be removed. Coniferous forest was removed due to collinearity with deciduous forest, reflecting the typical mutual exclusivity of these forest types in the study region. Pipelines and transmission lines were also highly collinear, so we combined these features into a single variable at all spatial scales since they share similar structure and ecological function.

2.3.6 Identifying best spatial scale

To identify the optimal spatial scale for modeling black bear habitat selection, we fit global generalized linear mixed models (GLMMs) at each spatial scale for each demographic group. For solitary adults, occurrence frequency was modelled with a binomial distribution and a logit-link function, including LU ID as a random effect:

$$\eta_{ij} = \beta_0 + \beta_1\text{Roads}_{ij} + \beta_2\text{Seismic}_{ij} + \beta_3\text{3DSeismic}_{ij} + \beta_4\text{Pipeline/Transmission}_{ij} + \beta_5\text{Trails}_{ij} + \beta_6\text{Cutblocks}_{ij} + \beta_7\text{Wells}_{ij} + \beta_8\text{Broadleaf}_{ij} + \beta_9\text{Mixed-wood}_{ij} + \beta_{10}\text{Grassland}_{ij} + \beta_{11}\text{Shrubland}_{ij} + \beta_{12}\text{White-tailed deer}_{ij} + \beta_{13}\text{Snowshoe hare}_{ij} + \beta_{14}\text{Moose}_{ij} + \text{LU}_j$$

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

$$\text{Solitary Adult Occurrence Frequency}_{\text{ij}} \sim \text{Bernoulli}(\theta_{ij})$$

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

where solitary adult occurrence frequency represents the i^{th} observation within LU j, and LU ID serves as a random intercept. Models were compared across spatial scales using AICc, evaluated both across all seasons combined and within individual seasons. In each case, the 250 m radius buffer yielded the lowest AICc (ΔAICc ≥ 2; Table 7) and was selected for all subsequent analyses. For females with young, an identical global model was evaluated across spatial scales but only at the combined-season level due to limited detections within individual seasons. The 250 m radius buffer was again best supported (Table 7). At this scale, we also examined the distributions of final predictor variables retained for modelling using histograms (Figure 17, 18).

2.3.7 Candidate model set

To evaluate which predictors best explained black bear occurrence frequency by season and demographic group, we developed a candidate set of GLMMs with a binomial distribution and logit-link function (Table 2). Each model represented a hypothesis about the influence of one or more predictor categories – linear disturbance features, polygonal disturbance features, natural landcover, and prey abundance – on occurrence frequency. For linear features, we included a model for total linear disturbance as well as separate models for roads and for off-highway vehicle (OHV)-accessible features (i.e., conventional seismic lines, 3D seismic lines, pipelines/transmission lines, and trails) to account for differences in disturbance type and vegetation structure. For natural landcover, we developed a “forest model” (deciduous and mixed-wood forest), an “open habitat model” (grassland and shrubland), and a model combining all natural landcover types. Polygonal disturbances (well pads and cutblocks) were included in a single model, and a prey model incorporated total detections of white-tailed deer, moose, and snowshoe hare. We also constructed combination models integrating multiple predictor categories, for example a "total anthropogenic disturbance" model (combining linear and polygonal features), as well as global and null models. All predictor variables were z-standardized (mean = 0, sd. = 1) using the 'scale' function in R to ensure ß estimate comparability.

For solitary adults, model selection was conducted by season and across all seasons combined for comparison. For females with young, limited detections necessitated analysis across the entire active season, with *Season* included as an interaction term (Table 3). This approach did not yield a top model for each season but allowed assessment of temporal variation in occurrence frequency. To evaluate seasonal effects, each interaction model was paired with a corresponding model lacking the interaction term, and we also included a model with *Season* as the sole predictor. The global model was excluded due to added complexity from interaction terms. To further reduce model complexity and high variance inflation, OHV-associated linear features were combined into a single covariate ("OHV linear features").

For each analysis, models were ranked in an information-theoretic framework using AICc to evaluate the strength of empirical support. Top models had the lowest AICc score by ΔAICc $\geq$ 2 barring uninformative parameters (Arnold 2010).

2.3.8 Random effect structure

For solitary adults, there was a single value of occurrence frequency per site in each seasonal analysis, and LU ID was included as a random effect to account for spatial variation in anthropogenic disturbance across the OSR. We evaluated the importance of this random effect by comparing AICc values of top models with and without it. In the summer and combined-season models, inclusion of LU improved model support (Table 8), indicating spatial heterogeneity in occurrence patterns. Although the top-ranked models for spring and fall excluded LU as a random effect, we retained it across all seasons to maintain consistency in model structure.

For females with young, the data were structured differently with three observations per site (one per season). To avoid pseudoreplication, we used a nested random effect structure with “site” nested within “LU.” AICc comparisons showed that this structure provided a better fit than models with only site or without random effects (Table 9).

2.3.9 Model validation

Top-ranked models were evaluated for fit using diagnostic plots generated in the *DHARMa* package (Figure 19, 20), and multicollinearity was evaluated using variance inflation factors (VIFs) from the *performance* package. All statistical analyses were conducted in R v. 4.4.1 (R Core Team 2024).

Table 2. Candidate generalized linear mixed models (GLMMs) used to predict the occurrence frequency of solitary adult black bears in the Oil Sands Region of western Canada. Models were developed within four thematic categories of predictor variables hypothesized to explain black bear occurrence frequency: anthropogenic polygonal features, anthropogenic linear features, natural landcover types, and prey species. Additional combination models integrated variables across thematic categories based on hypothesized ecological relationships. Models were evaluated separately within three seasons (spring, summer, fall) as well as across all seasons combined.

Category	**Occurrence best explained by:**	**Candidate model name**	**Predictor variables**
Polygonal features	Polygonal features	Polygonal	Cutblocks + wells
Linear features	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
Natural landcover	Forest	Forest	Deciduous forest + mixed forest
	Open natural habitat	Open natural	Grassland + shrubland
	All natural landcover	Open natural + Forest	Grassland + shrubland + deciduous forest + mixed forest
Prey species	Prey species	Prey	Moose + white-tailed deer + hare
Combination	Linear and polygonal features	Linear + Polygonal	Roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + cutblocks + wells
	Open foraging areas	Polygonal + Open natural	Cutblocks + wells + grassland + shrubland
	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 + cutblocks + wells
	Food sources without roads	Prey + OHV + Polygonal	Moose + white-tailed deer + hare + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + cutblocks + wells
Global	Global	Global	Moose + white-tailed deer + hare + roads + seismic lines + 3D seismic lines + pipelines and transmission lines + trails + cutblocks + wells + grassland + shrubland + deciduous forest + mixed forest
Null	Null	Null	1

Table 3. Candidate generalized linear mixed models (GLMMs) used to predict the occurrence frequency of female black bears with young in the Oil Sands Region of western Canada. Models were grouped into four thematic categories of predictor variables hypothesized to explain black bear occurrence frequency: anthropogenic polygonal features, anthropogenic linear features, natural landcover types, and prey species. To reduce model complexity, off-highway vehicle (OHV) linear features (comprising conventional seismic lines, 3D seismic lines, pipelines/transmission lines, and trails) were combined into a single variable. Each model was duplicated to include a version with season (spring, summer, and fall) as an interaction term, and a model with season as the sole predictor was also included. Additional combination models integrated variables across thematic categories based on hypothesized ecological relationships.

Category	Occurrence best explained by:	Candidate model name	Predictor variables
Polygonal features	Polygonal features	Polygonal	Cutblocks + wells
	Polygonal features with season interaction	Polygonal x Season	Cutblocks x season + wells x season
Linear features	Roads	Roads	Roads
	Roads with season interaction	Roads x Season	Roads x season
	Linear features used by OHVs	OHV	OHV linear features
	Linear features used by OHVs with season interaction	OHV x Season	OHV linear features x season
	All linear features (Roads + OHV)	Linear	Roads + OHV linear features
	All linear features (Roads + OHV) with season interaction	Linear x Season	Roads x season + OHV linear features x season
	Forest	Forest	Deciduous forest + mixed forest
	Forest with season interaction	Forest x Season	Deciduous forest x season + mixed forest x season

Natural landcover	Open natural habitat	Open natural	Grassland + shrubland
	Open natural habitat with season interaction	Open natural x Season	Grassland x season + shrubland x season
	All natural landcover	Open natural + Forest	Grassland + shrubland + deciduous forest + mixed forest
	All natural landcover with season interaction	Open natural x Season + Forest x Season	Grassland x season + shrubland x season + deciduous forest x season + mixed forest x season
Prey species	Prey species	Prey	Moose + white-tailed deer + hare
	Prey species with season interaction	Prey x Season	Moose x season + white-tailed deer x season + hare x season
Combination	Linear and polygonal features	Linear + Polygonal	Roads + OHV linear features + cutblocks + wells
	Linear and polygonal features with season interaction	Linear x Season + Polygonal x Season	Roads x season + OHV linear features x season + cutblocks x season + wells x season
	Open foraging areas	Polygonal + Open natural	Cutblocks + wells + grassland + shrubland
	Open foraging areas with season interaction	Polygonal x Season + Open natural x Season	Cutblocks x season + wells x season + grassland x season + shrubland x season
	Prey and linear features	Prey + Linear	Moose + white-tailed deer + hare + roads + OHV linear features
	Prey and linear features with season interaction	Prey x Season + Linear x Season	Moose x season + white-tailed deer x season + hare x season + roads x season + OHV linear features x season
	Prey and roads	Prey + Roads	Moose + white-tailed deer + hare + roads

	Prey and roads with season interaction	Prey x Season + Roads x Season	Moose x season + white-tailed deer x season + hare x season + roads x season
	Food sources (forage and prey)	Prey + Linear + Polygonal	Moose + white-tailed deer + hare + roads + OHV linear features + cutblocks + wells
	Food sources (forage and prey) with season interaction	Prey x Season + Linear x Season + Polygonal x Season	Moose x season + white-tailed deer x season + hare x season + roads x season + OHV linear features x season + cutblocks x season + wells x season
	Food sources without roads	Prey + OHV + Polygonal	Moose + white-tailed deer + hare + OHV linear features + cutblocks + wells
	Food sources without roads with season interaction	Prey x Season + OHV x Season + Polygonal x Season	Moose x season + white-tailed deer x season + hare x season + OHV linear features x season + cutblocks x season + wells x season
Season	Season	Season	Season
Null	Null	Null	1

2.4 Results

2.4.1 Black bear occurrence frequency

Across the six LUs, 46,306 black bear images were collected from 233 sites over a cumulative total of 82,027 camera trap days. Occurrence frequency, defined as the proportion of 15-day occasion periods with detections at each site, varied by season and demographic group (Figure 3). For solitary adults, mean (± standard deviation SD) occurrence frequency was 0.19 ± 0.23 in spring, 0.33 ± 0.28 in summer, and 0.17 ± 0.21 in fall. For females with young, mean occurrence frequencies were lower: 0.05 ± 0.13 in spring, 0.13 ± 0.20 in summer, and 0.04 ± 0.10 in fall.

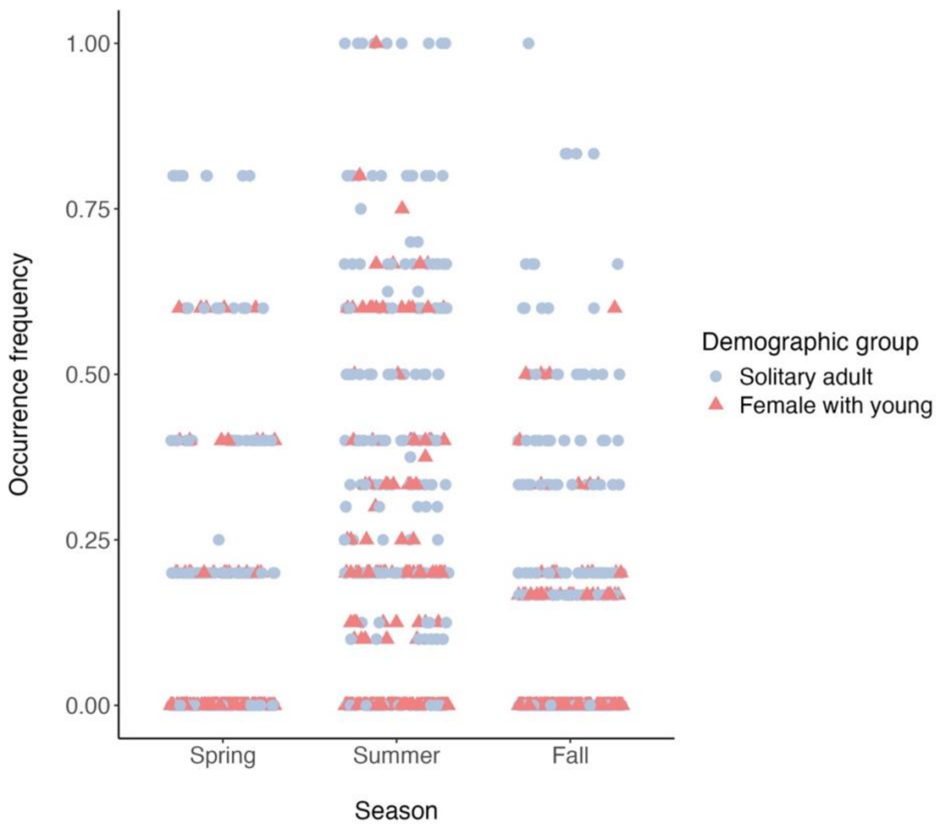

Figure 3. Seasonal black bear occurrence frequencies, measured as the proportion of 15-day sampling occasions with detections at each camera site (n = 233) in the Oil Sands Region of western Canada. Occurrence frequencies were calculated for two demographic groups: solitary adults and females with young.

2.4.2 Solitary adult habitat selection

2.4.2.1 Spring: Prey and roads best explained solitary adult occurrence frequency

In spring, the *Prey + Roads* model best explained solitary adult occurrence frequency (AICcw = 0.83; Table 4) and LU ID contributed little to model variation (SD < 0.01; Table 11). We report on covariates whose 95% confidence intervals did not overlap zero. Occurrence frequency declined strongly with increasing road proportion (β = -0.36, [CI: -0.55 – -0.17]; Figure 4), indicating lower predicted use of sites with greater road coverage (Figure 5). In contrast, occurrence frequency increased with prey relative abundance, most strongly for moose (β = 0.29, [95% CI: 0.15 – 0.44]; Figure 4), corresponding to higher predicted use of sites with greater moose detections (Figure 6). A weaker positive association was observed for white-tailed deer (β = 0.16, [CI: 0.01 – 0.32]; Figure 4). Complete parameter estimates for the *Prey + Roads* model, and for other top models described below, are provided in Table 12.

2.4.2.2 Summer: OHV-accessible linear features best explained solitary adult occurrence frequency

In summer, the *OHV* model received the strongest support (AICcw = 0.67; Table 4), and inclusion of LU ID as a random effect improved model fit (SD = 0.27; Table 11). The *Linear* model (Roads + OHV) was within 2 ΔAICc units of the top model; however *Roads* was an uninformative parameter (β = -0.04 [CI: -0.18 – 10]; Figure 5) and was not considered ecologically meaningful (Arnold 2010). As such, we did not consider the *Linear* model further. Within the top *OHV* model, occurrence frequency decreased with increasing proportions of 3D seismic lines (β = -0.17 [CI: -0.34 – -0.01]; Figure 4) and pipelines/transmission lines (β = -0.17

[CI: -0.34 – 0.00]; Figure 4), but increased with trail proportion (β = 0.17 [CI: 0.06 – 0.29]; Figure 4).

2.4.2.3 Fall: Prey and linear features best explained solitary adult occurrence frequency

In fall, the *Prey + Linear* model was best supported (AICcw = 0.43; Table 4), and inclusion of LU ID did not improve model fit (SD < 0.01; Table 11). The *Linear* model was within 2 ΔAICc units of the top model, indicating that, despite the parameter penalty, the addition of prey covariates increased explanatory power. Because the *Prey + Linear* model encompassed all covariates from both models, we report estimates from this model. Occurrence frequency declined strongly with increasing road proportion (β = -0.37 [CI: -0.55 – -0.19]; Figure 4), indicating lower predicted use of sites with greater road coverage and mirroring the pattern in spring (Figure 5). Occurrence frequency also decreased with increasing proportions of conventional seismic lines (β = -0.19 [CI: -0.35 – -0.03]; Figure 4) and pipelines/transmission lines (β = -0.30 [CI: -0.53 – -0.07]; Figure 4). Among prey covariates, occurrence frequency increased with higher snowshoe hare relative abundance (β = 0.14 [CI: 0.01 – 0.27]; Figure 4), whereas associations with moose and white-tailed deer were weak or negligible.

2.4.2.4 All seasons combined: Prey and linear features best explained solitary adult occurrence frequency

Model selection across all seasons combined was conducted to compare results with season-specific analyses. In this analysis, the *Prey + Linear* model was best supported (AICcw = 0.69; Table 4), and inclusion of LU ID improved model fit (SD = 0.19; Table 11). Occurrence frequency declined with increasing proportions of roads (β = -0.14 [CI: -0.25 – -0.04]; Figure 7), conventional seismic lines (β = -0.12 [CI: -0.21 – -0.03]; Figure 7), and 3D seismic lines (β = -0.17 [CI: -0.28 – -0.06]; Figure 7), but increased with trails (β = 0.09, [CI: 0.02 – 0.17]; Figure 7). Occurrence frequency also increased with higher relative abundance of moose (β = 0.15 [CI: 0.07 – 0.23]; Figure 7) and snowshoe hare (β = 0.08 [CI: 0.01 – 0.15]; Figure 7).

2.4.3 Female with young habitat selection

2.4.3.1 Linear features and season best explained female with young occurrence frequency

The *Linear x Season* model best explained occurrence frequency of females with young across the three seasons (AICcw = 0.77; Table 4). Inclusion of site ID improved model fit (SD = 1.16; Table 11), whereas inclusion of LU ID did not (SD = 0.00006; Table 11). Occurrence frequency decreased with increasing road proportion during the summer (reference; non-hunting) season (β = -0.66, [CI: -0.93 – -0.38]; Figure 8). Similar but weaker negative relationships were observed in spring (β = 0.37; P = 0.08) and fall (β = 0.24; P = 0.22). This pattern resulted in consistently lower predicted use of sites with greater road coverage across seasons (Figure 9). OHV-accessible linear features had negligible influence on occurrence frequency during summer (β = 0.07, [CI: -0.19 – 0.33]; Figure 8), but interaction terms signalled a negative association in fall (β = -0.67, [CI: -1.27 – -0.06]).

Table 4. Top generalized linear mixed models (within 2 ΔAICc) explaining solitary adult black bear occurrence frequency by season, and female black bear with young occurrence frequency across seasons, in the Oil Sands Region of western Canada. See Table 10 (Appendix A) for full rankings of all candidate models evaluated in each analysis. Reported metrics are model degrees of freedom (*df*), negative log-likelihood (*Log-Lik*), Akaike information criterion corrected for small sample size (*AICc*), difference *AICc* score from the top model (Δ*AICc*), and model weight (*AICc*w).

Demographic	Season	Top buffer radius (m)	Top models	df	log-lik	AICc	ΔAICc	AICcw
Solitary adult	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
	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
Female with young	All	250	Linear x Season	11	-483.19	988.78	0.00	0.77

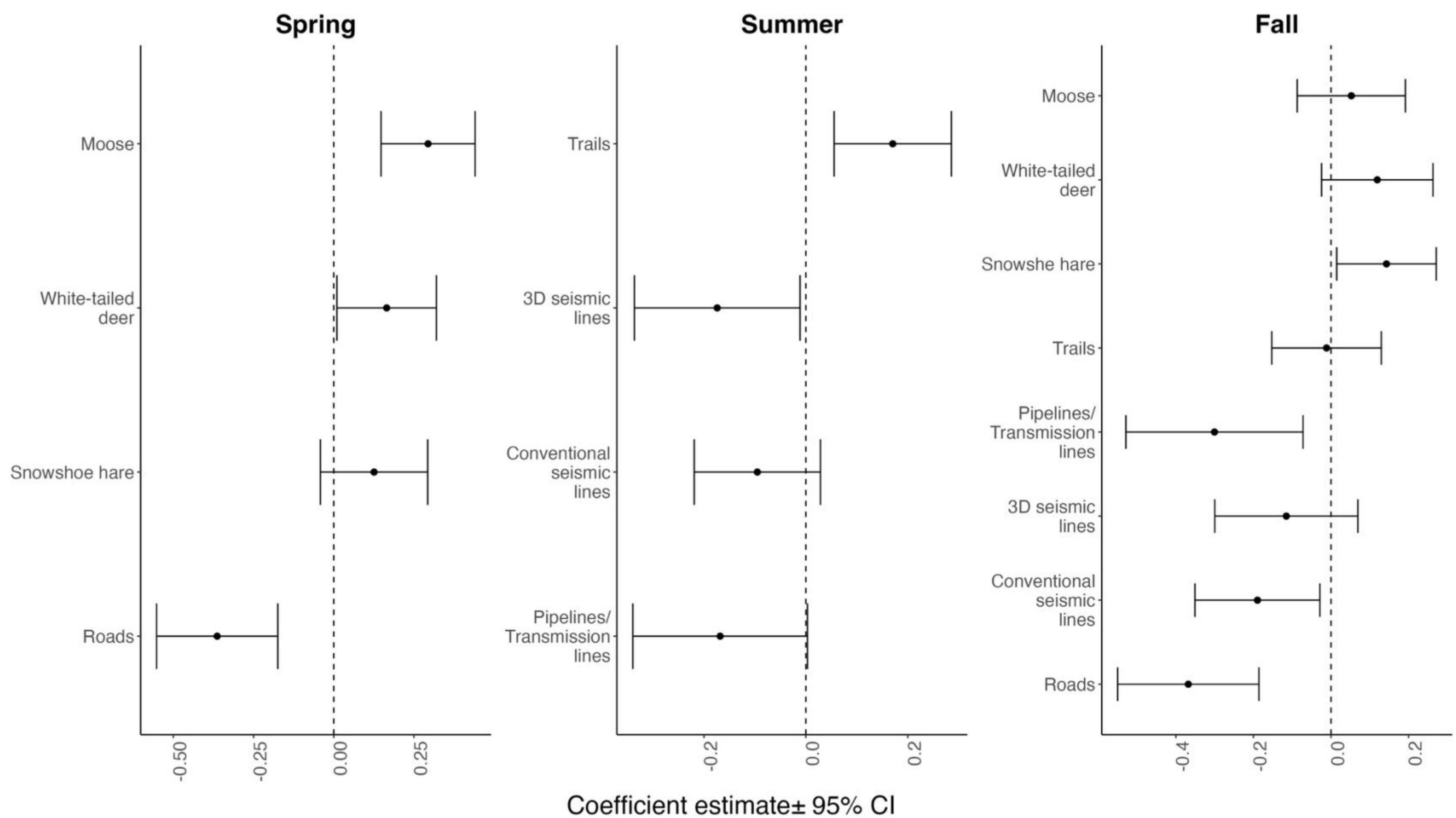

Figure 4. Beta coefficient estimates from the best supported generalized linear mixed models explaining solitary adult black bear occurrence frequency in the Oil Sands Region of western Canada for each season (spring: *Prey* + *Roads*; summer: *OHV*; fall: *Prey* + *Linear*). Coefficients < 0 indicate negative predictors of occurrence frequency, and coefficients > 0 indicate positive predictors. Error bars represent 95% confidence intervals.

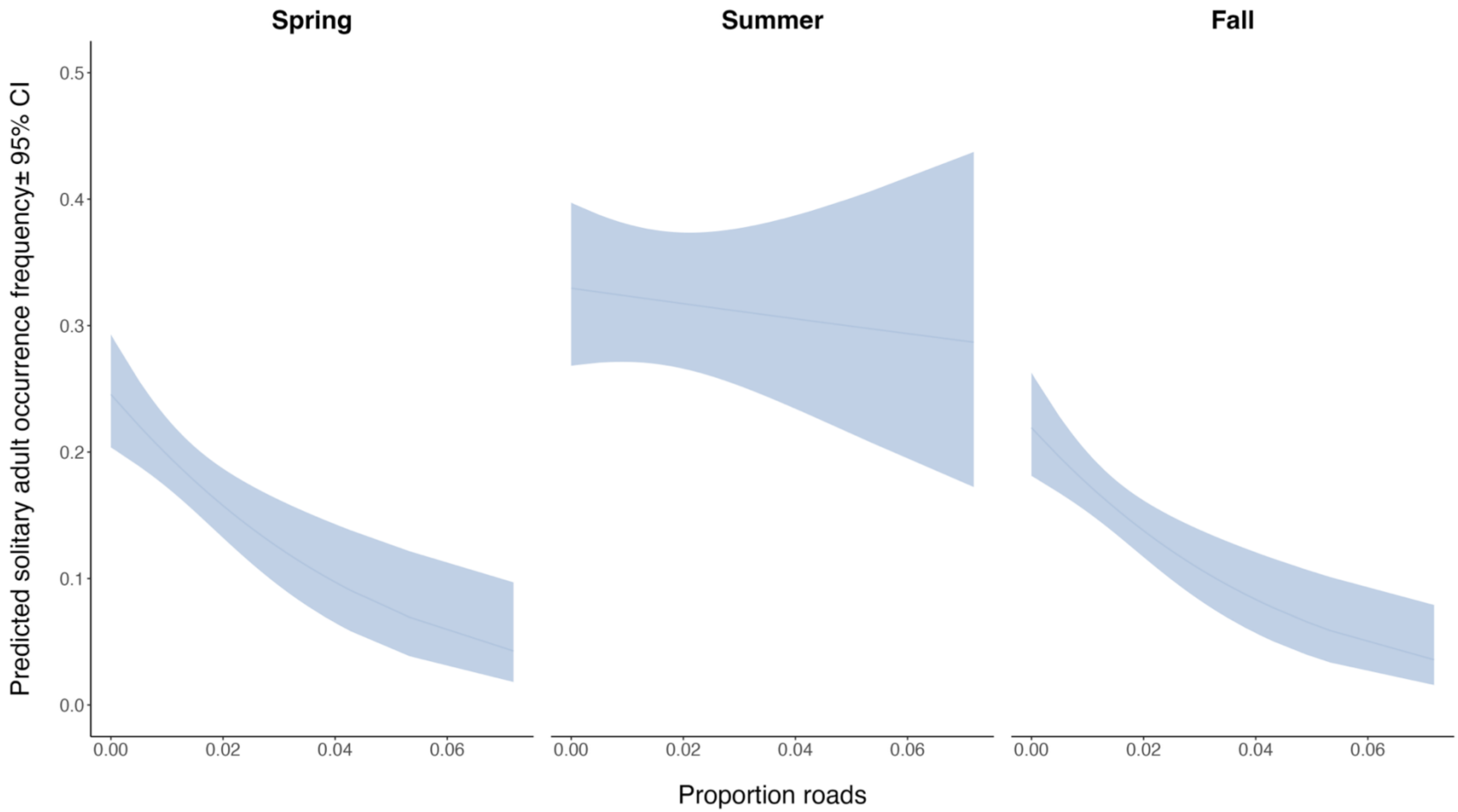

Figure 5. Predicted changes in occurrence frequency of solitary adult black bears in the Oil Sands Region of western Canada with increasing proportion of roads within a 250-m radius buffer around cameras sites, shown by season. Estimates were derived from the best-supported generalized linear mixed models: *Prey + Roads* in spring, *Prey + Linear* in fall, and the *Linear* model in summer, in which roads were an uninformative parameter with a negligible effect size. Shaded ribbons represent 95% confidence intervals. Predicted occurrence frequency decreases with increasing road proportion in spring and fall but remains relatively unaffected in the summer non-hunting season.

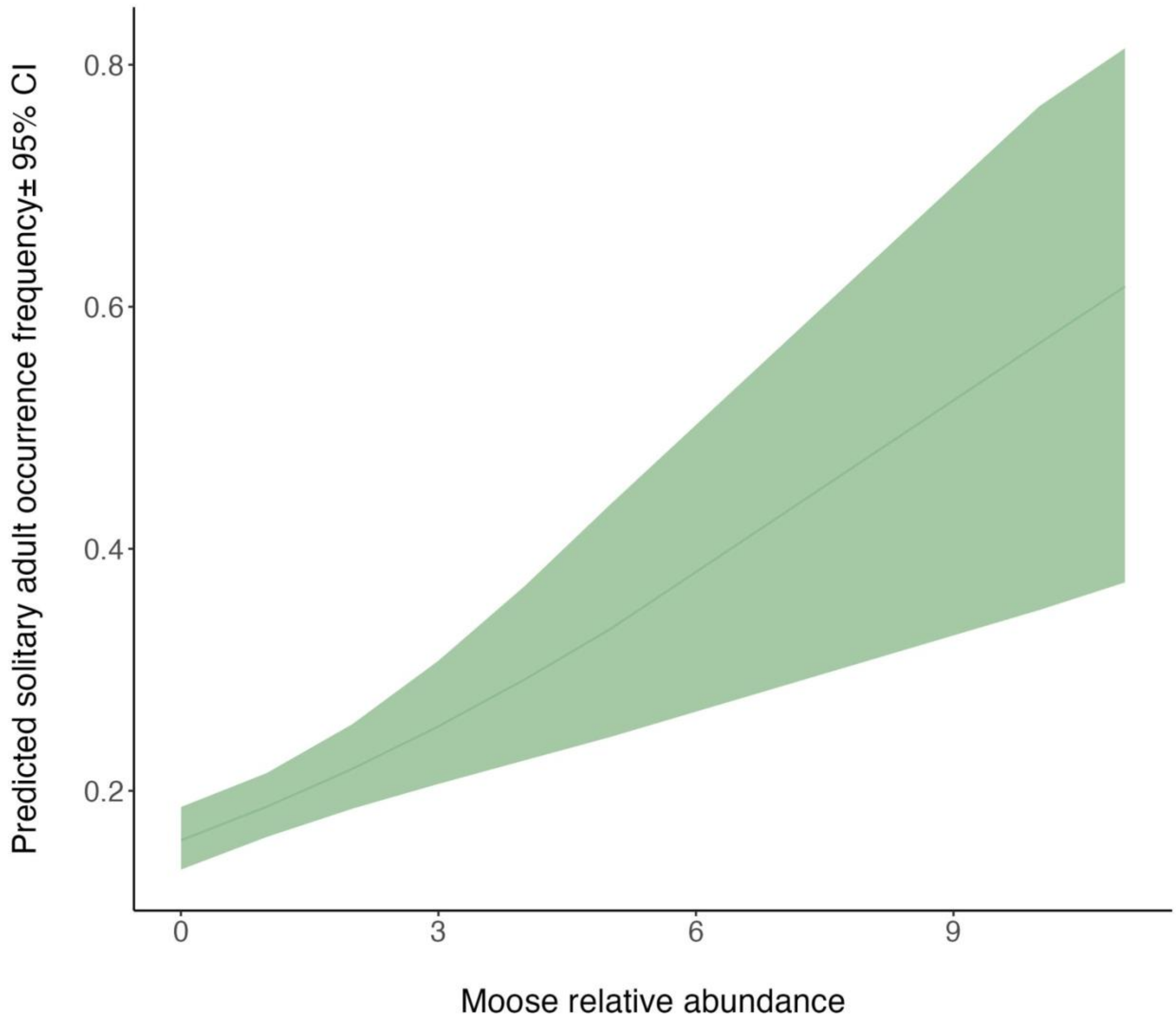

Figure 6. Predicted relationship between solitary adult black bear occurrence frequency and moose relative abundance in spring within the Oil Sands Region of western Canada, based on the *Prey + Roads* model (the best-supported generalized linear mixed model for spring). Predicted occurrence frequency increases with higher moose relative abundance. The shaded ribbon represents the 95% confidence interval.

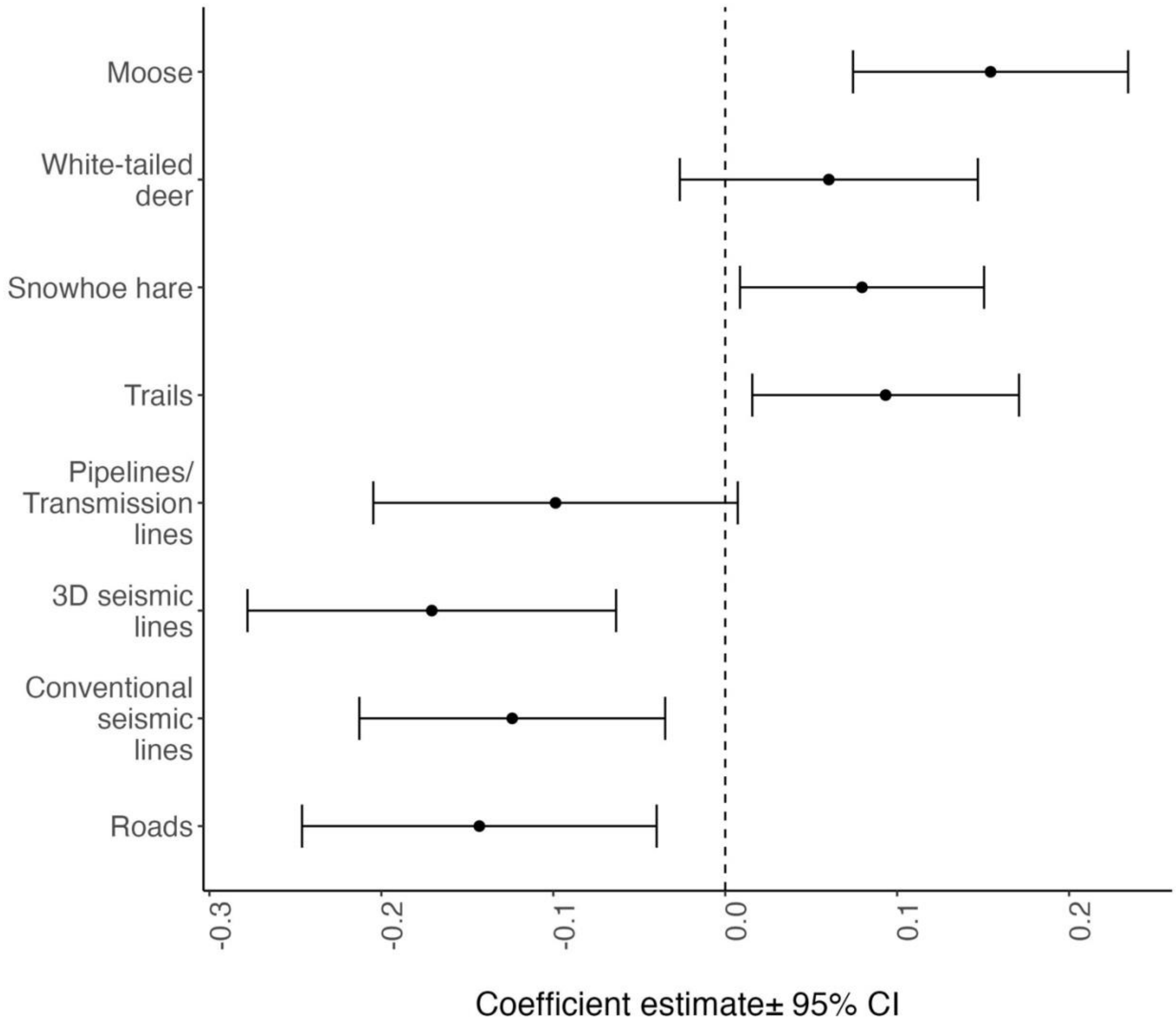

Figure 7. Beta coefficient estimates from the best supported generalized linear mixed model explaining solitary adult black bear occurrence frequency in the Oil Sands Region of western Canada across all seasons combined (*Prey + Linear*). Coefficients < 0 indicate negative predictors of occurrence frequency, and coefficients > 0 indicate positive predictors. Error bars represent 95% confidence intervals.

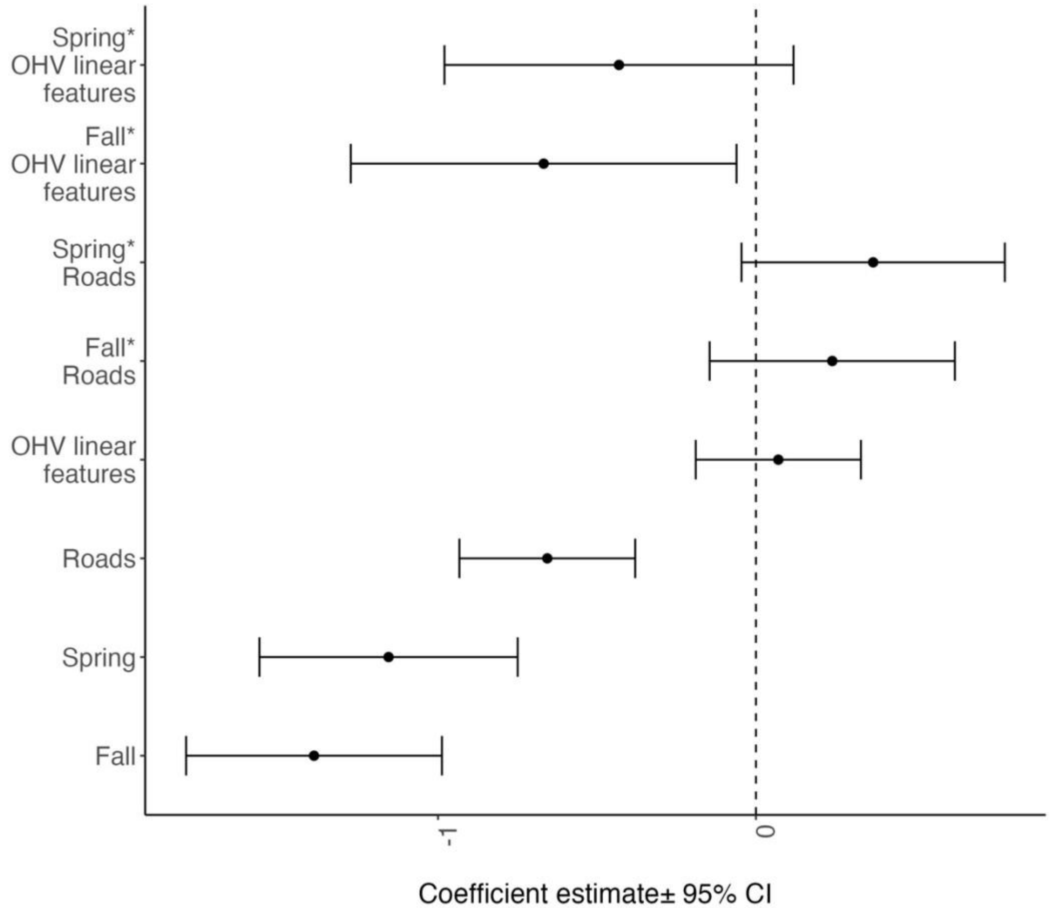

Figure 8. Beta coefficient estimates from the best-supported generalized linear mixed model (*Linear x Season*) explaining occurrence frequency of female black bears with young in the Oil Sands Region of western Canada. "Summer" was the reference season, representing the non-hunting period. Coefficients < 0 indicate negative predictors of occurrence frequency, and coefficients > 0 indicate positive predictors. Error bars represent 95% confidence intervals.

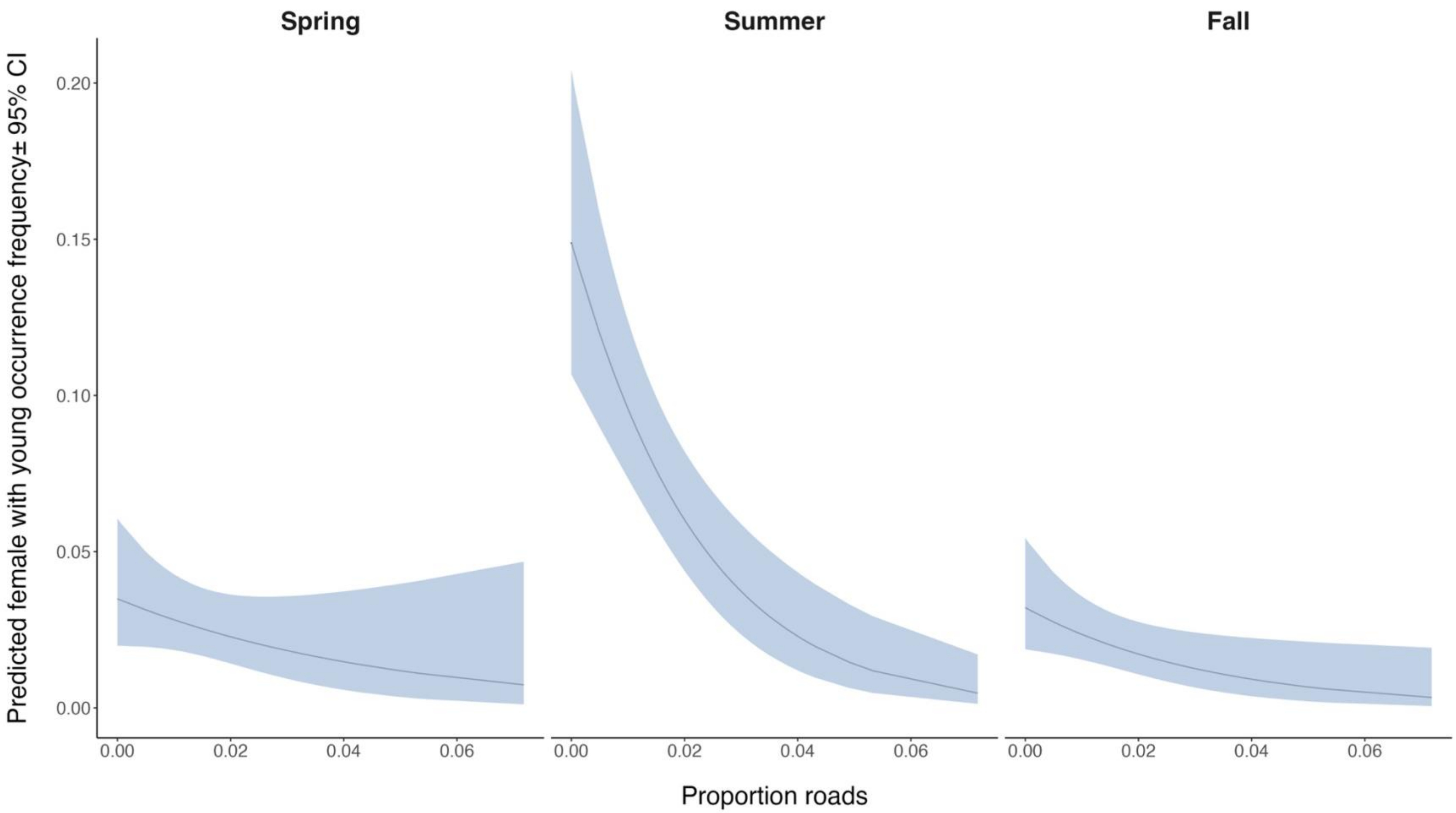

Figure 9. Predicted changes in occurrence frequency of female black bears with young in the Oil Sands Region of western Canada with increasing proportion of roads within a 250-m radius buffer around cameras sites, shown by season. Estimates were derived from the best-supported generalized linear mixed model (*Linear x Season*) explaining female black bear with young occurrence frequency. Predicted occurrence frequency decreases with increasing road proportion across seasons. The shaded ribbon represents the 95% confidence interval.

2.5 Discussion

Anthropogenic landscape change is pervasive worldwide, and the OSR of the western Canadian boreal forest is a particularly striking example (Pickell et al. 2016). Landscape alterations in this region are reshaping the spatial distribution and abundance of mammals (Roberts et al. 2022), underscoring the need to understand species-specific responses so that the underlying mechanisms can be addressed through management and restoration. We show that black bear responses to disturbance features varied by both season and demographic group, consistent with theoretical predictions of dynamic risk-reward trade-offs (Lima and Dill 1990). Linear features, particularly roads, exerted strong and generally negative effects on occurrence frequency for both demographic groups across seasons. However, solitary adults no longer exhibited this negative association in summer, supporting trade-off theory: roads present elevated anthropogenic mortality risk, especially during the hunting seasons, but also provide early seral forage opportunities. Prey availability further emerged as a positive driver of solitary adult occurrence frequency, particularly in spring and fall, reinforcing the role of energetic reward in habitat selection. Contrary to expectations, polygonal features did not have important influence on the occurrence frequency of either demographic group in any season.

2.5.1 Occurrence frequency of both demographic groups decreased with linear features

Occurrence frequency of both age-sex classes was strongly influenced by linear features across seasons. For solitary adults, roads and/or OHV-accessible linear features were consistently retained in the top model explaining occurrence frequency in every season, and the *Linear x Season* model best described patterns for females with young.

For solitary adults, seasonal associations with roads matched predictions: occurrence frequency declined with increasing road proportions during spring and fall but not in summer. Because roads serve as primary access routes for hunters during spring and fall hunting seasons, this pattern likely reflects a risk-avoidance response. These findings are consistent with Stillfried et al. (2015), who reported greater road avoidance by black bears during hunting periods, and with studies showing that bears recognize hunting threats and modify their behaviour to reduce encounters with hunters (Ordiz et al. 2012, Price et al. 2024).

Associations between solitary adults and other OHV-accessible linear features did not always mirror those observed for roads. In fall, solitary adults were negatively associated with conventional seismic lines and pipelines/transmission lines, consistent with predicted hunting risk aversion. Conversely, in spring, OHV linear features were not retained in the top model, suggesting minimal influence during this season. Given the high energetic demands and limited forage availability in spring, black bears may rely more on linear features as movement corridors or forage sources (Young and Ruff 1982), representing a situation where the need for energetic reward outweighs perceived risks (Holbrook and Schmitt 1988). Alternatively, reduced motorized access due to muddy conditions may lower associated disturbance. In summer, we predicted that solitary adults would be attracted to linear features for forage subsidies in the absence of hunting risk. Indeed, solitary adults were positively associated with trails; however, they were unexpectedly negatively associated 3D seismic lines and pipelines/transmission lines. This may reflect avoidance of other human disturbances, such as recreational vehicle activity, that offset potential foraging benefits. Differences in behavioural response may also arise from variation in fine-scale linear feature characteristics, such as forage composition or vegetation height (Sun et al. 2021, Tattersall et al. 2023), which were not captured in our analysis.

In partial support of our hypothesis, occurrence frequency of females with young decreased with increasing road proportions across all seasons. We infer that roads – characterized by consistent and high levels of human activity – are perceived as risky by mothers regardless of season. This negative association persisted despite potential benefits such as roadside forage or the hypothesized "human shield" effect, which could reduce infanticide risk when solitary adults are negatively associated with roads during hunting seasons. We suggest that females with young in these landscapes may not recognize the protection afforded to them from hunting, as previously proposed (Ordiz et al. 2012, Stillfried et al. 2015), and that perceived risk is heightened by the presence of cubs. It is important to note, however, that neither of these studies explicitly demonstrated hunting-related behavioural responses by female black bears with young. Ordiz et al. (2012) examined European brown bears with cubs, while Stillfried et al. (2015) found that female black bears occurred closer to roads during hunting seasons than males but were unable to distinguish females with cubs due to small sample size. Hunting may represent a particularly significant threat for females, as a recent review of black bear life-history traits found hunting to be the strongest predictor of adult female mortality, surpassing even food resource availability (Metthé et al. 2025).

Interestingly, females with young did not show the same consistent negative association with OHV-accessible linear features as they did with roads. They were negatively associated with these features in the fall (and spring, though the 95% confidence interval marginally overlapped zero) but not in summer. If avoidance of linear features reflects perceived human risk, this seasonal variation may correspond to differences in the type or intensity of disturbance: roads are used consistently across seasons, whereas OHV activity may be more sporadic or less disruptive in summer (e.g., no gunshots). As with solitary adults, fine-scale characteristics of linear features may also modulate these relationships (Sun et al. 2021, Tattersall et al. 2023).

2.5.2 Solitary adult occurrence frequency was seasonally influenced by prey

Solitary adults were more likely to occur at sites with higher relative abundance of white-tailed deer and moose in the spring, and snowshoe hare in the fall. In spring, when vegetation quality is low and berries are unavailable, animal prey may be a more important source of calories (Young and Ruff 1982, Zager and Beecham 2006). The positive association with moose relative abundance during this period aligns with well-documented predation on moose calves by black bears shortly after calving (Garneau et al. 2007, Bastille-Rousseau et al. 2011, Moore et al. 2024). In fall, the positive association with snowshoe hare relative abundance suggests that this species may also serve as an important dietary component later in the active season.

In contrast, females with young did not exhibit strong associations with prey abundance. Even in the best-supported model that included prey covariates (*Prey x Season + Linear x Season*) prey availability was unimportant for explaining occurrence frequency. This may indicate that females with dependent young, constrained by mobility or risk sensitivity, have reduced hunting efficiency and rely more heavily on other food resources.

2.5.3 Polygonal features did not best explain black bear occurrence frequency

Well pads and cutblocks did not strongly influence occurrence frequency of either demographic group and were not retained in any top models. For solitary adults, seasonal responses to these polygonal features were largely absent (Table 13), contrary to our prediction that individuals would avoid them during the hunting seasons due to increased exposure and use them for foraging in summer. The lack of positive associations in summer was unexpected, given that previous studies have documented the presence of shade-intolerant, berry-producing species in these areas (Brodeur et al. 2008, Nielsen et al. 2020), and reported black bear foraging activity within them (Brodeur et al. 2008, Mosnier et al. 2008, Lesmerises et al. 2015). Likewise, females with young showed no association with polygonal features in any season.

We propose several follow-up hypotheses for future research. First, polygonal features differ in human activity levels: active well pads are frequently serviced, whereas spent or dry wells are typically abandoned to natural succession. Black bears may preferentially use low-activity features, but this variation may have been obscured when all polygonal features were analyzed together. Second, the application of herbicides (e.g., glyphosate) to cutblocks as a common post-harvest management practice may reduce the availability and quality of forage for black bears, as has been suggested for moose (Carroll et al. 2024). Finally, natural habitats with abundant berry resources, such as open pine stands (Pelchat and Ruff 1986), may diminish the relative attractiveness of anthropogenic polygonal features as foraging sites.

2.5.4 Value of a seasonal modelling approach

When the full model set was analyzed across all seasons combined for solitary adults, the top model (*Prey + Linear*) masked important temporal variation. For instance, while the combined model indicated an overall negative association with roads, this relationship was absent in summer and stronger in spring and fall. Similarly, the positive association with moose relative abundance occurred only in spring rather than across the entire active period. These findings emphasize the value of a seasonal modelling approach for revealing biologically meaningful temporal patterns that would otherwise be obscured in aggregated analyses.

2.5.5 Caveats

Several technical caveats must be acknowledged. First, although we took care to avoid false cub absences in our image classifying procedure, misclassification could have occurred if cubs did not pass in front of the camera field of view during female detections. However, such an error would need to occur repeatedly during the primary sampling occasion (15 days) to alter model estimates, and even then, would only increase error (not entrain bias) unless this happened asymmetrically with some landscape feature variable.

Second, the low number of detections for females with young prevented season-specific modelling. Increased sample sizes would allow us to identify seasonal top models and increase the resolution of our findings.

Third, it is important to acknowledge that model selection using AIC is a predictive inference technique. As such, causal inference from estimated effects should be made with caution (Arif and MacNeil 2022).

Finally, our ability to infer hunting pressure was limited by the lack of spatially explicit hunter distribution data across the study area. Although annual provincial reports (Alberta Government 2024) summarize black bear harvest numbers by wildlife management unit (WMU), there is no finer-scale information on where hunters concentrate their efforts within each WMU. Consequently, our use of linear features as a proxy for hunting intensity was necessarily assumption-based rather than derived from direct observation. Because cameras were positioned to avoid human access routes, we also lacked direct measures of human activity. Future research could address these limitations by pairing camera traps with autonomous recording units (ARUs) to detect gunshots and OHV noise, thereby generating a “soundscape” (Shonfield and Bayne 2017, Hedley et al. 2022) for quantifying human disturbance.

There are also aspects of black bear behaviour that our study may not have captured. For example, diel variation in feature use could reveal avoidance strategies; in other systems, brown bears have shifted their activity to nocturnal hours following hunting onset (Ordiz et al. 2012). Although our analysis distinguished between demographic groups, it is likely that as habitat generalists, significant individual variation in behaviour influences habitat use (Latham et al. 2011b). Finally, while we consider infanticide as a potential risk influencing habitat selection, our study was not designed to directly assess behaviours associated with this risk, but rather to draw inferences about its role as a possible underlying driver of observed spatial patterns.

2.6 Conclusion

Black bear responses to anthropogenic disturbance features in the OSR varied across seasons and demographic groups, with linear features consistently emerging as key predictors of occurrence frequency. Some seasonal shifts in feature associations appeared linked to hunting activity, emphasizing the need to incorporate direct measures of human presence in future research. By clarifying how black bears navigate human-modified landscapes, this study advances not only our understanding of their spatial ecology but also provides broader insights into how wildlife respond to dynamic risk-reward trade-offs. Ultimately, these findings can inform more effective access management and restoration planning- benefitting not only black bears, but other at-risk species like woodland caribou.

Chapter 3: Structural equation modelling reveals causal inferences about moose (*Alces alces*) responses to industrial landscape change

3.1 Abstract

Anthropogenic landscape change affects wildlife both directly through habitat loss, and indirectly by altering interspecies interactions in ways that can propagate throughout ecosystems. Causal inference methodologies, such as structural equation modelling (SEM), offer a valuable framework for simultaneously evaluating direct and indirect effects within networks of pathways linking landscape features and species. We used a piecewise SEM to investigate potential top-down and bottom-up drivers of moose population declines in the highly disturbed Oil Sands Region (OSR) of western Canada. Guided by prior knowledge, we developed a causal model linking natural habitat, disturbance features, predator species and moose, which we tested using species occurrence data derived from 430 camera traps deployed across ten landscapes in the OSR. The model showed good fit to the data, supporting the inclusion of our hypothesized pathways. We found a strong negative effect of roads on moose occurrence, which outweighed the positive effects of other potential forage-subsidizing features such as 3D seismic lines, suggesting an overall net-negative impact of industrial disturbance. Moose were more likely to occur in areas dominated by deciduous forest and wetlands, highlighting the importance of maintaining these habitats to support populations. Wolves were more likely to occur in areas with higher moose detections, likely reflecting successful prey tracking behaviour, and their spatial associations with landscape features were influenced by moose presence. Future research should integrate complementary data sources to enable stronger inference on the reverse causal pathway (predator to prey), allowing identification of indirect effects of landscape features on moose mediated by wolves. Overall, SEM provides a flexible and powerful tool for ecological

inference, and we recommend its broader application as a mechanism-oriented alternative to traditional predictive modelling in ecological studies.

3.2 Introduction

Humans have profoundly transformed terrestrial environments, with at least three-quarters of Earth's ice-free land now impacted by anthropogenic landscape change (Ellis and Navin 2008). Widespread and rapidly expanding landscape modification is having adverse implications for wildlife, driving global biodiversity loss (Maxwell et al. 2016). Mammal species have been particularly affected, with observed population declines (Crooks 2002, Johnson et al. 2017) and behavioural changes in response to disturbance (Beirne et al. 2024). In addition to direct effects of disturbance, species-specific responses also impact the larger mammal community through interspecies interactions, resulting in complex indirect effects that may propagate throughout the system (Fisher and Ladle 2022).

Quantifying mammalian responses to anthropogenic landscape change typically relies on observational data, such as those derived from camera traps or GPS collars (Trolliet et al. 2014, Burton et al. 2015, Solène et al. 2020). Following data collection, statistical inference techniques are applied to estimate ecological relationships. Predominantly, predictive inference methodologies are employed (Arif and MacNeil 2022), often using multiple regression models ranked using model selection procedures (Burnham and Anderson 2002) based on information theory (Akaike 1973). Here, the top-ranked model from a candidate set is assumed to best explain relationships between predictor and response variables, and estimated ß coefficients are used to predict, for example, species responses to specific disturbances. While predictive methods are valuable and widely implemented, they are, however, not explicitly designed to address causal questions (Arif and MacNeil 2022). Causal inference methodologies offer an alternate approach that has yet to be widely adopted in the field of ecology and are specifically developed to better isolate and evaluate causal relationships (Arif and MacNeil 2023). One analytical tool seeing increased use is structural equation modelling (SEM), which integrates extensive prior knowledge of an ecological system to construct hypothesized causal pathways between predictors and responses (Lefcheck and Freckleton 2016). SEMs enable simultaneous evaluation of individual pathways and the overall fit of the causal network (Lefcheck and Freckleton 2016). A key advantage of SEMs is the capacity to treat variables as both predictors and responses, allowing for the evaluation of indirect effects in addition to direct effects (Lefcheck and Freckleton 2016), for example how an anthropogenic landscape change may affect a species through its impact on another species (Curveira-Santos et al. 2024). However, SEMs are data-intensive and thus benefit from large sample sizes, which have historically been rare for mammalian studies.

The Oil Sands Region (OSR) of western Canada represents a prime example of extensive human-induced landscape change. Spanning over 100,000's of km^2, landscapes in the OSR have been profoundly altered by forestry and petroleum extraction industries, resulting in fragmentation of natural forests by disturbance features such as cutblocks, well pads, roads, exploration "seismic" lines, and pipelines (Pickell et al. 2016). Caught amid these disturbances is a diverse mammal community, including black bear (*Ursus americanus*), moose (*Alces alces*), caribou (*Rangifer tarandus caribou*), grey wolf (*Canis lupus*), snowshoe hare (*Lepus americanus*), lynx (*Lynx canadensis*), and coyote (*Canis latrans*). The effects of landscape change on these species has been the target of abundant research efforts (Beirne et al. 2021, Wittische et al. 2021, Roberts et al. 2022, Barnas et al. 2024), which demonstrate that disturbances have variable positive and negative impacts, resulting in species that generally "win" or "lose" (Fisher and Burton 2018). Beyond altering habitat structure, such widespread industrial activity can reshape predator-prey dynamics and the balance of top-down and bottom-up controls within mammal communities. For example, cleared linear features have been shown to enhance grey wolf travel efficiency and ability to predate caribou (Dickie et al. 2017) and moose (Boucher et al. 2022).

Research on mammal response to disturbance in the OSR has been primarily conducted using predictive frameworks (Roberts et al. 2022). SEMs can provide inferential evidence to identify mechanisms linking species responses to habitat change and identify indirect effects to reveal more intricate underlying interactions in the mammal community. The extensive body of existing research also provides an ideal opportunity to use this foundation for constructing a network of causal hypotheses needed to formulate an SEM. Recently, Curveira-Santos et al. (2024) performed a network analysis in the OSR, using camera-trap data (O'Connell et al. 2011) and SEMs to test causal pathways linking disturbance features (grouped by shape into linear and polygonal features), prey species, and predator species. Their work revealed both direct and indirect effects of disturbance for species and a network of important causal paths throughout the broader community (Curveira-Santos et al. 2024). However, their study was constrained by a relatively small sample size and limited disturbance gradients.

To address these limitations, we expanded both sample size and the range of natural heterogeneity and disturbance measures (430 wildlife cameras across ten landscapes, versus 183 cameras across three landscapes), and applied an SEM framework similar to Curveira-Santos et al. (2024), with a new focus on moose and their interacting species. Moose occupy a central role in western boreal food webs, as major browsers, key prey for large carnivores (Connor et al. 2000), and culturally important subsistence species for First Nations (Carroll et al. 2024). However, concerns have been raised about ongoing moose populations declines across western Canada (Kuzyk et al. 2018). Reports from Wildlife Management Units show that populations in this region have been decreasing since the 1980s (Lamy and Finnegan 2019), and First Nations have expressed concern, indicating they are finding it increasingly difficult to locate moose during hunts (Parlee et al. 2012, Carroll et al. 2024). Past research implicates industrial landscape change as a potential contributing mechanism (Fisher and Burton 2018, Finnegan et al. 2023, Ethier et al. 2024, Johnson and Rea 2024). Yet, the net effects of landscape change on moose are uncertain: while forest clearing reduces mature cover and increases early seral vegetation (Pickell et al. 2013) that should enhance forage availability (Fisher and Wilkinson 2005), elevated mortality along anthropogenic linear features used by both predators (Dickie et al. 2017, Boucher et al. 2022) and hunters (Luymes et al. 2024, Hessami et al. 2025) may offset these benefits and contribute to local declines.

These competing mechanisms suggest that moose responses to disturbance are shaped by an interplay of bottom-up and top-down forces, highlighting the need to evaluate the relative strength of each in this modified landscape. We used documented associations between moose, landscape features, and predators to construct hypothesized causal pathways (see *Hypothesized pathways*), which we evaluated using camera trap data in an SEM framework. As network analyses are limited by the degree of complexity that can be considered in models, we limited the number of species incorporated and focused on key predictors for moose, enabling us to accommodate a variety of landscape features and heterogeneity in their characteristics. Recognizing that predator-prey relationships are inherently dynamic, we explicitly accounted for the possibility of bidirectional influence, where the balance between prey tracking by predators and predator avoidance by prey may shift depending on scale and context. To reflect this, we evaluated both directions of influence (predator to prey, and prey to predator) in separate SEMs. Specifically, our objectives were to disentangle (1) bottom-up and top-down processes, and (2) direct and indirect effects of landscape changes on moose and their predators. We hypothesized that anthropogenic linear features, which facilitate predator and hunter movement, would negatively affect moose occurrence, whereas polygonal features that promote early seral vegetation would have positive effects. We further expected that natural landcover types providing high-quality moose habitat would have positive effects, and that the spatial associations between predators and prey would influence respective associations with landscape features through indirect effects.

3.3 Methods

3.3.1 Study area

Our study was situated in the boreal forest of northeastern Alberta, Canada. This region is characterized by a mosaic of upland forests dominated by jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), aspen (*Populus tremuloides*), and lodgepole pine (*Pinus contorta*), interspersed with lowland muskegs of larch (*Larix laricina*) and black spruce (*Picea mariana*) (Pickell et al. 2013). The boreal landscape is naturally dynamic, presenting as a patchwork of stands at varying successional stages driven by recurring disturbances such as wildfire and insect outbreaks (Pickell et al. 2013). Beneath this landscape lies one of the world's largest hydrocarbon deposits, which led to the development of the OSR (Alberta Government 2023). The OSR encompasses approximately 142,200 km^2 (Alberta Government 2023) and has undergone extensive industrial development resulting in widespread landscape change without global or historic analogues (Pickell et al. 2016). Surface mining of bitumen occurs over roughly 3.4% of the OSR (Alberta Government 2023), while in situ extraction predominates elsewhere, creating dense networks of anthropogenic disturbance features such as roads, seismic lines, pipelines, and well pads (Bayne 2021).

3.3.2 Camera trap arrays

To investigate moose-habitat relationships, we used detection data collected from remote camera traps (O'Connell et al. 2011, Burton et al. 2015). Cameras were deployed across ten distinct study landscapes ("landscape units" or LUs) within the OSR (Figure 10) as part of the Oil Sands Monitoring Program (Bayne 2021). LUs were delineated across the OSR using watershed boundaries and selected by stratifying watersheds based on disturbance magnitude, followed by random selection from each stratum (Bayne 2021). The sampled LUs each encompassed approximately 1500 km^2 and spanned a gradient of anthropogenic disturbance intensity (Bayne 2021).

To determine camera deployment locations (i.e., “sites”), each LU was first stratified by dominant forest class (>50% composition: conifer, deciduous, or mixed-wood) to account for natural variation in sampling locations. Then, a 2-km^2 hexagonal grid was overlaid across each LU in ArcGIS Desktop (ESRI 2014), with grid cell size selected to ensure adequate spacing between cameras for spatial independence in species-habitat models (Zuckerberg et al. 2020). From each forest class stratum, 30 grid cells were randomly selected, yielding a total of 60 potential sampling sites per LU. To facilitate site access, grid cells were constrained to within 100 m of accessible roads (when possible), except in LU21 and LU14, where some sites were accessed by helicopter (Figure 10).

Among the selected cells in each LU, 40 – 50 Reconyx PC900 Hyperfire infrared remote digital cameras (Holmen, WI) were deployed, with one camera per cell. Cameras were placed approximately 1 m above the ground, and a minimum of 100 m from active roads and 1 km from other cameras. To enhance detection probability, cameras were positioned along active game trails (Fisher and Burton 2018) and scent lure (O’Gorman’s™ Long Distance Call, Broadus, MT, USA) was applied to a tree 4-7 m in front of each unit, sensu Fisher and Bradbury (2014). 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 noon daily to monitor functionality.

A total of 430 cameras were deployed across 10 LUs sampled over three years from 2021 – 2024. In 2021, 78 cameras were deployed across LU2 and LU3 in July and retrieved in either

February or September 2022 as weather permitted (Figure 21). In 2022, 155 cameras were deployed across LU13, LU21, LU15, and LU1 in September/October, and retrieved in September/October 2023 (Figure 21). In 2023, 199 cameras were deployed across the remaining LUs – LU16, LU14, LU22, and LU9 – in September/October and retrieved September/October 2024 (Figure 21). Once collected, images were manually classified by trained reviewers using *Timelapse Image Analyzer 2.0* (Greenberg et al. 2019) to determine species identities and characteristics.

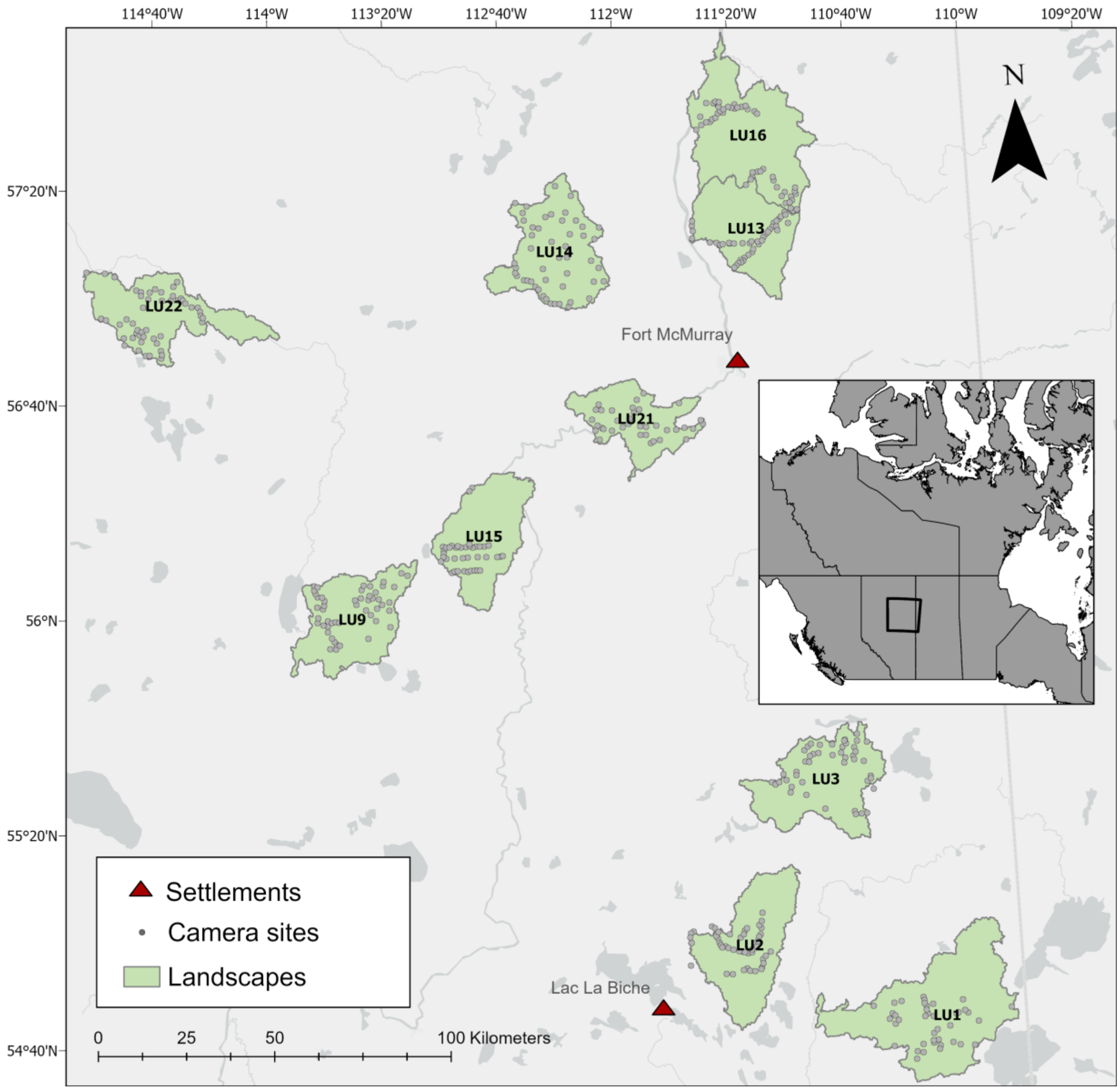

Figure 10. The ten landscape units (LUs) surveyed (green polygons) and camera site locations (grey dots) in the study. The inset map indicates the extent of the Oil Sands Region in Alberta, Canada. Number of camera sites per LU were: LU16: n = 48, LU14: n = 49, LU13: n = 41, LU22: n = 50, LU21: n = 36, LU15: n = 39, LU9: n = 50, LU3: n = 36, LU2: n = 42, LU1: n = 39.

3.3.3 Model variables

We considered both species and landcover variables with established empirical linkages to moose for inclusion in our SEM (Table 5). Landcover variables, both natural and anthropogenic, were treated as exogenous variables, functioning solely as predictors in the SEM. Natural landcover data was derived from the Satellite Based Forest Inventory by Wulder et al. (2024), while anthropogenic landcover data was sourced from the current version of Alberta Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory (Alberta Biodiversity Monitoring Institute 2022). All landcover variables were extracted within a 250 m buffer radius around each camera site, as this spatial scale is suggested to best explain moose-habitat relationships in the OSR (Dyck et al. 2025a). Species were treated as endogenous variables – those influenced by other variables in the model framework – and species "occurrence" metrics were derived by first calculating independent detections (images detected > 30 minutes apart) from the raw camera data, then summing these per site (Figure 11).

Table 5. Descriptions of variables considered in the piecewise structural equation model (SEM) containing causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada. Landscape variables are grouped into anthropogenic linear features, polygonal disturbance features, and natural landcover types, with variable descriptions derived from the metadata of their respective sources. Animal species occurrence data was derived from camera traps deployed in the study area.

Category	**Variable**	**Description**	**Source**
Anthropogenic linear features	Roads	Non-vegetated, impermeable surfaces used for motorized vehicle or aircraft transportation or access	ABMI Wall-to-Wall Human Footprint Inventory (2022)
	Conventional seismic lines	Cleared corridors created during hydrocarbon exploration 6 m wide	
	3D seismic lines	Cleared corridors created during hydrocarbon exploration 3 m wide	
	Pipelines	A line of underground and overground pipes, of substantial length and capacity, used to convey petrochemicals. The physical clearing contains underground and above-ground high-pressure pipelines	
	Transmission lines	Cleared corridors designated for the location of power transmission line infrastructure	
Polygonal disturbance features	Wells	Ground cleared for an oil/gas well pad (separated by active/inactive status)	ABMI Wall-to-Wall Human Footprint Inventory (2022)
	Cutblocks	Areas where forestry operations have occurred (clear-cut, selective harvest, salvage logging, etc.)	
	Burn sites	Areas impacted by fire disturbances	Satellite Based Forest Inventory (2020)
Natural landcover	Deciduous forest	Areas covered by deciduous forest	Satellite Based Forest Inventory (2020)
	Conifer forest	Areas covered by conifer forest	
	Wetland	Areas covered by wetland	
Animal species	Moose	Detections from deployed cameras	Camera arrays
	Wolf		
	Coyote		

A)

B)

C)

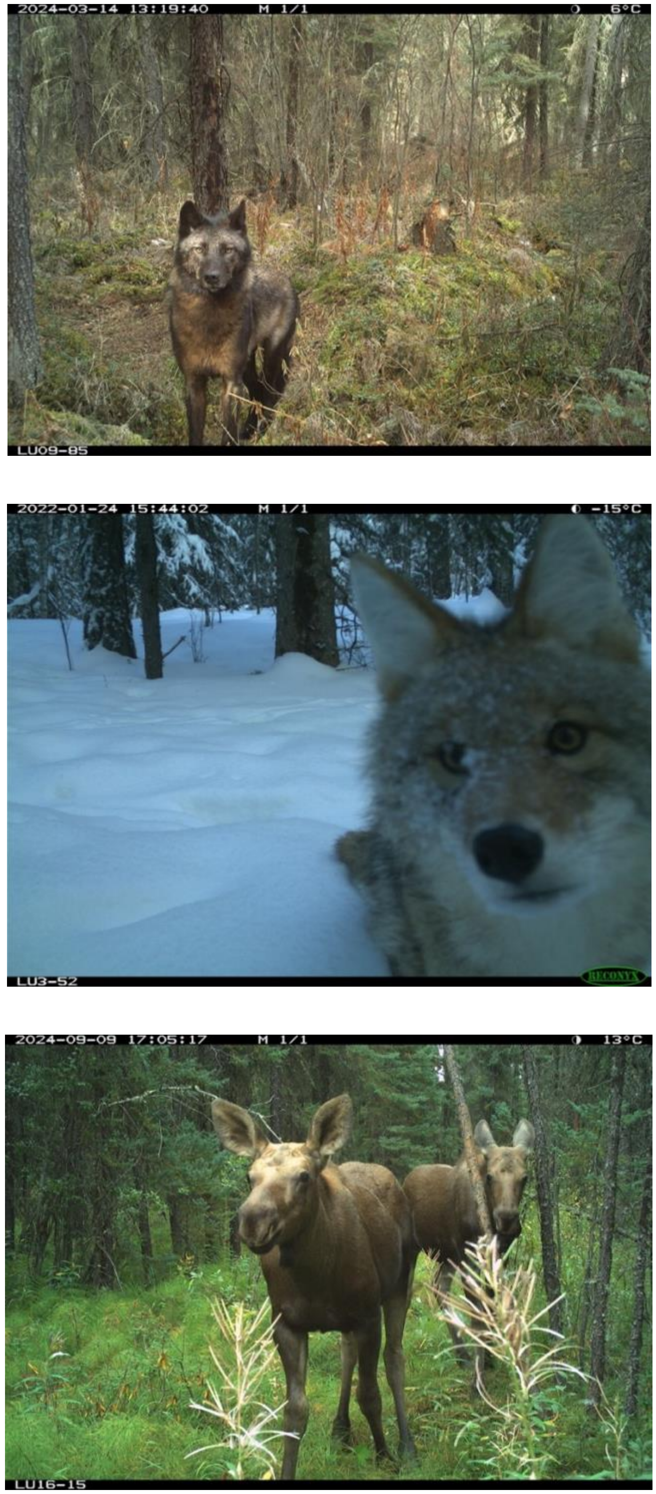

Figure 11. Camera images of the three animal species included in the piecewise structural equation model containing causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada. A) Wolf, B) Coyote, C) Moose.

Species and landcover features included in the SEMs were selected based on two, *a priori* path diagrams (Figure 12). These diagrams depict hypothesized causal pathways – based on past studies – linking landcover features, predators, and moose. The first, a top-down configuration (A), represents causal pathways from predators to moose, while the second, a bottom-up configuration (B), represents pathways from moose to predators. We examined distributions of all model covariates at the 250 m scale using histograms (Figure 22).

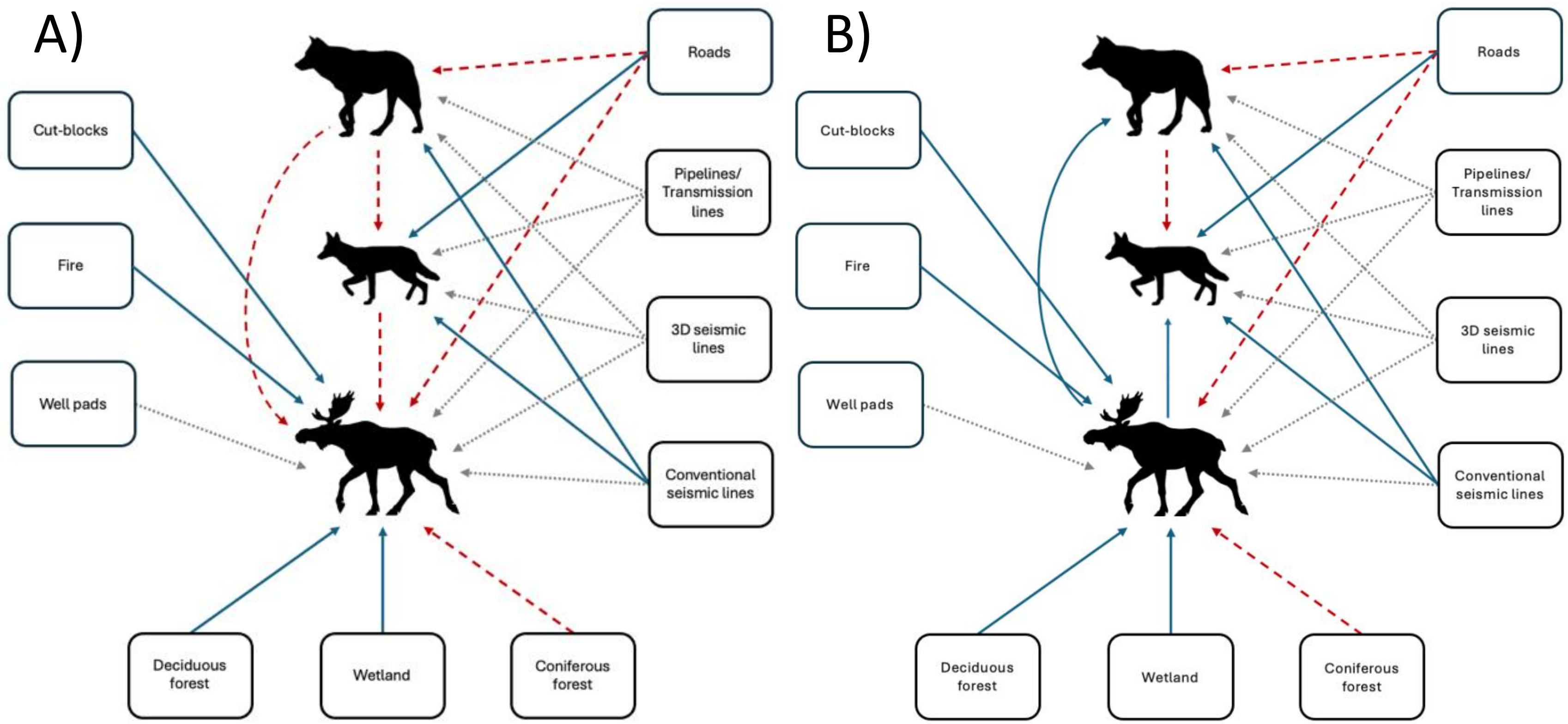

Figure 12. Path diagrams of hypothesized causal relationships explaining species occurrence data for moose, coyotes, and wolves from camera traps deployed in the Oil Sands Region of western Canada. The hypothesized causal direction of the relationship between moose and predators differs between diagrams: A) predators to moose, and B) moose to predators. Landcover variables, measured as proportions within 250-m radius buffers around camera sites, are shown in boxes around the perimeter, organized by polygonal disturbances (left), natural landcover (bottom), and linear disturbances (right). Solid (blue) lines indicate positive pathways, dashed (red) lines indicate negative pathways, and dotted (grey) lines indicate pathways with uncertain effect sign.

3.3.4 Hypothesized pathways

3.3.4.1 Moose

Natural landcover – We predicted a positive causal pathway from deciduous forest to moose. This landcover is typically considered primary moose habitat (Stewart et al. 2010), where there is abundant browse (Timmermann and McNicol 1988, Koetke et al. 2023), and has shown to be selected relative to other natural landcover types on the landscape (Stewart et al. 2010, Wasser et al. 2011). We also predicted a positive causal pathway from wetland to moose, where they forage on aquatic vegetation (Fraser et al. 1982), and with which they are also positively associated (Lamy and Finnegan 2019). Conversely, we predicted a negative causal pathway from conifer forest to moose, with which they tend to negatively associate (Telfer 1970, Stewart et al. 2010, Wasser et al. 2011), likely due to lack of browse (Telfer 1970).

Disturbance features- For linear features, we predicted a negative causal pathway from roads to moose, as the majority of studies indicate that moose negatively associate with roads (Wasser et al. 2011, Eldegard et al. 2012, Mumma et al. 2019, McKay and Finnegan 2023, Ethier et al. 2024, Johnson and Rea 2024), with suggested causal mechanisms including vehicle disturbance (Eldegard et al. 2012) and increased hunter activity from ease of access (Timmermann et al. 1998). We also predicted causal pathways from conventional seismic lines and 3D seismic lines to moose, but we were uncertain whether this effect would be positive or negative since this association has varied among studies: positive (Fisher and Burton 2018, Finnegan et al. 2023), negative (Ethier et al. 2024) and negligible (Toews et al. 2018, Mumma et al. 2019). Use of seismic lines by moose likely depends on a trade-off between the benefits of movement subsidies (Dickie et al. 2020) and early seral forage (Dabros et al. 2018, Tattersall et al. 2023) and the risk of predator and human hunter presence, which also benefit from movement subsidies (Dickie et al. 2017, Dabros et al. 2018). For the same reasons, we also expected a causal pathway from pipelines/transmission lines to moose with an uncertain effect sign.

With respect to polygonal features, we predicted positive causal pathways from cutblocks and burns to moose, which typically contain abundant early seral vegetation favoured as forage (Fisher and Wilkinson 2005, Newbury et al. 2007, Lamy and Finnegan 2019). Moose have shown positive associations with both features: cutblocks (Newbury et al. 2007, Toews et al. 2018, Lamy and Finnegan 2019, Mumma et al. 2021, McKay and Finnegan 2023), and burns (Maier et al. 2005, Kyle et al. 2016). We also expected a causal pathway from well pads to moose but were uncertain about the effect sign of this relationship. Moose have been reported to associate both positively (Ethier et al. 2024) and negatively (Fisher and Burton 2018) with well pads, which may depend on the well's activity status.

Predators – We considered two predators – wolves and coyotes – in our analysis. Although black bears also predate moose in this region (Moore et al. 2024), we did not include them due to challenges in modelling their hibernation, and because predation is typically restricted to calves. Given the potential for bidirectional interactions between moose and their predators, we adopted an exploratory approach, testing two alternative scenarios in separates SEMs to evaluate which causal direction was more strongly supported. The first scenario represented top-down control, with negative pathways from predators to moose. The second represented bottom-up influence, with positive pathways from moose to wolves and coyotes, reflecting prey availability driving predator occurrence. Empirical evidence supports the plausibility of both directions. Wolves are a primary predator of moose across North America (Wasser et al. 2011, Neilson and Boutin 2017), and moose have been shown to adjust habitat selection to reduce overlap with wolves (Dussault et al. 2005, Ethier et al. 2024). Coyotes also have been documented predating moose in packs (Benson and Patterson 2013, Balluffi-Fry et al. 2020), though direct evidence of predation in the western boreal is lacking.

3.3.4.2 Wolves and coyotes

Disturbance features – We predicted causal pathways from linear disturbance features to both predator species. Specifically, we expected positive causal pathways from conventional seismic lines to wolves and coyotes, as both species have been shown to positively associate these features (Latham et al. 2011c, Toews et al. 2018, Clarke et al. 2025), likely due to movement subsidies that facilitate efficient travel and increase prey encounter rates (Dickie et al. 2017). We also predicted a positive causal pathway from roads to coyotes, which similarly show positive associations with roads (Toews et al. 2018, Fisher and Ladle 2022, Clarke et al. 2025). Conversely, we predicted a negative causal pathway from roads to wolves, as multiple studies have reported negative associations in the study region (Fisher and Burton 2018, Toews et al. 2018, McKay and Finnegan 2022, Baillie-David et al. 2024). This avoidance may be driven by elevated human activity occurring along roads (Muhly et al. 2011), particularly in areas where predator control programs are actively implemented (Baillie-David et al. 2024). For other linear features – pipelines/transmission lines and 3D seismic lines – we also predicted causal pathways to both predators, but with uncertain effect signs. Pipelines are typically less travelled than roads, and 3D seismic lines, deployed in dense, crosshatched ("#") patterns, may not facilitate movement as effectively. These features are less frequently studied independently and are often grouped into broader "linear disturbance" categories (Wasser et al. 2011, Demars and Boutin 2018, Curveira-Santos et al. 2024), though they nonetheless may also serve as movement corridors.

Path from wolves to coyotes – We predicted a negative causal pathway from wolves to coyotes, based on the expectation that wolves, as the dominant predator, suppress coyotes as the subordinate, leading to spatial segregation (Arjo and Pletscher 1999, Berger and Gese 2007, Levi and Wilmers 2012).

3.3.5 Statistical analysis

We constructed both SEMs using a piecewise SEM framework. In piecewise (or local) SEM, the path diagram is deconstructed into a series of linear structured equations which are solved independently, differing from the traditional "global" approach where all paths are solved simultaneously (Grace et al. 2015, Lefcheck and Freckleton 2016). The piecewise approach offers several advantages, including the ability to accommodate smaller datasets and incorporate various non-normal distributions (Lefcheck and Freckleton 2016). In our analysis, we derived three structured equations from the *a priori* path diagram, one for total detections of each species (i.e. moose, wolf, and coyote). Each equation was modelled using generalized linear mixed models (GLMMs) with a negative binomial distribution and a log-link function, and landscape unit included as a random effect. For example, the moose model from the top-down scenario was specified as follows:

$$\eta_{ij} = \beta_0 + \beta_1\text{Roads}_{ij} + \beta_2\text{Seismic}_{ij} + \beta_3\text{3DSeismic}_{ij} + \beta_4\text{Pipeline/Transmission}_{ij} + \beta_5\text{Wells}_{ij} + \beta_6\text{Harvest}_{ij} + \beta_7\text{Fire}_{ij} + \beta_8\text{Deciduous}_{ij} + \beta_9\text{Wetland}_{ij} + \beta_{10}\text{Conifer}_{ij} + \beta_{11}\text{Wolf}_{ij} + \beta_{12}\text{Coyote}_{ij} + \text{LU}_j$$

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

$$\text{Moose Total Detections}_{ij} \sim \text{NegativeBinomial}(\lambda_{ij}, \theta)$$

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

where moose total detections are modelled as the i^{th} observation within LU j, and LU ID is a random intercept with j^{th} level j = individual LU. LU was specified as a random effect to account for variation across space and degree of disturbance. For all species, the inclusion of this random effect improved model support (ΔAICc $\geq$ 2) relative to an identical model without it (Table 14). We also ensured that each structured equation met the d-rule (Grace et al. 2015) for number of parameters allowed given the sample size (430 cameras/(fixed + random effects) > 5).

We assessed correlations among raw variables using Pearson's correlation coefficient (Figure 23), ensuring that all pairwise combinations were below a threshold absolute value of 0.7 (Zuur et al. 2010). The number of camera trap days was also included in the correlation analysis, as total species detections at each site were influenced by varying durations of camera operation. No strong correlations were found between camera days and any other variables, suggesting that while variation in camera effort may introduce some model error, it does not systematically bias relationships among predictors. As such, and because offset variables are not yet accommodated in piecewise SEMs, we did not further consider camera trap days as a covariate.

We fit the structural equation models (SEMs) using the *piecewiseSEM* package in R version 4.4.1 (R Core Team 2024). Examination of the path coefficients revealed that, in the top-down model, the pathway from wolves to moose was significant and positive – contrary to expectations of a negative relationship if it represented predator-avoidance behaviour. Similarly, in the bottom-up model, the reverse pathway (moose to wolves) was also positive. Spatial associations between moose and wolves on the landscape likely reflect a balance between prey-tracking and predator-avoidance behaviour, and these results suggest the relationship leans more strongly toward prey-tracking at the 250-m scale. Consequently, we did not pursue the top-down model further and focused subsequent analyses on the bottom-up model.

To assess whether the model satisfied the assumption of conditional independence – i.e., that no omitted relationships existed between unlinked variables (Shipley 2000) – we applied tests of directed separation using the "d-sep" function in "piecewiseSEM." No significant independence claims ($p < 0.05$) emerged, so we did not add any additional pathways (Lefcheck and Freckleton 2016, Dyck et al. 2025b).

We evaluated the SEM using chi square (χ^2) and Fisher's *C* goodness-of-fit measures, where low scores and high, non-significant p-values ($p > 0.05$) indicate a good model fit (Lefcheck and Freckleton 2016). In addition, we computed Nagelkerke's Pseudo R^2 values for each structured equation to evaluate their respective model fits (Nagelkerke 1991). The effect size for each causal pathway was inferred from standardized ß coefficient estimates.

3.4 Results

Across the ten LUs, there were a cumulative 149,273 camera trap days across 430 sites. Of the three focal species, coyotes had the most independent detections (2461) followed by moose (1000) and wolves (424). Total independent detections for each species varied by site (Figure 13).

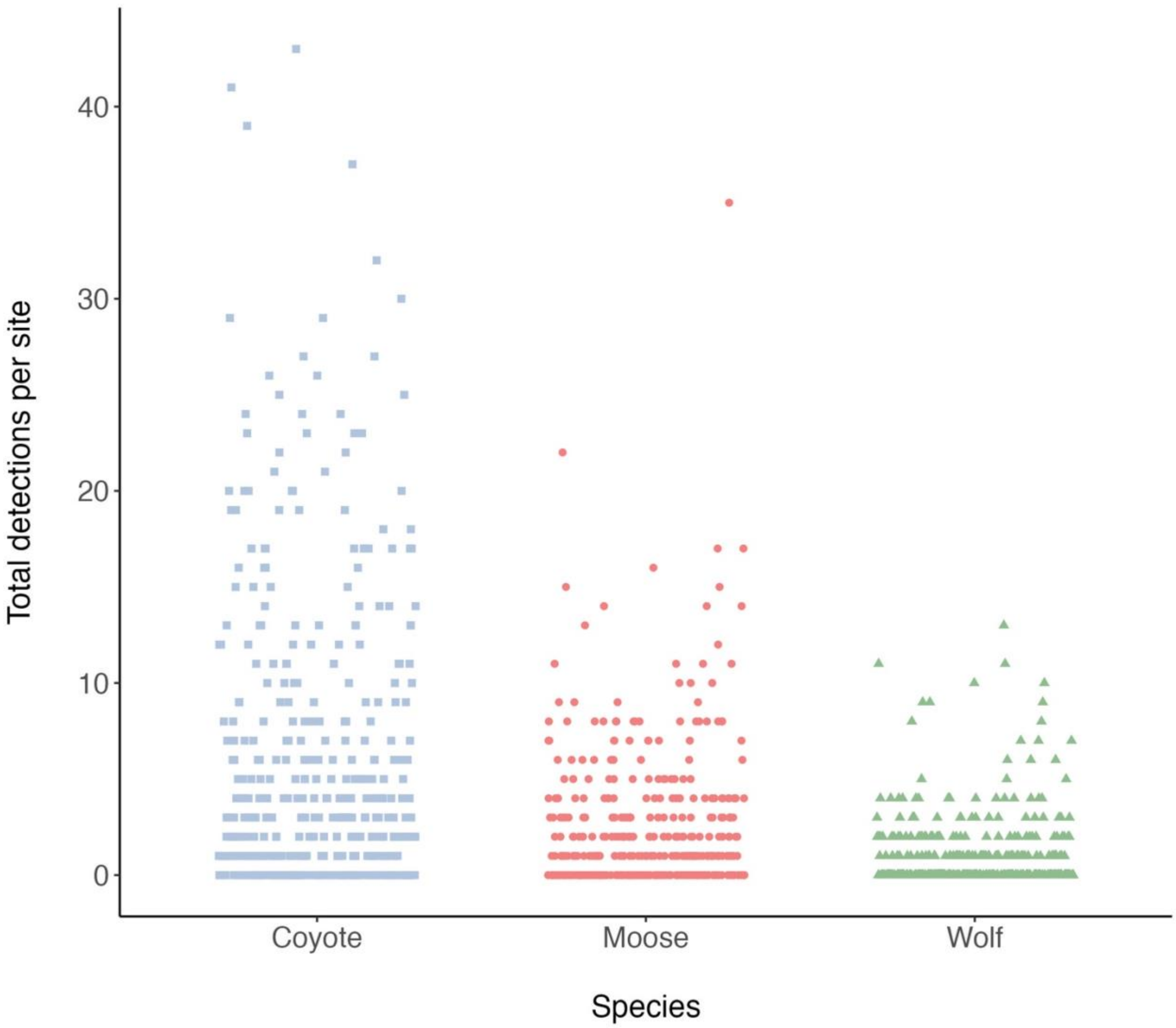

Figure 13. Total independent detections of coyotes, moose, and wolves at each camera site (n = 430) in the Oil Sands Region of western Canada.

3.4.1 SEM model fit

The final SEM bottom-up configuration demonstrated good model fit based on Fisher' *C* and chi-square tests (C_{24} = 15.03, p = 0.92; χ^2_{12} = 9.38, p = 0.67), as indicated by low test statistics and the high, non-significant p-values ($p > 0.05$). The individual pseudo R^2 value was high for moose (0.62), suggesting the structured equation (GLMM) explained a substantial portion of variation relative to the null model. Pseudo R^2 values were slightly lower for coyote (0.45) and wolf (0.19) structured equations.

3.4.2 Direct effects: Evidence for bottom-up and top-down mechanisms

The direct pathways in the SEM from predictors to moose largely aligned with our predictions, with some exceptions (Figure 14). As predicted, deciduous forest and wetland had strong positive direct effects on moose occurrence ($\beta_{\text{Deciduous}}$ = 0.17, β_{Wetland} = 0.11; Table 6), while roads had a strong negative direct effect (β_{Roads} = -0.19, Table 6). Interestingly, 3D seismic lines also had a strong positive direct effect on moose occurrence ($\beta_{\text{3Dseismic}}$ = 0.10, Table 6), which was unexpected given the inconclusive evidence reported in the literature. Effect sizes for other linear features and all polygonal features were relatively small.

For predators, the strongest direct effects from linear features included the expected positive effect of roads on coyote occurrence (β_{Roads} = 0.10; Table 6), and an unexpected negative effect of 3D seismic lines on wolf occurrence ($\beta_{\text{3Dseismic}}$ = -0.14; Table 6). Roads also had a relatively weaker negative direct effect on wolves (β_{Roads} = -0.09; Table 6). Moose occurrence had the expected positive effect on wolf occurrence (β_{Moose} = 0.10; Table 6), but no meaningful effect on coyotes (β_{Moose} = 0.01; Table 6).

3.4.3 *Indirect effects explain wolf-landscape feature associations mediated by moose*

We interpreted indirect pathways from landscape features to wolves using moose as a mediator, but did not do so for coyotes, as there was no ecologically justified direct relationship with moose. Indirect effects were calculated only for landscape features that had a strong direct effect on either moose or wolves. These were estimated by multiplying the coefficient for the direct effect of moose on wolves (β_{Moose} = 0.10) by the direct effect of the landscape feature on moose (Lefcheck and Freckleton 2016).

Deciduous forest and wetland both had positive indirect effects on wolves acting through moose ($\beta_{\text{Deciduous}}$ = 0.02; β_{Wetland} = 0.01), reflecting their positive influence on moose occurrence. Roads had a negative indirect effect on wolves through moose (β_{Roads} = -0.02), consistent with the negative direct effect of roads on wolves. Interestingly, 3D seismic lines had a positive indirect effect on wolves through moose ($\beta_{\text{3Dseismic}}$ = 0.01), which contrasts with their negative direct effect on wolves.

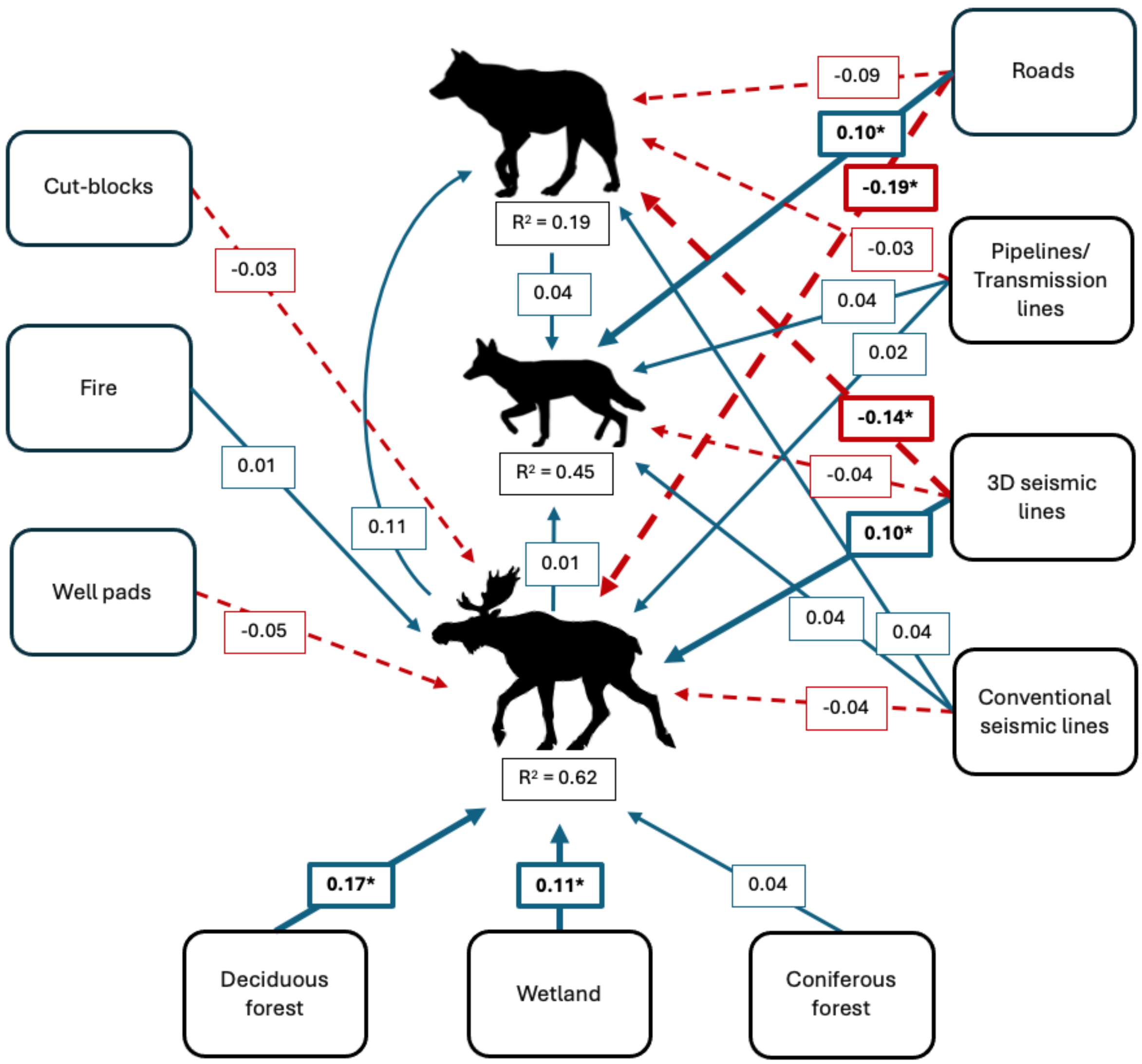

Figure 14. Optimized piecewise structural equation model containing causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada. Landcover variables, measured as proportions within a 250-m radius buffer around camera sites, are shown in boxes around the perimeter, organized by polygonal disturbances (left), natural landcover types (bottom), and linear disturbances (right). Solid (blue) lines indicate positive pathways and dashed (red) lines indicate negative pathways. Standardized coefficient estimates are given for each pathway, bolded estimates with a '*' have $p < 0.05$. Pseudo R-squared values were computed for each component model.

Table 6. Coefficient estimates (raw and standardized) and corresponding standard error and p-values for predictor variables included in the optimized piecewise structural equation model predicting causal pathways for moose, coyote, and wolf occurrence data from camera traps deployed in the Oil Sands Region of western Canada. Standardized coefficient estimates, rather than raw estimates, should be interpreted for comparability. Bolded estimates have $p < 0.05$.

Response	Predictor	Raw estimate	Standard error	P value	Standardized estimate
Moose	**Roads**	**-0.39**	**0.08**	**0.00**	**-0.19**
	Wells	-0.10	0.08	0.17	-0.05
	Conventional seismic lines	-0.07	0.07	0.30	-0.04
	Harvest sites	-0.06	0.07	0.40	-0.03
	Burn sites	0.02	0.07	0.83	0.01
	Pipelines/Transmission lines	0.04	0.07	0.58	0.02
	Conifer forest	0.08	0.08	0.33	0.04
	3D seismic lines	**0.21**	**0.06**	**0.00**	**0.10**
	Wetland	**0.23**	**0.08**	**0.00**	**0.11**
	Deciduous forest	**0.34**	**0.10**	**0.00**	**0.17**
Coyote	3D seismic lines	-0.06	0.06	0.37	-0.04
	Moose	0.00	0.02	0.79	0.01
	Wolf	0.04	0.03	0.29	0.04
	Pipelines/Transmission lines	0.07	0.07	0.33	0.04
	Conventional seismic lines	0.07	0.07	0.31	0.04
	Roads	**0.15**	**0.07**	**0.02**	**0.10**
Wolf	**3D seismic lines**	**-0.22**	**0.10**	**0.03**	**-0.14**
	Roads	-0.13	0.10	0.18	-0.09
	Pipelines/Transmission lines	-0.05	0.10	0.60	-0.03
	Moose	0.04	0.02	0.07	0.10
	Conventional seismic lines	0.07	0.10	0.51	0.04

3.5 Discussion

3.5.1 Identifying mechanistic linkages to understand effects of anthropogenic landscape change

Anthropogenic landscape change is a primary driver of global biodiversity loss (Maxwell et al. 2016), affecting mammals not only through habitat loss but also via the introduction of novel disturbance features. These features modify the distribution of risk and reward across landscapes (Fisher and Burton 2018), thereby influencing both the relative abundance and spatial patterns of species. Understanding the top-down and bottom-up mechanisms underlying these responses is essential for guiding effective conservation and management strategies. We conclude that both mechanisms operate concurrently for moose in the western boreal, offering forage subsidies that could support population growth, while simultaneously increasing exposure to predators and hunters, which may suppress populations.

Among linear disturbance features, we found a strong negative direct effect of roads on moose occurrence (despite the early seral forage they offer on edges, as well as salt subsidies (Laurian et al. 2008, Grosman et al. 2011)), and a strong positive direct effect of 3D seismic lines. These effects align with trade-off theory (Holbrook and Schmitt 1988, Frid and Dill 2002): wide features that are heavily trafficked by humans and predators may present high perceived risk and be avoided, while narrower, less-trafficked features may pose less risk and offer potential benefits such as travel corridors or foraging opportunities. As expected, we also found strong positive direct effects of deciduous forest and wetland on moose occurrence, both of which are natural habitats with abundant forage.

Camera data have limited capacity to characterize predator–prey dynamics, as predators and prey may exhibit spatial co-occurrence even when prey actively avoid predators (Muhly et al. 2011). We were unable to directly assess the effects of predator occurrence on moose and the resulting indirect effects. However, we were able to evaluate reverse pathways and found that moose occurrence positively affected wolf occurrence.

3.5.2 Several landscape features had strong direct effects on moose occurrence

Results from our SEM indicated that two linear features, roads and 3D seismic lines, had strong direct effects on moose occurrence. As predicted, roads had a strong negative effect, consistent with previous studies (Wasser et al. 2011, Eldegard et al. 2012, Mumma et al. 2019, McKay and Finnegan 2023, Ethier et al. 2024, Johnson and Rea 2024). Roads may be perceived by moose as particularly risky due to high levels of vehicle disturbance (Eldegard et al. 2012) and concentrated hunting activity during the fall (Timmermann et al. 1998), despite the forage and salt subsidies they offer (Laurian et al. 2008, Grosman et al. 2011).

In contrast, 3D seismic lines had a positive effect on moose occurrence, which was unexpected given the mixed findings in the literature (Fisher and Burton 2018, Ethier et al. 2024). However, few studies have explicitly examined 3D seismic lines independently from conventional seismic lines. Fisher and Burton (2018) also reported a positive association, whereas Ethier et al. (2024) found a negative relationship, though this effect was only strong at broader spatial scales and was influenced by wolf culls. Structurally, 3D seismic lines differ from conventional seismic lines and other linear features in ways that may reflect a more favourable risk-reward trade-off for moose. Like other vegetated linear features, they can offer early seral forage (Dabros et al. 2018) and possibly facilitate movement, but they may also provide greater snow interception and thermal shelter compared to wider, more open features (Weiland et al. 2024). Furthermore, the narrow width and typically lower maintenance of 3D seismic lines may reduce use by humans (e.g., hunters, recreationalists) and predators (Dickie et al. 2017), decreasing perceived risk. Notably, we found a strong negative direct effect of 3D seismic lines on wolves, the primary predator of moose, suggesting these features promote spatial segregation.

We found no strong relationships between moose and any polygonal disturbance features. This was unexpected, particularly for burns and cutblocks, where we anticipated increased occurrence due to abundant early seral vegetation subsidies. However, several factors could explain these weak or absent signals. First, associations are likely influenced by time since disturbance, which reflects the successional stage of vegetation (Fisher and Wilkinson 2005). Forage availability typically peaks in mid-age sites (10 – 25 years post-disturbance), potentially increasing moose use during this period (Fisher and Wilkinson 2005, Mumma et al. 2021). In contrast, younger features may be less preferred due to limited shrub regeneration (Poole and Stuart-Smith 2004), or a lack of forest cover, which provides protection from weather and predators (Thompson and Vukelich 1981). Similarly, moose have shown a negative relationship with older features (Mumma et al. 2021, Sand et al. 2021), likely because available browse has declined or grown beyond reach (Lamy and Finnegan 2019). We initially attempted to classify cutblocks and burns into these three age classes, but our data was too zero-heavy to support this analysis.

Second, especially for burns, forage availability is shaped by the pre-disturbance vegetation composition (DeMars et al. 2019). For example, post-disturbance vegetation biomass tends to be high in aspen-dominated areas but lower in peatlands (MacCracken and Viereck 1990). Third, seasonality may influence polygonal feature use, with reduced winter occurrence possibly linked to increased snow accumulation (McKay and Finnegan 2023). Finally, post-harvest management practices such as the application of herbicide (e.g., glyphosate) to cutblocks can alter forage availability and consumption patterns (Koetke et al. 2023).

Moose associations with natural landcover types were as anticipated, with strong positive effects of their primary habitat, deciduous forest and wetlands, on occurrence. Preference for deciduous forest is likely driven by forage, with leaves from deciduous trees and shrubs like aspen, willow, and birch composing the majority of a moose's diet (Timmermann and McNicol 1988, Koetke et al. 2023). Moose also forage on aquatic vegetation, most intensively in early summer (Fraser et al. 1982), which can provide higher levels of nutrients like sodium and iron than woody browse (Fraser et al. 1984). Conifer forest did not have a negative effect as expected due to minimal browse, and may provide some benefits like snow interception (Telfer 1970).

3.5.3 Indirect effects reveal additional insights in a causal approach

A key advantage of the SEM approach is its ability to identify indirect pathways (Lefcheck and Freckleton 2016), which can reveal more intricate ecological interactions than direct pathways alone. Identifying such mediating processes can offer opportunities for more targeted management interventions, as they clarify how and through which species or landscape features certain effects are transmitted.

Of the two topologies tested, the bottom-up SEM, with pathways from moose to predators, was best supported. This model indicated a positive effect of moose on wolves, which was expected given moose are a key prey species (Wasser et al. 2011). In contrast, the top-down model yielded a positive effect of wolves on moose, which is not biologically plausible because predators are unlikely to increase prey occurrence. Although we were therefore unable to evaluate indirect effects of landscape features on moose mediated by wolves, the reverse relationships revealed how anthropogenic disturbances may indirectly influence predator occurrence through their effects on moose.

We suggest this directional outcome may indicate that wolf-moose interactions at the 250 m scale are more strongly driven by prey-tracking by wolves than by predator avoidance by moose – though our data cannot definitively distinguish between these mechanisms. Predator-prey interactions are difficult to characterize using co-occurrence data (Blanchet et al. 2020), but successfully searching predators typically manifest as positively co-occurring with prey (e.g., Darlington (2018)). However, it is unlikely that moose do not attempt predator avoidance at all. Ethier et al. (2024) found that moose occurrence in this region was best explained by security-related habitat features prior to a wolf cull and by forage availability post-cull, suggesting wolves do influence moose distribution. Similarly, Dussault et al. (2005) found that moose avoided areas used by wolf packs. It is also possible that moose have limited capacity to avoid wolves in landscapes dominated by linear features, similar to patterns observed in woodland caribou (Mumma et al. 2019).

In this western boreal system, deciduous forest and wetland cover had small but positive indirect effects on wolf occurrence, mediated by their positive effects on moose. Tests of directed separation indicated that direct pathways from these landcover types to wolves were not important, but the positive indirect effects are consistent with these landcover types being primary moose habitat. Interestingly, 3D seismic lines had a strong negative direct effect on wolves, yet a positive indirect effect due to their positive direct effect on moose occurrence. This pattern suggests the possibility of an unmeasured variable driving the negative direct effect on wolves. Alternatively, as wolves have other prey options besides moose, they may find 3D seismic lines less favourable than wider linear features, potentially due to reduced mobility in these narrow corridors, despite increased moose occurrence.

Moose occurrence had a very weak positive effect on coyotes, suggesting no meaningful ecological relationship in our analysis. We included coyotes in the SEM due to documented cases of eastern coyotes preying on moose (Benson and Patterson 2013, Balluffi-Fry et al. 2020), and because increasing coyote populations have been proposed via personal communications as a factor in moose declines in the western boreal. However, our results do not support strong predator-prey interactions between coyotes and moose. It is possible that western boreal coyotes, which are typically smaller than their eastern counterparts, do not prey on moose. Coyotes may prefer smaller prey, and dietary analyses in Alberta have shown moose absent from their diet (Latham et al. 2011a). That said, our co-occurrence measure alone is insufficient to definitively assess predation, and future research should investigate this relationship using finer-scale data.

3.5.4 Caveats

A key limitation of our study is the limited capacity of camera trap data to capture fine-scale dynamics of predator avoidance and prey tracking behaviour. While patterns of co-occurrence, such as the positive association between wolves and moose, likely reflect the net outcome of predator-prey interactions, they operate at spatial and temporal scales that are probably too coarse to detect subtle avoidance responses by moose. This limits our ability to make inferences about predator avoidance within a causal framework, and we were unable to assign a causal pathway for wolves to moose. Incorporating finer-scale data, such as GPS collar data, which has also been successfully used in piecewise SEM (Cowan et al. 2024), may help address this limitation.

There are also other factors known to influence mammalian responses to landscape change that we did not consider, due to both data limitations and constraints on complexity that can be accommodated in an SEM. Spatial associations can be influenced by the density, configuration, and characteristics of disturbance features (e.g., vegetation height), and may vary by season or demographic group (Demars and Boutin 2018, Mumma et al. 2019, McKay and Finnegan 2023, Tattersall et al. 2023). In addition, black bears, which we excluded from our analysis, are important predators of moose calves (Moore et al. 2024) and may influence occurrence, particularly in spring.

3.6 Conclusion

Across multiple landscapes spanning a wide gradient of landscape change in the western boreal forest, direct and indirect effects of top-down mortality risk likely play a large role in moose relative abundance, despite forage subsidies created by anthropogenic landscape features. The strong negative effect size of roads eclipses the positive effects of other forage-subsidizing features, suggesting a net negative outcome. Moose are more likely to occur in in places with low road densities, and natural habitats characterized by extensive deciduous forest and wetland cover. These findings underscore the importance of maintaining and restoring (Tattersall et al. 2020, Dickie et al. 2022) natural boreal habitat conditions to support moose populations.

Future research would benefit from incorporating finer-scale data on predator–prey interactions, which could be more effectively integrated into a causal modeling framework. The SEM approach used here is highly flexible and capable of accommodating multiple data types, spatial scales, and hierarchical structures. This flexibility makes it broadly applicable to other ecological systems involving different species, habitat types, and disturbance gradients.

Moreover, the use of path diagrams provides an intuitive visual representation of complex relationships, making SEM a powerful tool for communicating ecological mechanisms to diverse audiences. By emphasizing causal pathways rather than solely predictive performance, SEM offers a mechanism-focused framework that can substantially advance ecological understanding and support more informed wildlife management and conservation decision-making.

Chapter 4: Conclusion

4.1 Overview of results

With widespread and rapidly expanding anthropogenic landscape modification contributing to biodiversity declines worldwide (Maxwell et al. 2016), understanding how these changes are affecting species is essential to inform effective wildlife management. The objective of my thesis was to investigate the impacts of industrial landscape disturbance on the spatial distributions of black bears and moose in the highly altered Oil Sands Region (OSR) of western Canada. To meet this objective, I conducted two independent studies – one for each species (Chapters 2 and 3) – aimed at addressing key ecological knowledge gaps and examining how industrial development alters risk-reward trade-offs in habitat use. Both studies used data from camera traps (Burton et al. 2015) deployed across ten landscapes within the OSR, representing a gradient of industrial development. The results provide new insights into how these species respond to anthropogenic disturbance, supporting more informed restoration planning and wildlife management in boreal ecosystems.

In Chapter Two, I examined black bear associations with anthropogenic disturbance features and investigated whether these relationships varied seasonally and by demographic group. Notably, I found that linear disturbance features, especially roads, generally had strong negative influences on both solitary adult and female with young occurrence frequency. However, solitary adult occurrence frequency did not decline with increasing road density during the summer non-hunting season, suggesting a potential trade-off with using roads for early seral forage that fluctuates with seasonal variation in mortality risk. In contrast, female with young occurrence frequency consistently declined with increasing road density across seasons. This pattern suggests a lower risk tolerance to human disturbance and does not support the hypothesis that these bears use roads as “human shields” from infanticidal adult bears during the hunting season, despite being legally protected from hunting. Solitary adult occurrence frequency also increased strongly with higher ungulate relative abundance in spring, likely reflecting neonate predation. These findings offer key insights into how demographic and seasonal variation in risk–reward trade-offs shape wildlife responses to landscape change and highlight the need to consider these dynamics in management and conservation planning.

In Chapter 3, I used structural equation modelling (SEM) to investigate the direct effects of disturbance features on moose and their predators, while simultaneously examining how indirect effects with landscape features might manifest through species direct associations. I found a very strong negative direct effect of roads on moose, which overshadowed the positive effects of potential forage-subsidizing features – indicating an overall net-negative impact of landscape change on moose. Additionally, strong positive direct effects of wetland and deciduous forest on moose occurrence highlight the importance of maintaining and restoring such habitats to support moose populations. I also found that wolves were more likely to occur in areas with higher moose detections, likely reflecting successful prey tracking behaviour, and their spatial associations with landscape features were influenced by moose presence. Future research should integrate complementary data sources to enable stronger inference on the reverse causal pathway (predator to prey), allowing identification of indirect effects of landscape features on moose mediated by wolves. As a mechanism-oriented alternative to purely predictive models, I recommend SEMs for other ecological studies as a tool for advancing ecological understanding.

4.2 Fine-scale ecological considerations may better identify patterns of response to landscape change, particularly in generalist species

Generalist species, characterized by their adaptability in resource use, may experience highly dynamic risk-reward trade-offs across landscapes that fluctuate temporally due to ecological factors like seasonality or demographic status. Accounting for these fine-scale variables may help clarify patterns of habitat use, particularly in anthropogenically modified environments. This was demonstrated with black bears in Chapter 2, where clearer patterns emerged when analyses were stratified by demographic group and biologically relevant seasons. For example, when all seasons were analyzed together, solitary adults showed a negative association with roads; however, this pattern was not evident in summer. Although not tested explicitly, this shift may reflect the influence of hunter presence – as summer is the non-hunting season – providing insight into the risk-reward dynamics shaping bear habitat use. Incorporating biologically meaningful, finer-scale factors into habitat use analyses, especially for generalist species, may therefore help uncover important ecological patterns that would otherwise remain obscured.

4.3 Moving beyond predictive models: Causal inference in the OSR

The analysis presented in Chapter 3 represents one of the first applications of a causal modelling framework to examine the effects of landscape change on mammals in the OSR. Unlike traditional predictive methods such as generalized linear models (GLMs), SEM is explicitly designed to investigate causal relationships, offering deeper insight into species-landscape interactions. This work provides a practical example of how SEMs can be used to assess both direct and indirect effects of industrial disturbance on mammal species, and the approach developed here can be readily adapted to other ecological systems. There is also considerable potential to build on this framework, for example by incorporating multiple data sources (e.g., camera trap and GPS telemetry data) into SEMs, to improve the resolution and robustness of ecological inference. Future research should continue to advance and apply causal inference methodologies, rather than continually defaulting to GLMs, particularly when addressing the complex dynamics of ecosystems undergoing anthropogenic change.

4.4 Negative associations with linear features, unclear patterns for polygonal features

A common finding across Chapters 2 and 3 was the largely negative effect of linear features on both black bear and moose occurrence, with the strongest effects associated with roads. This pattern demonstrates the importance of restoring linear features and regulating human access (Alberta Sustainable Resource Development Forum 2012), particularly to support declining moose populations.

In contrast, another shared outcome was the limited influence of polygonal features on the occurrence of both species. For both black bears and moose, I had expected a largely positive association with polygonal disturbances due to the availability of early-seral vegetation subsides (Fisher and Wilkinson 2005, Nielsen et al. 2020). However, neither species showed strong responses. Each chapter outlined several plausible explanations for this net-zero outcome, including variation in the successional stage of disturbances, post-harvest management practices such as glyphosate application, and differences in human activity levels (e.g., active vs. inactive wells). Due to zero-heavy data and constraints on model complexity, I was unable to explore this heterogeneity in polygonal features in detail. Future studies specifically designed to address the variation may be able to better detect underlying patterns of association.

4.5 Improving hunter distribution data to better explain wildlife spatial patterns

Both black bears and moose are hunted in Alberta, and in each case, I suggested hunter activity as a potential causal mechanism driving negative associations with wide linear features, which are commonly used as access routes (Timmermann et al. 1998, Dabros et al. 2018). However, fine-scale data on hunter spatial distributions were not available, aside from species harvest totals reported at the Wildlife Management Unit (WMU) level (Alberta Government 2024). Access to more spatially and temporally explicit data on hunter presence would improve our ability to directly assess its influence on species behaviour and associations with disturbance features. One possible approach would be to pair wildlife camera traps with autonomous recording units (ARUs) to detect indirect indicators of hunter activity, such as the number of gunshots or level of ATV traffic, which could then be used to approximate hunter presence at camera sites. These data would also be valuable for explaining spatial patterns of other hunted species in the region.

4.6 Conclusions

As human activity continues to reshape ecosystems, it not only drives species declines but also initiates complex, cascading effects throughout ecological communities. To guide effective conservation, it is essential to understand how individual species interact with and respond to landscape change, and how these responses influence broader ecosystem dynamics. In this thesis, I examined the spatial associations of black bears and moose in the OSR, providing new insights into how industrial disturbances alter species distributions through shifting risk-reward trade-offs. These findings underscore the value of fine-scale, theory-informed analyses in revealing patterns that may be obscured in coarser assessments. Going forward, applying similar approaches across additional species in the OSR will be critical for building a more complete picture of how landscape change reshapes community structure and function. This is especially important given that even generalist species can be pushed beyond the limits of their ecological flexibility under sustained anthropogenic pressure. The insights gained from this work contribute not only to regional management and restoration planning but also offer frameworks and considerations relevant to other rapidly developing ecosystems worldwide. As global biodiversity loss accelerates, research that integrates ecological theory, species-specific responses, and community-level perspectives will be increasingly vital to sustaining ecosystem integrity and guiding meaningful conservation action.

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Appendix A: Chapter 2 supplementary results

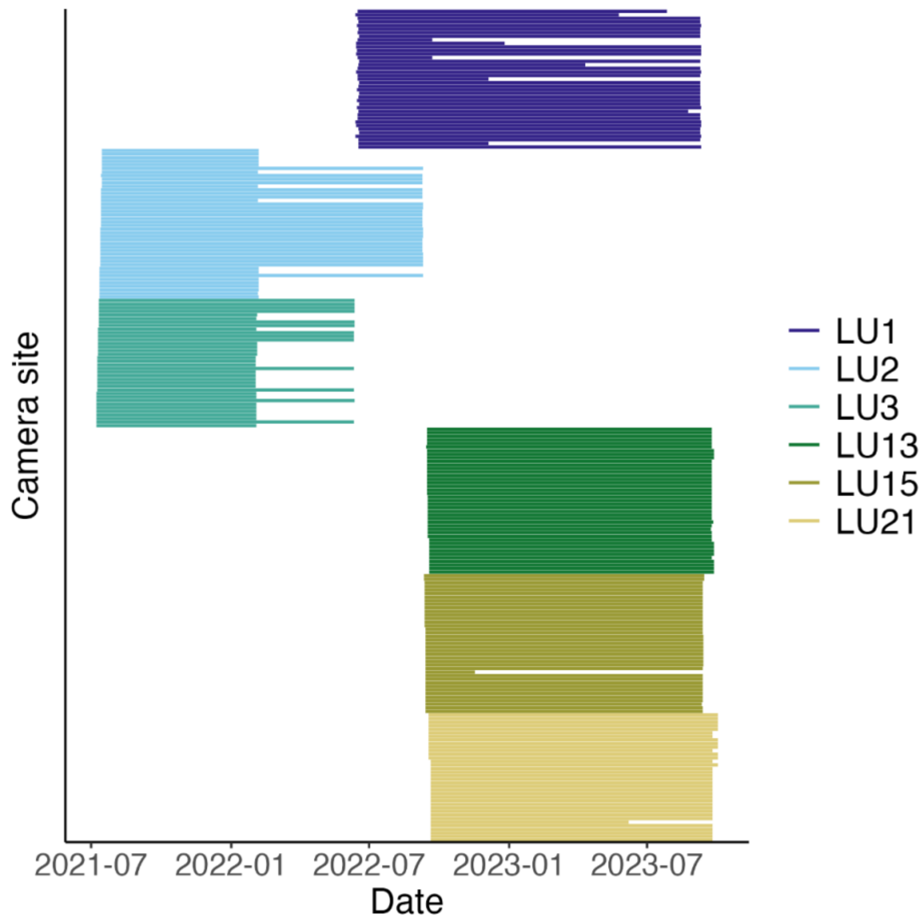

Figure 15. Operability plot across the study period for camera sites (n = 233) deployed in the Oil Sands Region of western Canada, with each line representing one camera. Bars indicate the time each camera was active, categorized and coloured by landscape unit (LU).

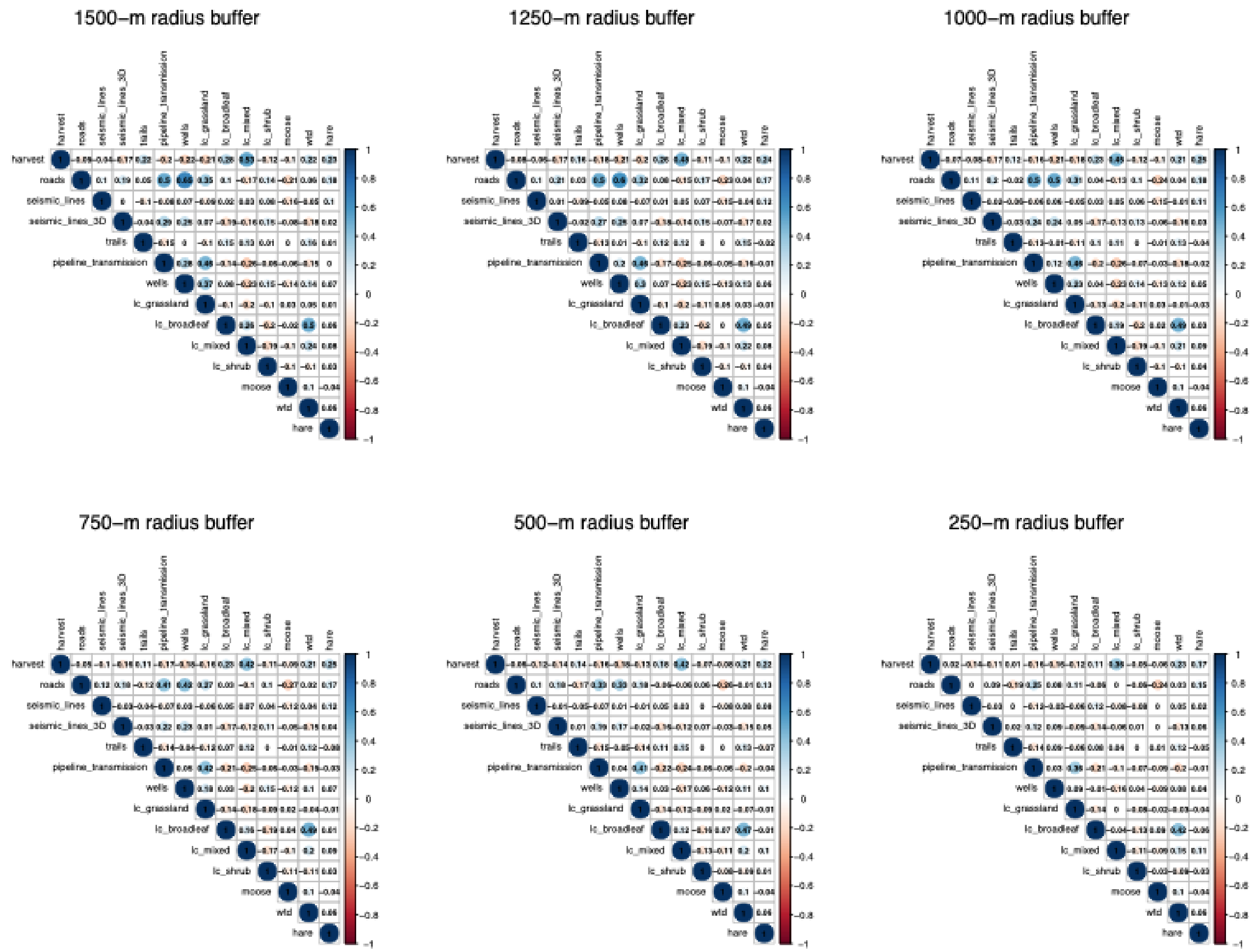

Figure 16. Pearson's correlation coefficient plots for the unscaled landscape variables and species total detections included in the candidate generalized linear mixed models explaining black bear occurrence frequency in the Oil Sands Region of western Canada. Correlation coefficients were calculated at six buffer radii around camera sites. For species variables, correlations were based on total detections across all seasons combined.

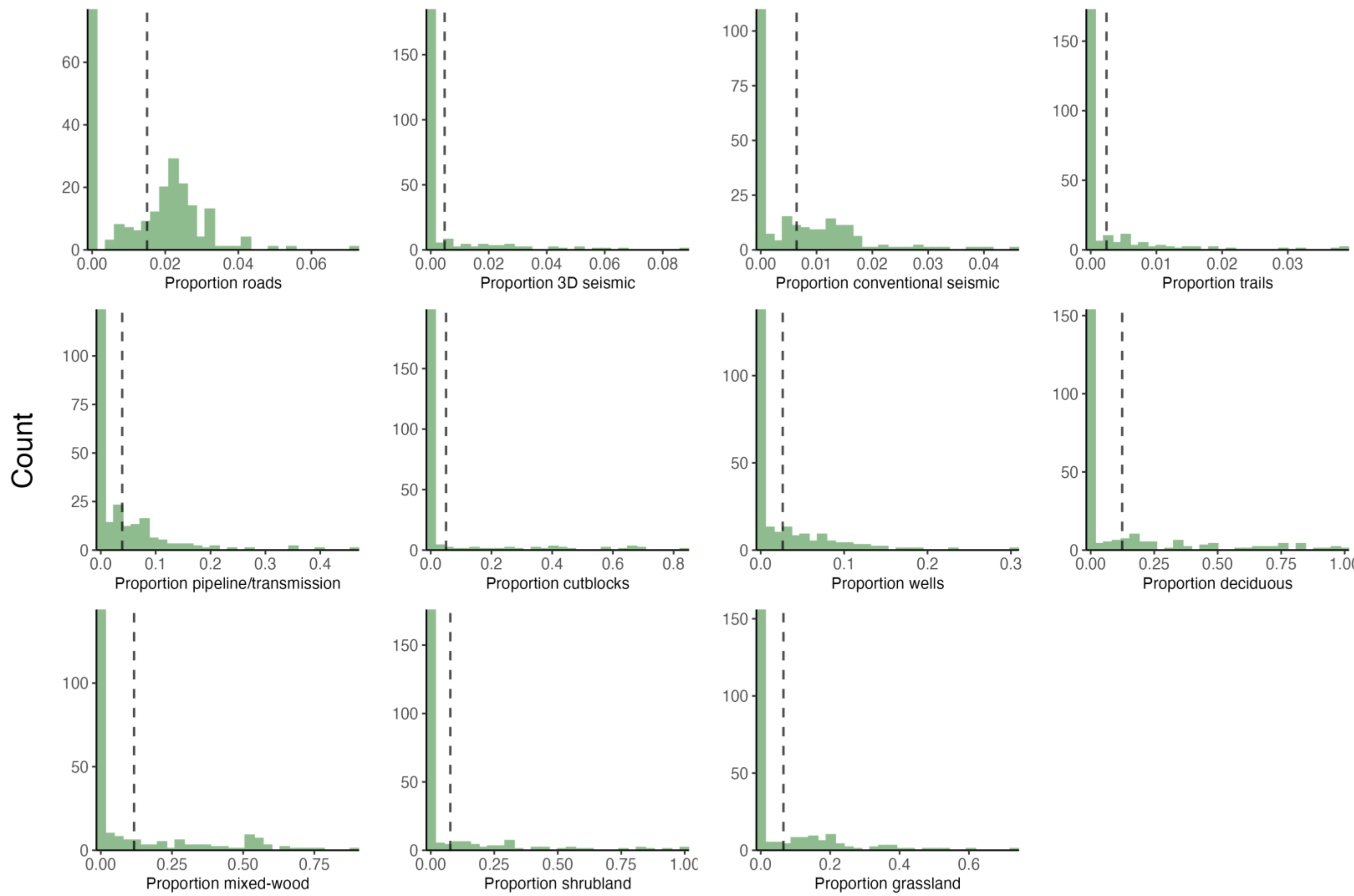

Figure 17. Histograms showing the proportion of landscape covariates within a 250-m radius buffer around camera sites (n = 233) in the Oil Sands Region of western Canada. "Count" is the number of sites within each bin. Dashed lines indicate the mean proportion of each covariate across all sites.

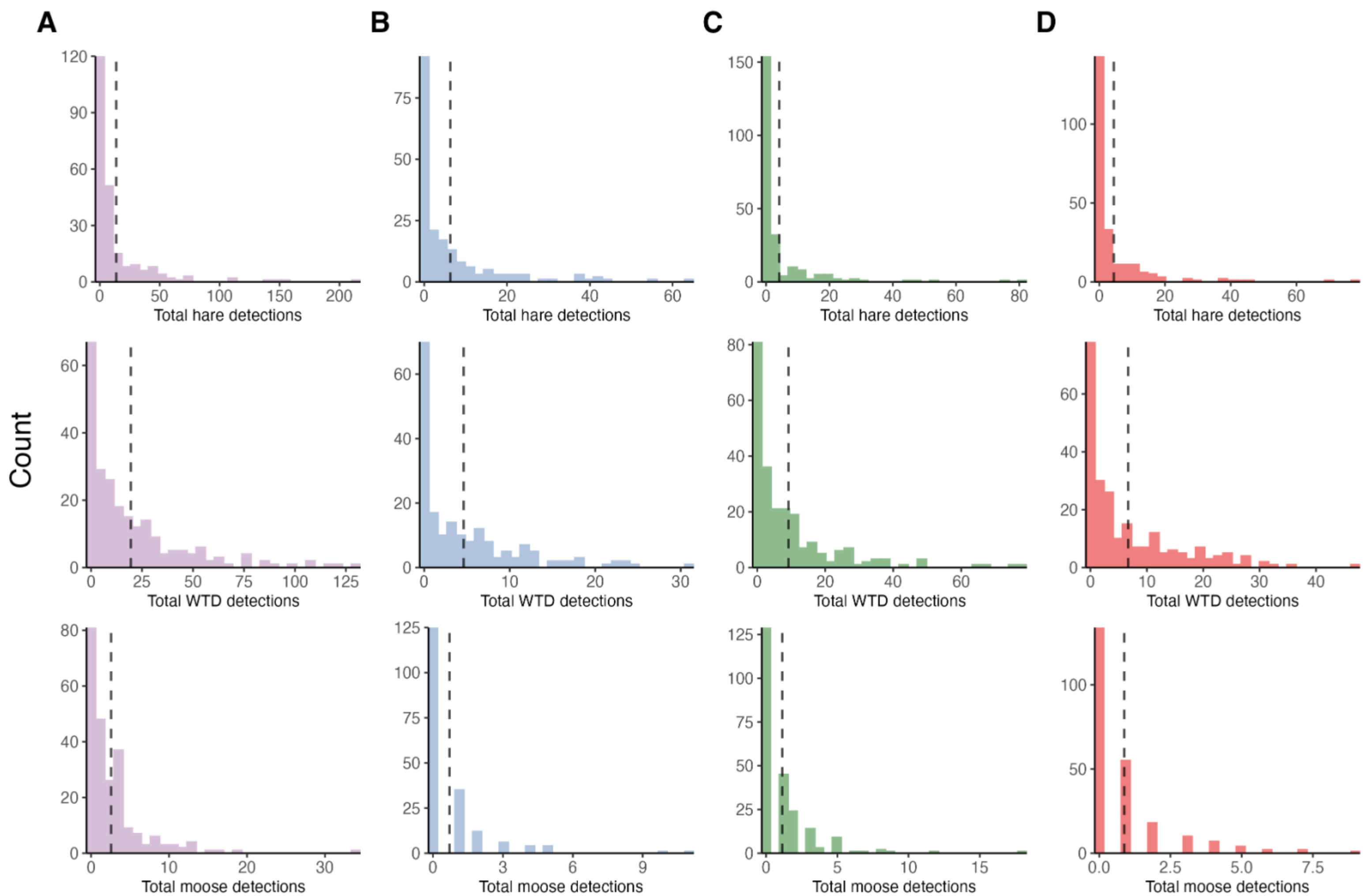

Figure 18. Histograms showing the distribution of total independent detections for moose, white-tailed deer (WTD), and snowshoe hare at camera sites (n = 233) in the Oil Sands Region of western Canada. “Count” is the number of sites within each bin. Dashed lines indicate the mean total detections across all sites. Columns are labelled and coloured by sampling period: A) All seasons combined (n = 233), B) Spring (n = 188), C) Summer (n = 231), D) Fall (n = 233).

Table 7. Model selection results for the global generalized linear mixed model explaining black bear occurrence frequency in the Oil Sands Region of western Canada at six spatial scales. Model selection was conducted by season and across seasons for solitary adult black bears, and across seasons for female with young black bears. Reported metrics are negative log-likelihood (*Log-Lik*), Akaike information criterion corrected for small sample size (*AICc*), difference in *AICc* score from the top model (Δ*AICc*), and model weight (*AICc*w). All models had 16 degrees of freedom.

Demographic	Season	Buffer radius (m)	Log-Lik	AICc	ΔAICc	AICcw
Solitary adult	Spring	**250**	**-238.20**	**511.58**	**0.00**	**0.95**
		500	-241.35	517.87	6.29	0.04
		1500	-243.42	522.02	10.43	0.01
		1250	-245.33	525.84	14.26	0.00
		1000	-246.12	527.41	15.83	0.00
		750	-246.37	527.92	16.34	0.00
Solitary adult	Summer	**250**	**-392.67**	**819.87**	**0.00**	**0.38**
		1000	-392.96	820.46	0.58	0.28
		1250	-393.23	820.99	1.12	0.22
		1500	-394.09	822.71	2.84	0.09
		750	-395.74	826.03	6.15	0.02
		500	-396.69	827.91	8.04	0.01
		250	**-299.32**	**633.17**	**0.00**	**0.99**
		1000	-305.29	645.09	11.92	0.00
		1250	-305.64	645.80	12.63	0.00

Demographic	Season	Buffer radius (m)	Log-Lik	AICc	ΔAICc	AICcw
Solitary adult	Fall	500	-305.80	646.13	12.96	0.00
		1500	-306.20	646.92	13.76	0.00
		750	-306.48	647.48	14.31	0.00
Solitary adult	All	**250**	**-572.03**	**1,178.58**	**0.00**	**1.00**
		500	-581.91	1,198.34	19.76	0.00
		1000	-582.23	1,198.98	20.41	0.00
		1250	-582.28	1,199.08	20.50	0.00
		1500	-582.59	1,199.69	21.12	0.00
		750	-584.94	1,204.40	25.82	0.00
Female with young	All	**250**	**-521.08**	**1,077.13**	**0.00**	**0.55**
		1500	-522.19	1,079.36	2.23	0.18
		1000	-522.98	1,080.93	3.81	0.08
		1250	-523.11	1,081.18	4.05	0.07
		500	-523.35	1,081.66	4.53	0.06
		750	-523.40	1,081.76	4.64	0.05

Table 8. The top candidate model identified to explain solitary adult black bear occurrence in each season with and without including a random effect of landscape unit (LU). Reported metrics are degrees of freedom (*df*), negative log-likelihood (*Log-Lik*), Akaike information criterion corrected for small sample size (*AICc*), difference in *AICc* score from the top model (Δ*AICc*), and model weight (*AICc*w). All models had 16 degrees of freedom.

Season	Top model	Random effect (LU)	df	Log-Lik	AICc	ΔAICc	AICcw
Spring	Prey + Roads	No	**5**	**-244.06**	**498.44**	**0.00**	**0.74**
		Yes	6	-244.06	500.58	2.13	0.26
Summer	OHV	Yes	**6**	**-395.47**	**803.31**	**0.00**	**0.85**
		No	5	-398.24	806.74	3.44	0.15
Fall	Prey + Linear	No	**9**	**-302.66**	**624.12**	**0.00**	**0.75**
		Yes	10	-302.66	626.31	2.18	0.25
All	Prey + Linear	Yes	**10**	**-577.77**	**1,176.54**	**0.00**	**0.87**
		No	9	-580.75	1,180.31	3.77	0.13

Table 9. Intercept-only models used to determine the appropriate random effects structure for modelling the female with young black bear dataset in the Oil Sands Region of western Canada. Candidate structures included camera site only, landscape unit (LU) only, camera site nested within LU, and a null model. Reported metrics are model degrees of freedom (*df*), negative log-likelihood (*Log-Lik*), Akaike information criterion corrected for small sample size (*AICc*), difference in *AICc* score from the top model (Δ*AICc*), and model weight (*AICc*w).

Model	**df**	**Log-Lik**	**AICc**	**ΔAICc**	**AICcw**
LU and site (nested)	**3**	**-537.30**	**1,080.64**	**0.00**	**0.61**
Site only	2	-538.78	1,081.57	0.93	0.39
LU only	2	-581.62	1,167.27	86.63	0.00
Null	1	-598.71	1,199.42	118.78	0.00

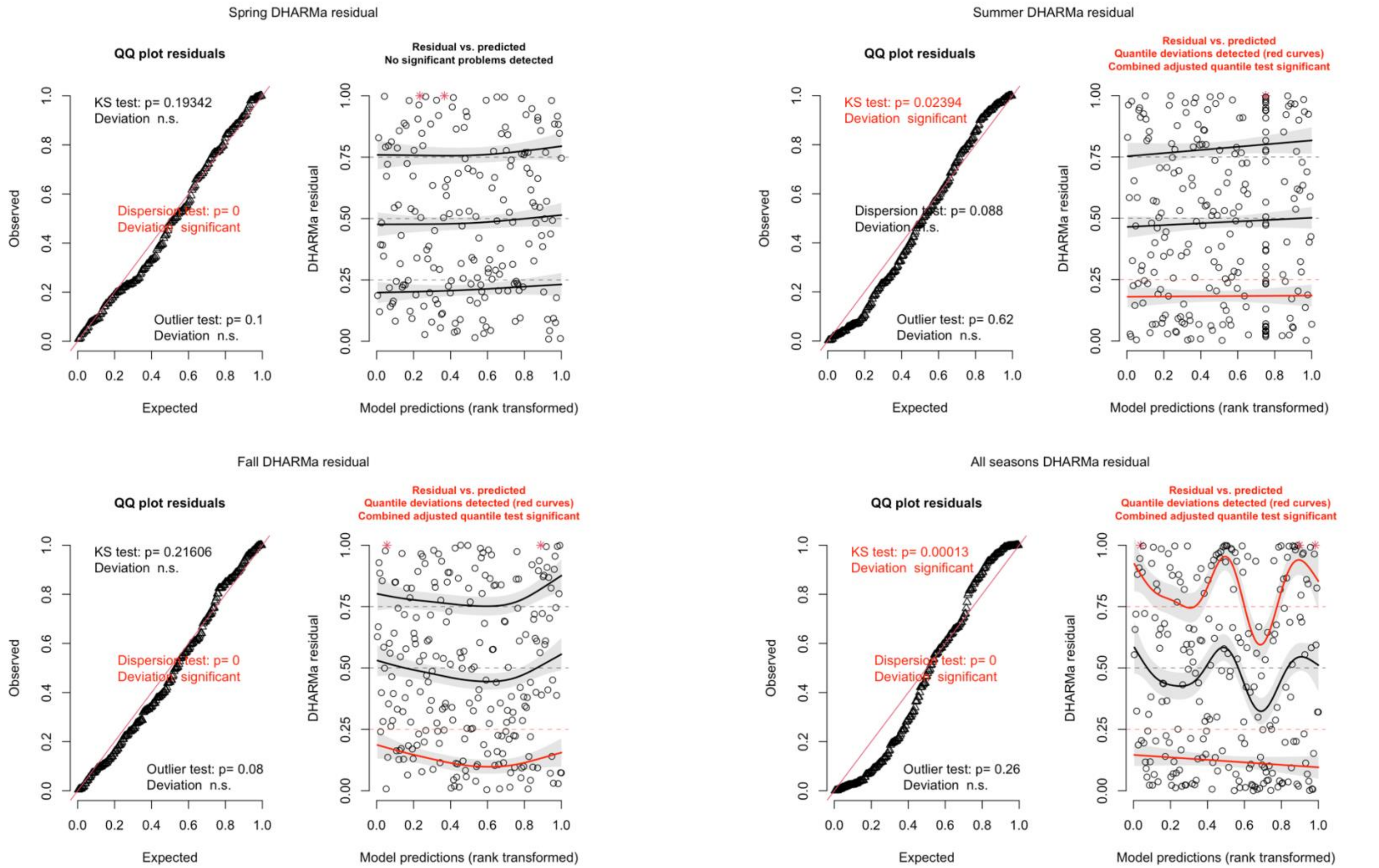

Figure 19. Model diagnostic plots for the top model explaining solitary adult black bear occurrence in the spring, summer, fall, and across all seasons combined. Plots were generated using simulated residuals from the *DHARMa* package in R to assess fit and potential violations of model assumptions.

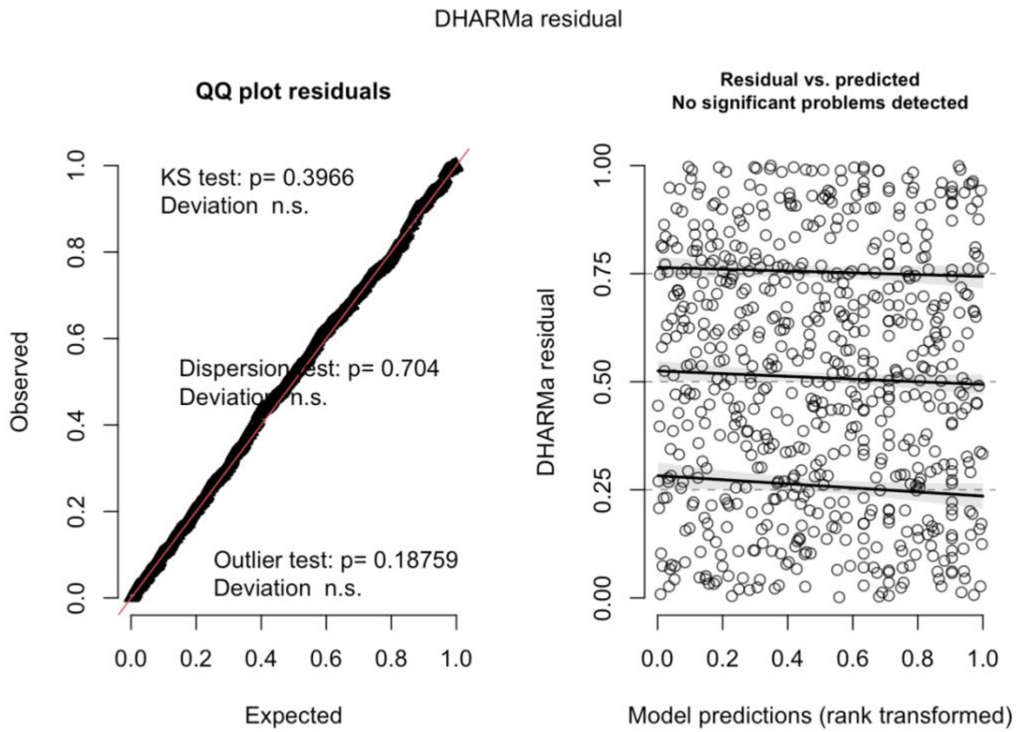

Figure 20. Model diagnostic plot for the top model explaining female with young black bear occurrence frequency. The plot was generated using simulated residuals from the *DHARMa* package in R to assess fit and potential violations of model assumptions.

Table 10. Model selection results for generalized linear mixed models (GLMMs; see Tables 2 and 3) assessing black bear occurrence frequency by demographic group and season in the Oil Sands Region of western Canada. Reported metrics are model degrees of freedom (*df*), negative log-likelihood (*Log-Lik*), Akaike information criterion corrected for small sample size (*AICc*), difference in *AICc* score from the top model (Δ*AICc*), and model weight (*AICc*w).

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
Solitary adult	Spring	**Prey + Roads**	**6**	**-244.06**	**500.58**	**0.00**	**0.83**
		Prey + Linear	10	-241.40	504.04	3.46	0.15
		Prey + Linear + Polygonal	12	-241.15	508.07	7.50	0.02
		Prey	5	-250.74	511.81	11.23	0.00
		Global	16	-238.46	512.10	11.52	0.00
		Roads	3	-254.76	515.65	15.08	0.00
		Prey + OHV + Polygonal	11	-246.98	517.46	16.88	0.00
		Linear	7	-252.28	519.18	18.60	0.00
		Linear + Polygonal	9	-251.94	522.88	22.31	0.00
		Open natural	4	-259.79	527.80	27.22	0.00
		Polygonal + Open natural	6	-259.19	530.84	30.27	0.00
		Open natural + Forest	6	-259.25	530.97	30.39	0.00
		Null	1	-265.07	532.16	31.58	0.00
		OHV	6	-259.98	532.42	31.84	0.00
		Polygonal	4	-262.38	532.97	32.40	0.00
		Forest	4	-262.47	533.15	32.57	0.00

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
		OHV	**6**	**-395.47**	**803.31**	**0.00**	**0.67**
		Linear	7	-395.34	805.18	1.87	0.26
		Linear + Polygonal	9	-395.33	809.47	6.17	0.03
		Prey + Linear	10	-394.60	810.21	6.90	0.02
		Prey + OHV + Polygonal	11	-394.69	812.59	9.28	0.01
		Roads	3	-404.21	814.53	11.22	0.00
		Prey + Linear + Polygonal	12	-394.60	814.63	11.33	0.00
Solitary adult	Summer	Open natural	4	-403.80	815.77	12.46	0.00
		Forest	4	-404.87	817.91	14.60	0.00
		Open natural + Forest	6	-403.07	818.52	15.22	0.00
		Polygonal	4	-405.25	818.67	15.37	0.00
		Polygonal + Open natural	6	-403.60	819.58	16.27	0.00
		Prey	5	-404.73	819.73	16.42	0.00
		Prey + Roads	6	-403.70	819.78	16.48	0.00
		Global	16	-392.67	819.89	16.58	0.00
		Null	1	-411.76	825.53	22.23	0.00
		Prey + Linear	**10**	**-302.66**	**626.31**	**0.00**	**0.43**
		Linear	7	-306.57	627.63	1.33	0.22
		Prey + Linear + Polygonal	12	-301.59	628.59	2.28	0.14

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
		Prey + Roads	6	-308.63	629.63	3.33	0.08
		Linear + Polygonal	9	-305.56	629.93	3.63	0.07
		Roads	3	-312.37	630.84	4.53	0.04
		Global	16	-299.68	633.87	7.57	0.01
Solitary adult	Fall	OHV	6	-311.68	635.73	9.43	0.00
		Prey + OHV + Polygonal	11	-307.17	637.54	11.24	0.00
		Open natural	4	-315.22	638.62	12.31	0.00
		Polygonal + Open natural	6	-314.08	640.53	14.22	0.00
		Prey	5	-315.17	640.61	14.30	0.00
		Open natural + Forest	6	-315.12	642.61	16.30	0.00
		Polygonal	4	-317.24	642.66	16.36	0.00
		Forest	4	-318.49	645.15	18.84	0.00
		Null	1	-331.32	664.66	38.36	0.00
		Prey + Linear	**10**	**-577.77**	**1,176.54**	**0.00**	**0.69**
		Global	16	-572.40	1,179.32	2.78	0.17
		Prey + Linear + Polygonal	12	-577.29	1,180.01	3.47	0.12
		Prey + OHV + Polygonal	11	-581.00	1,185.20	8.66	0.01
		Linear	7	-589.36	1,193.22	16.68	0.00
		Prey + Roads	6	-590.46	1,193.29	16.75	0.00

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
		Linear + Polygonal	9	-588.55	1,195.90	19.36	0.00
Solitary adult	All	OHV	6	-594.41	1,201.20	24.66	0.00
		Prey	5	-597.13	1,204.52	27.98	0.00
		Roads	3	-600.66	1,207.43	30.89	0.00
		Open natural	4	-602.29	1,212.75	36.21	0.00
		Polygonal + Open natural	6	-601.42	1,215.22	38.68	0.00
		Open natural + Forest	6	-601.63	1,215.64	39.10	0.00
		Polygonal	4	-608.60	1,225.38	48.84	0.00
		Forest	4	-608.99	1,226.16	49.62	0.00
		Null	1	-631.22	1,264.46	87.92	0.00
		Linear x Season	**11**	**-483.19**	**988.78**	**0.00**	**0.78**
		Roads x Season	8	-487.69	991.60	2.81	0.19
		Linear x Season + Polygonal x Season	17	-480.24	995.45	6.67	0.03
		Prey x Season + Linear x Season	20	-479.92	1,001.17	12.39	0.00
		Prey x Season + Roads x Season	17	-484.62	1,004.20	15.42	0.00
		Roads + Prey	17	-484.62	1,004.20	15.42	0.00
		OHV x Season	8	-494.13	1,004.49	15.70	0.00
		Open natural x Season	11	-491.85	1,006.11	17.32	0.00
		Season	5	-498.39	1,006.87	18.08	0.00

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
		Prey x Season + Linear x Season + Polygonal x Season	26	-477.18	1,008.62	19.83	0.00
		Open natural x Season + Forest x Season	17	-488.07	1,011.10	22.32	0.00
		Forest x Season	11	-494.78	1,011.98	23.19	0.00
		Polygonal x Season + Open natural x Season	17	-489.70	1,014.37	25.58	0.00
		Polygonal x Season	11	-496.33	1,015.07	26.29	0.00
		Prey x Season	14	-494.63	1,017.92	29.14	0.00
		Prey x Season + OHV x Season + Polygonal x Season	23	-487.46	1,022.68	33.90	0.00
Female with young	All	Roads	4	-528.76	1,065.59	76.81	0.00
		Prey + Linear	8	-525.02	1,066.27	77.48	0.00
		Linear	5	-528.34	1,066.77	77.99	0.00
		Prey + Linear + Polygonal	10	-524.44	1,069.22	80.43	0.00
		Linear + Polygonal	7	-527.83	1,069.84	81.06	0.00
		Forest	5	-534.09	1,078.27	89.48	0.00
		Prey	6	-533.15	1,078.43	89.64	0.00
		OHV	4	-536.34	1,080.75	91.96	0.00
		Prey + OHV + Polygonal	9	-531.39	1,081.06	92.27	0.00

Demographic	Season	Model name	df	Log-Lik	AICc	ΔAICc	AICcw
		Open natural + Forest	7	-533.85	1,081.87	93.09	0.00
		Polygonal	5	-536.49	1,083.07	94.29	0.00
		Open natural	5	-537.20	1,084.50	95.71	0.00
		Polygonal + Open natural	7	-536.41	1,086.98	98.20	0.00
		Null	1	-598.71	1,199.42	210.64	0.00

Table 11. Standard deviation of random effect terms included in the top models explaining black bear occurrence frequency by demographic group and season in the Oil Sands Region of western Canada. For solitary adults, the landscape unit (LU) where cameras were deployed was included as a random effect to account for spatial structure. For females with young, camera site was nested within LU due to differences in data structure (i.e., multiple rows per site across seasons) to avoid pseudoreplication.

Demographic	Season	Top model	Random effect	Standard deviation
Solitary adult	Spring	Prey + Roads	LU	0.00004
	Summer	OHV	LU	0.27
	Fall	Prey + Linear	LU	0.00006
		Linear	LU	0.08
	All	Prey + Linear	LU	0.19
Female with young	All	Linear x Season	Site	1.16
			LU	0.00006

Table 12. Beta coefficient estimates for fixed effects from the best-supported models (within 2 ΔAICc of the top model) in the candidate sets (see Table 2 and Table 3) predicting black bear occurrence frequency by season and demographic group in the Oil Sands Region of western Canada. Confidence intervals are 95%.

Demographic	Season	Model name	Variable	Beta estimate	Standard error	P-value	Lower CI	Upper CI	VIF
Solitary adult	Spring	Prey + Roads	(Intercept)	-1.53	0.09	0.00	-1.70	-1.35	NA
			Roads	-0.36	0.10	0.00	-0.55	-0.17	1.09
			Hare	0.13	0.09	0.14	-0.04	0.29	1.09
			White-tailed deer	0.16	0.08	0.04	0.01	0.32	1.00
			Moose	0.29	0.07	0.00	0.15	0.44	1.05
Solitary adult	Summer	OHV	(Intercept)	-0.75	0.13	0.00	-1.00	-0.51	NA
			Pipelines/ Transmission lines	-0.17	0.09	0.05	-0.34	0.00	1.08
			Seismic lines	-0.10	0.06	0.13	-0.22	0.03	1.05
			3D Seismic lines	-0.17	0.08	0.04	-0.34	-0.01	1.02
			Trails	0.17	0.06	0.00	0.06	0.29	1.03
			(Intercept)	-1.69	0.08	0.00	-1.86	-1.53	NA
			Roads	-0.37	0.09	0.00	-0.55	-0.19	1.29
			Seismic lines	-0.19	0.08	0.02	-0.35	-0.03	1.01
			3D Seismic lines	-0.12	0.09	0.22	-0.30	0.07	1.05

			Pipelines/ Transmission lines	-0.30	0.12	0.01	-0.53	-0.07	1.16
		Prey + Linear	Trails	-0.01	0.07	0.87	-0.15	0.13	1.06
			Hare	0.14	0.07	0.03	0.01	0.27	1.06
			White-tailed deer	0.12	0.07	0.10	-0.02	0.26	1.07
Solitary adult	Fall		Moose	0.05	0.07	0.46	-0.09	0.19	1.10
			(Intercept)	-1.68	0.09	0.00	-1.85	-1.50	NA
			Pipelines/ Transmission lines	-0.33	0.13	0.01	-0.59	-0.07	1.15
			Roads	-0.33	0.10	0.00	-0.51	-0.14	1.12
		Linear	Seismic lines	-0.18	0.09	0.05	-0.36	0.00	1.10
			3D Seismic lines	-0.11	0.09	0.22	-0.29	0.07	1.02
			Trails	-0.01	0.08	0.92	-0.16	0.14	1.15
			(Intercept)	-1.24	0.09	0.00	-1.41	-1.07	NA
			Roads	-0.14	0.05	0.01	-0.25	-0.04	1.19
			Seismic lines	-0.12	0.05	0.01	-0.21	-0.03	1.07
			3D Seismic lines	-0.17	0.05	0.00	-0.28	-0.06	1.05
Solitary adult	All	Prey + Linear	Pipelines/ Transmission lines	-0.10	0.05	0.07	-0.20	0.01	1.11
			Trails	0.09	0.04	0.02	0.02	0.17	1.15
			Hare	0.08	0.04	0.03	0.01	0.15	1.04

			White-tailed deer	0.06	0.04	0.17	-0.03	0.15	1.11
			Moose	0.15	0.04	0.00	0.07	0.23	1.12
Female with young	All	Linear x Season	(Intercept)	-2.49	0.15	0.00	-2.79	-2.20	NA
			Fall	-1.39	0.21	0.00	-1.79	-0.99	1.75
			Spring	-1.16	0.21	0.00	-1.56	-0.75	1.75
			Roads	-0.66	0.14	0.00	-0.93	-0.38	1.37
			OHV linear features	0.07	0.13	0.60	-0.19	0.33	1.19
			Fall x Roads	0.24	0.20	0.22	-0.15	0.63	1.95
			Spring x Roads	0.37	0.21	0.08	-0.05	0.78	1.95
			Fall x OHV linear features	-0.67	0.31	0.03	-1.27	-0.06	2.17
			Spring x OHV linear features	-0.43	0.28	0.12	-0.98	0.12	2.17

Table 13. Beta coefficient estimates for fixed effects from the polygonal features model predicting solitary adult black bear occurrence in the Oil Sands Region of western Canada. The model was run separately per season (spring, summer, fall).

Season	Variable	Beta estimate	Standard error	P-value
Spring	(Intercept)	-1.49	0.13	0.00
	Cutblocks	0.03	0.09	0.72
	Wells	-0.12	0.11	0.27
Summer	(Intercept)	-0.73	0.14	0.00
	Cutblocks	0.03	0.06	0.64
	Wells	0.03	0.06	0.69
Fall	(Intercept)	-1.62	0.19	0.00
	Cutblocks	0.08	0.07	0.25
	Wells	-0.12	0.10	0.22

Appendix B: Chapter 3 supplementary results

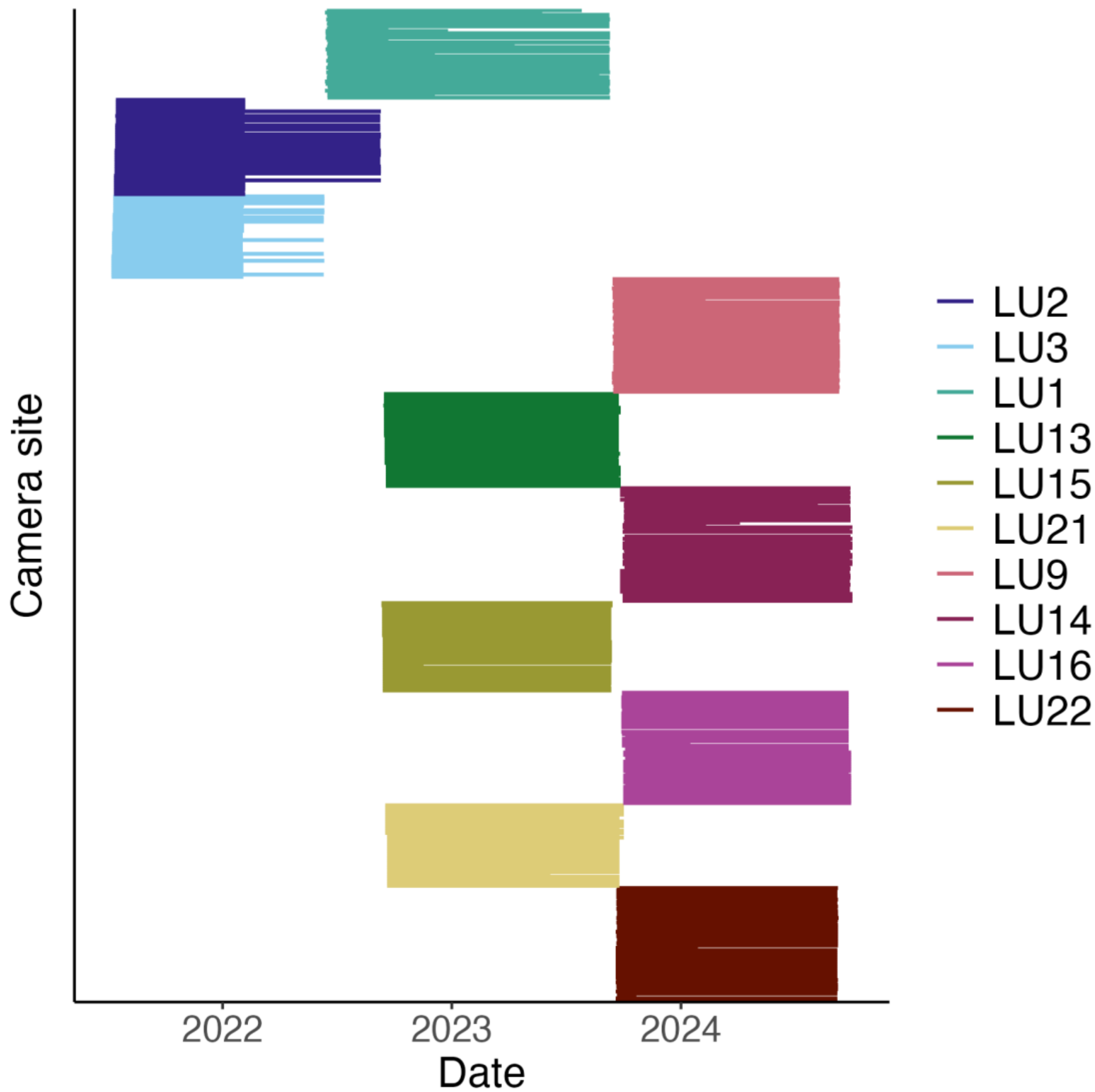

Figure 21. Operability plot across the study period for camera sites (n = 430) deployed in the Oil Sands Region of western Canada, with each line representing one camera. Bars indicate the time each camera was active, categorized and coloured by landscape unit (LU).

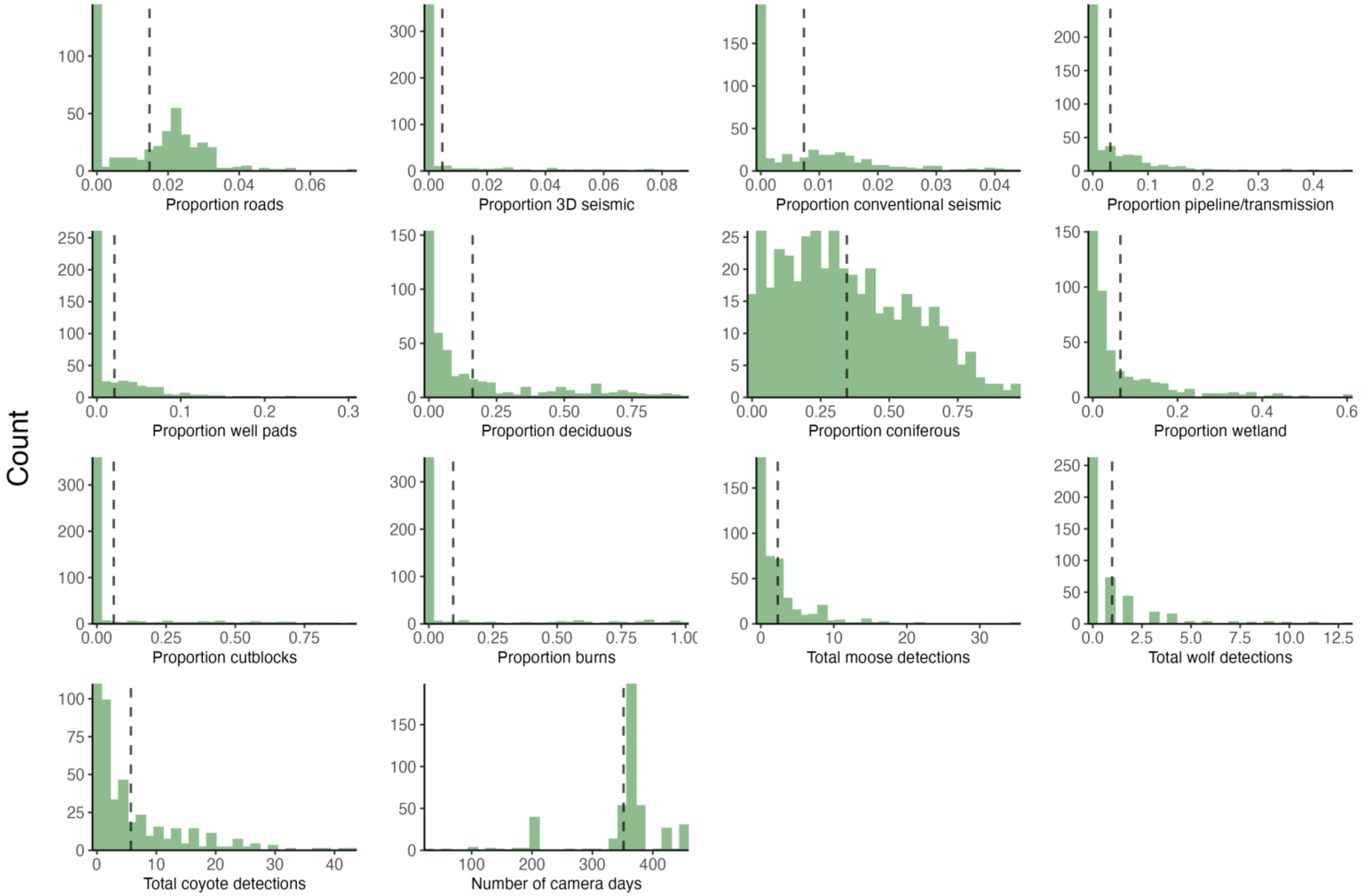

Figure 22. Histograms showing the proportion of landscape covariates within 250-m radius buffer and total detections of species at each camera site included in the piecewise structural equation model with causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada. Number of camera days per site is also included. "Count" is the number of sites (n = 430), and dashed lines represent the mean value across sites.

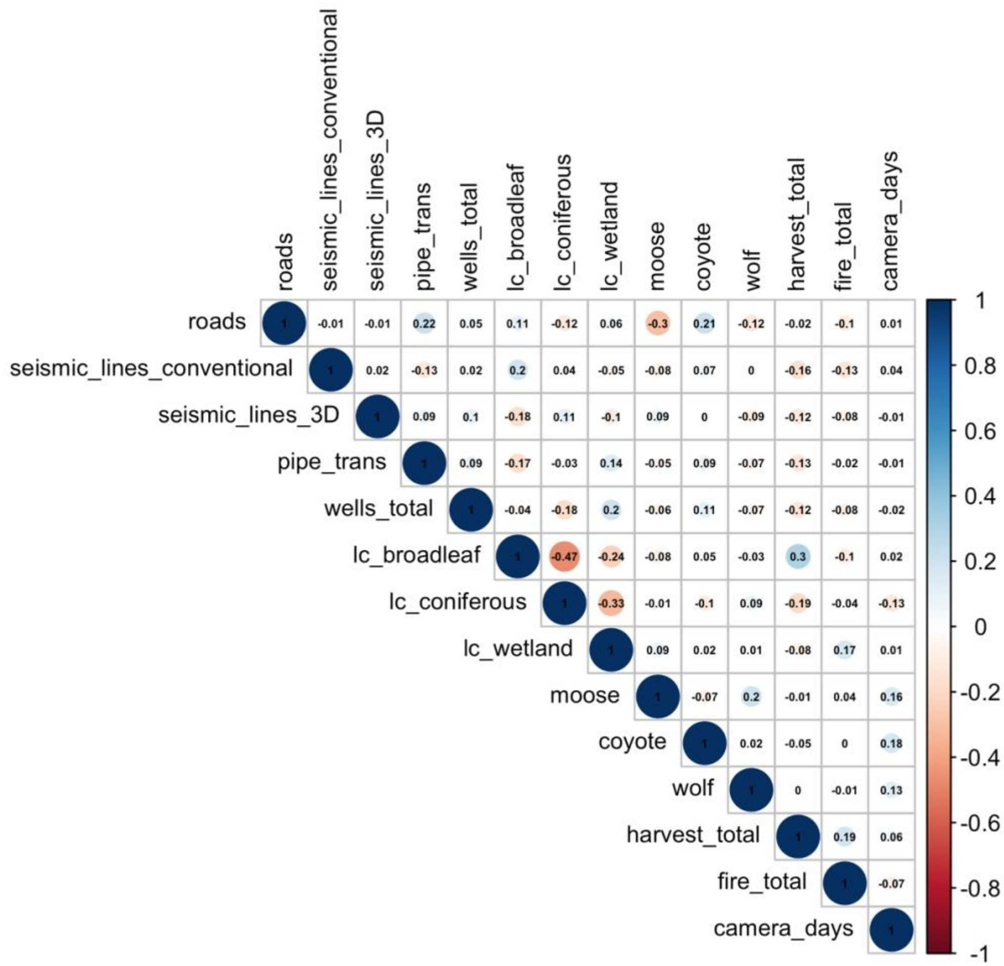

Figure 23. Pearson's correlation coefficient plots for the unscaled landscape variables and species total detections included in the component generalized linear mixed models for each species at the 250-m spatial scale. Component models were combined in a piecewise structural equation model containing causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada

Table 14. The component model for each species with and without including the random effect of landscape unit (LU). Component models were combined in a piecewise structural equation model containing causal pathways predicted to influence moose occurrence in the Oil Sands Region of western Canada. Per model, *df* is the degrees of freedom, *Log-Lik* is the negative log-likelihood, *AICc* is the Akaike information criteria score corrected for small sample size, Δ*AICc* is the difference in the AICc score from the best supported model, and *AICcw* is the AIC weight.

Species	Random effect (LU)	df	Log-Lik	AICc	ΔAICc	AICcw
Moose	Yes	**21**	**-754.92**	**1554.10**	**0.00**	**1**
	No	20	-801.19	1644.40	90.33	0
Wolf	Yes	**7**	**-558.376**	**1131.00**	**0.00**	**0.98**
	No	6	-563.350	1138.90	7.88	0.02
Coyote	Yes	**7**	**-1126.28**	**2266.80**	**0.00**	**1**
	No	6	-1176.53	2365.30	98.43	0