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# Grey wolves (*Canis lupus*) shift selection of anthropogenic landscape features following predator control in the Nearctic boreal forest

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ABSTRACT

Conserving endangered species sometimes involves killing their predators. In the case of Nearctic wolves (*Canis lupus*), rarely are lethal control measures examined for ancillary effects on predator behaviour or community responses in a before-after design. We examined wolf relative abundance and spatial distribution in a northwestern boreal forest landscape for three years before and after the onset of wolf culling intended to conserve threatened woodland caribou (*Rangifer tarandus caribou*). We hypothesized that wolf occurrence would increase with density of anthropogenic features created by landscape development before the cull, but that wolves would avoid anthropogenic features after the cull due to associated mortality risk. We used generalized linear models in an information-theoretic framework to weigh evidence for our hypotheses. Post-control, independent wolf detections decreased to 24 % of pre-cull numbers, but wolves maintained 75 % of their distribution. Pre-control, wolves were positively associated with linear features, presumably for hunting efficiency, but post-cull wolves were negatively associated with these features. Thus, wolf control caused not only a numerical reduction of wolf numbers, but also a functional change in wolf behaviour that could further reduce predation pressure on caribou. However, post cull wolf occurrence was more strongly associated with anthropogenic block features which provide forage for alternate prey, potentially subsidizing their fast recovery. Conservation actions involving predator mortality alter landscape-scale distributions and behaviors of surviving predators, with potential indirect effects for the mammal community.

## 1. Introduction

Predator control is a common tool for managing prey populations and conserving species at-risk (Boertje et al., 1996; Hayes et al., 2003; Hervieux et al., 2014). It has been criticized for lacking rigorous accompanying research, such as the responses of non-target sympatric species (Johnson et al., 2022; Lennox et al., 2018; Treves et al., 2016). Apex predators regulate ecosystem structure through consumptive effects (e.g. predation) and non-consumptive effects (e.g. fear, competition) on both prey and mesopredators (Terborgh and Estes, 2010), thus impacting heterospecifics' abundance and distribution (Hairston et al., 1960; Soulé et al., 1988). Despite predators' importance they are often perceived as negatively impacting humans (Lennox et al., 2018); predators were, and are now, lethally controlled for hunting, livestock, or conservation objectives (Clark and Hebblewhite, 2021; Packer et al., 2009; Reynolds and Tapper, 1996). Extant research has focused on target species' numerical changes (Brown and Conover, 2011; Hayes et al., 2003; Hervieux et al., 2014) and recently on "mesopredator release" (Berger et al., 2008; Crooks and Soulé, 1999). There is less information on whether predator control induces behavioural changes within the surviving predator populations (Treves et al., 2016). For example, habitat selection behaviour may be altered after a lethal population reduction, wherein a new risk is induced that changes risk/reward trade-offs (Sih, 1984; Sih and Del Giudice, 2012).

Habitat selection is driven by endogenous traits such as movement ability (Avgar et al., 2011), animal personality (Leclerc et al., 2016; Stamps and Groothuis, 2010), and by exogenous factors such as resource availability, (Langvatn and Hanley, 1993), intra- and interspecific competition (Morris, 2003; Rosenzweig, 1981) and predation risk (Brown, 1999; Gilliam and Fraser, 1987; Lima and Dill, 1990). Predator habitat use is driven largely by prey availability, in that predators select habitat that will maximize encounters with prey (Lima and Dill, 1990) – typically areas with high prey densities (Carbone and Gittleman, 2002) and/or their prey's preferred resources (Mitchell and Lima, 2002). In

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addition, predators will select habitat such as linear features that facilitate movement across the landscape (Avgar et al., 2011) to reduce search times and increase prey encounter rates (McKenzie et al., 2012). However, with human-induced mortality risk intensified (and made aerial) via predator control tactics such as aerial gunning, predator habitat selection criteria could shift from prey availability only, to a trade-off between prey acquisition and perceived risk avoidance (Lima and Dill, 1990; Rosenzweig, 1991; Ruprecht et al., 2021). Moreover, anthropogenic landscape features have the potential to amplify this risk vs. reward trade-off simply due to the presence of humans (Khan et al., 2023; Lesmerises et al., 2012). While anthropogenic features may be beneficial for predators by increasing movement, prey encounter, and predation rates (McKenzie et al., 2012), these features may also be associated with increased exposure risk via reduced escape cover, thus increasing perceived risk of human-induced mortality (Cristescu et al., 2013; Llaneza et al., 2016; Mysterud and Ostbye, 1999; Ordiz et al., 2011).

### 1.1. *Grey wolf population reduction to aid boreal woodland caribou recovery*

Woodland caribou are one of the most threatened prey species in the northern circumpolar region. Caribou population declines in the Canadian boreal forest are ultimately attributed to the loss of old-growth habitat due to increased industrial activity, and proximally to wolf predation (Boutin et al., 2012; Hebblewhite, 2017; Nagy-Reis et al., 2021): wolves use anthropogenic linear features to increase movement rates, encounter rates, and hence predation rates (Latham et al., 2011a; McKenzie et al., 2012). Ungulates including caribou (Dickie et al., 2020; Tattersall et al., 2020b), invasive white-tailed deer *Odocoileus virginianus* (Darlington et al., 2022; Fuller et al., 2023) and native moose (*Alces alces*) (Barnas et al., 2024; Fisher and Ladle, 2022) heavily use these linear features as well, so they are sources of wolf prey. Additionally, polygonal anthropogenic "block" features such as cutblocks, petroleum well sites, and open industrial sites also provide prey subsidies for these ungulates (though without the movement subsidies of linear features) (Darlington et al., 2022; Fisher et al., 2020). Ergo, wolves too are positively associated with these block features (Fisher and Burton, 2018; Fisher et al., 2021; Fisher and Ladle, 2022).

Artificially elevated grey wolf populations increase predation risk for caribou through apparent competition (Holt, 1977) with deer and moose (James et al., 2004; Latham et al., 2011a; Serrouya et al., 2021) and so wolf culls have been identified as the most timely approach to stemming caribou declines (Serrouya et al., 2019), with ongoing criticism (Darimont and Paquet, 2024). We had the opportunity to conduct the first before-and-after study of wolves' spatial response to culling. In a highly industrialized part of the Canadian boreal forest, we used a multi-year camera trap dataset collected before and after the onset of government-mandated wolf population control (Alberta Environment and Parks, 2017), independently of that control. We hypothesized that wolf control – which is largely done by aerial shooting in open areas, especially along linear features (Bridger, 2019) – would trigger a trade-off in wolf habitat selection between prey acquisition and exposure risk. We predicted wolves would adjust their use of landscapes (reflected in change in relative abundance, or rate of occurrence at camera traps) depending on the level of perceived risk from human persecution. Before wolf population reduction, we expected wolf occurrence to increase with linear features that facilitate movement and prey availability, as well as areal anthropogenic features and natural habitat associated with their primary prey. After the onset of wolf population reduction, we expected wolf occurrence to decrease with anthropogenic landscape features without escape cover, thus increasing their exposure risk to aerial gunning, at the expense of access to the primary prey in these landscape features.

As caribou predation risk is a function of both number of wolves and their behaviour, investigating survivors' use of landscapes post-control is key to understanding how the mechanisms of woodland caribou declines are reduced – or may persist – following this contentious management decision.

## 2. Methods

### 2.1. *Study area*

We examined wolf relative abundance and distribution in the Nearctic boreal forest of western Canada (Fig. 1) where energy development, forest harvesting, and transportation infrastructure have created a novel anthropogenic landscape (Barnas et al., 2024; Pickell et al., 2013; Pickell et al., 2015). Novel features include linear features – such as petroleum exploration "seismic" lines (Dabros et al., 2018), pipelines, and roads – and polygonal (block) features, such as well sites and cutblocks (Fig. 2). The 3500 km$^2$ study area of mixedwood boreal forest ca. 350 km northeast of Edmonton, Alberta is a mosaic of mixedwood, coniferous, and deciduous forest, as well as bogs, fens, lakes, and rivers. The area overlaps the Cold Lake and East Side Athabasca River (ESAR) caribou ranges (Appendix A.1) whose populations have consistently declined since monitoring began in 1999 (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010; Hervieux et al., 2013). Pursuant to recovery measures outlined in the Species at Risk Act's Recovery Strategy for boreal woodland caribou (Environment and Climate Change Canada, 2020), government-mandated wolf control programs were initiated across western Canada intended to reverse boreal woodland caribou population decline and achieve self-sustaining populations (Alberta Environment and Parks, 2017; Serrouya et al., 2021; Serrouya et al., 2019).

In the winter of 2016/2017, the wolf population reduction started in our study area, which we had previously researched extensively (Burgar et al., 2019; Fisher and Burton, 2018). The government deemed aerial gunning via helicopter in winter the most efficient and humane control method for wolves as it facilitates rapid removal and reduces the risk of collateral deaths of non-target species, compared to poisoning (Bridger, 2019). The pre-cull population was estimated at 7.7 wolves per 1000 km$^2$ but this number may represent distinct packs rather than total wolves (Burgar et al., 2019). Between 2017 and 2020, 92 wolves in the greater region were killed, with the target being 95 % wolf reduction (D. Hervieux, personal communication, March 18, 2021). Wolves were targeted by following GPS-collared wolves or snow tracks, and necessarily occurred in open (non-forested) areas, especially anthropogenic linear features; wolves use these preferentially for travel (Dickie et al., 2020; Dickie et al., 2017; Dickie et al., 2022).

### 2.2. *Wolf relative abundance and distribution*

Three years before the onset of wolf population reduction, we deployed a camera array in the study area to examine mammals' response to landscape change (Fisher and Burton, 2018, 2021; Wittische et al., 2021). We had used a stratified random design to capture natural heterogeneity (Fig. 1a). Sampling cells were determined by overlaying a 1 km × 1 km cell grid across the study area in ArcGIS 10.2 Spatial Analyst (ESRI Inc., Redlands, CA) and partitioned into strata defined by canopy cover, tree species, and topography. We randomly selected (constrained by access and a minimum of 2-km apart) an equal number of cells in each stratum; within those cells we deployed one unbaited Reconyx PC900 Hyperfire infrared remote digital camera facing an active game trail to maximize detection probability of medium- to large-sized mammals (Fisher and Burton, 2018). Cameras were set to high sensitivity and no delay between triggers. Cameras were accessed primarily by roads and trails, so these landscape features were disproportionately sampled within 250-m radius of each site. At >250-m radii these features are sampled as they occur in the landscape (see multiscale analysis in Fisher and Burton (2018)). "Site" is defined as the detection zone of an individual camera trap (about 30–50-m radius in a ca. 60$^0$

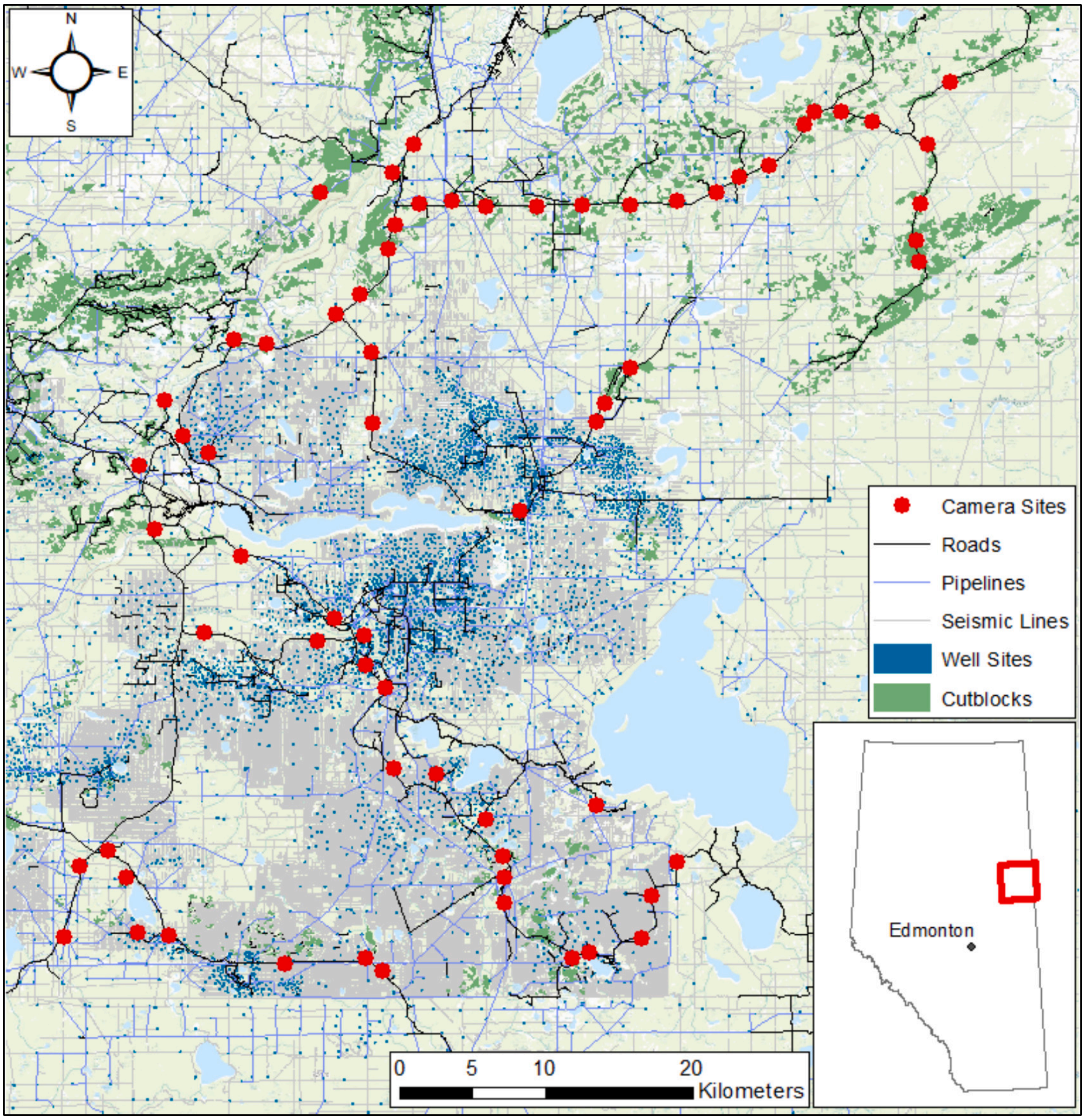

**Fig. 1.** Map of camera trap locations within the study area. The ~3500 km$^2$ study area is located approximately 350 km northeast of Edmonton, Alberta. The landscape has experienced significant disturbance from industrial practices, with high densities of anthropogenic features associated with oil and gas exploration and extraction and timber harvesting.

hemisphere), and "study area" is defined as the ~3500 km$^2$ polygon surrounding all sites.

Camera traps operated across 61 sites from October 2011 to October 2014. After the onset of wolf population reduction, we re-deployed 60 cameras at original locations (or within 250-m) between October 2017 and October 2020. Sites were visited annually to collect camera data and replace batteries. Wolf control began in the winter of 2016/2017; thus, we classified the camera data based on whether it was collected pre-control (2011–2014) or post-control (2017–2020). We processed camera trap images and extracted metadata using Timelapse 2 version 2.2.2.4 (Greenberg et al., 2019; http://saul.cpsc.ucalgary.ca/timelapse/).

In the R statistical package (R Core Team, 2017) we summed wolf detection events by month to create a proportional binomial response variable called "occurrence frequency" whereby a wolf was detected (1) or not (0) monthly at each site (Chow-Fraser et al., 2022; Fisher and Burton, 2021; Fisher et al., 2021). This variable is sufficiently sensitive to detect variation in site use imposed by temporary emigration, while reducing zero-inflation induced by absences caused by movement. Thus, a wolf absence within an entire month is considered a true zero and not a false absence (MacKenzie et al., 2017; Neilson et al., 2018; Stewart et al., 2018). Occurrence frequency was generated across 35 months pre-control (November 2011 – September 2014) and 35 months post-control (November 2017 – September 2020).

### 2.3. *Natural and anthropogenic landscape features*

We quantified the proportion of natural and anthropogenic landcover features within variably sized buffers around the camera traps. Natural landcover was quantified using Alberta Vegetation Inventory (Alberta Agriculture Forestry and Rural Economic Development, 2005). Anthropogenic landcover was derived from Alberta Biodiversity Monitoring Institute's (ABMI) Human Footprint Inventory (Alberta Biodiversity Monitoring Institute, 2017a, 2017b, 2019). These two data sources are disparate so sums of proportions can exceed 100 %. Given the growing industrial footprint throughout the study area, we accounted for temporal changes in anthropogenic landcover by calculating the amount of anthropogenic habitat classes from spatial data collected before (2010) and after (2016) the start of wolf population reduction (Appendix A2). Consistent with a rapidly developing landscape the proportion of roads, pipelines, forest cutblocks, and seismic lines increased, whereas exploration 3D seismic lines decreased; forest

**Fig. 2.** Anthropogenic features include linear features such as roads, pipelines, seismic lines, and 3-D seismic lines ("hashtag" patterned), and block (polygonal) features such as cutblocks (irregular shapes) and well sites (small square shapes).

cover decreased.

We derived landscape variables (Table 1) grouped according to three ecological mechanisms hypothesized to influence wolf occurrence: prey habitat, movement ability, and exposure risk (Table 2). We assumed all anthropogenic features and natural features with <6 % crown closure would have greater exposure to human persecution risk via aerial gunning due to lower vegetation height and canopy cover relative to other natural features (Llaneza et al., 2016). Prey availability was estimated as monthly occurrence of each large prey species– caribou, moose, and white-tailed deer.

We assessed collinearity among predictor variables by calculating variance inflation factor (VIF), and kept variable sets where VIF < 3 indicating a lack of collinearity among predictor variables (Zuur et al., 2010). We jointly scaled (mean = 0, s.d. = 1) pre-control and post-control predictor variables to allow for comparisons of coefficient estimates before and after wolf population reduction.

### 2.4. Statistical analysis

We modelled pre-control and post-control wolf occurrence to test whether habitat associations differed before and after the onset of wolf population reduction, and which associated ecological drivers most influenced observed patterns (Table 2). We used generalized linear models (GLM) (McCullagh and Nelder, 1989) with a binomial distribution (logit link function). All analyses were performed using R statistical software (R Core Team, 2017).

Species' habitat selection can vary depending on the spatial scale at which one quantifies available habitat (Fisher et al., 2011; Levin, 1992) so we modelled wolf occurrence at multiple spatial scales. Global generalized linear models included variables quantifying proportions of all natural and anthropogenic landcover within 250-m to 2000-m radii surrounding sites, in 250-m intervals. Akaike's Information Criterion corrected for small sample sizes (AICc) and AICc weights (Burnham and Anderson, 2002) were treated as evidence of the strength of habitat selection at that particular spatial scale, a common approach (Fisher et al., 2011; Holland et al., 2004; Holland et al., 2005) (Appendix A.3).

At the best-supported spatial scale, we built competing models for both pre-control and post-control periods based on our hypotheses (Table 2). Empirical support for each hypothesis was evaluated using AICc scores (Burnham and Anderson, 2002), model diagnostics plots, deviance explained, and k-fold cross validation from the *boot* package (Canty and Ripley, 2021) in R to evaluate prediction error (Appendix A.4).

## 3. Results

### 3.1. Effects of population reduction on wolf relative abundance and distribution

Although wolf spatial distribution only decreased by 25 % post-control (pre-control: 92 % of sites; post-control: 67 % of sites) (Fig. 3b), the number of independent wolf detections (truncated to 30-min intervals) decreased 76 % in the post-control sampling period (pre-control: 509 detections; post-control: 122 detections) (Fig. 3a).

**Table 1**

Landcover types quantified within the study area. Landcover data sources are as follows: AVI = Alberta Vegetation Inventory, 1987–2014; UALF = University of Alberta Linear Features Map Updated 2012; $^1$ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2010; $^2$ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2016; $^3$ABMI = Alberta Biodiversity Monitoring Unit Human Footprint Layer, updated 2017; Aw = Aspen; Pb = Poplar; Bw = White birch; Sb = Black spruce; Sw = White spruce; Fb = Balsam fir; Lt = Larch/tamarack; d = Dry; m = Mesic; w = Wet; a = Aquatic. $^4$Combined functionally similar landcover classes to reduce skew in distributions. $^5$Omitted from both pre-control and post-control analysis to prevent collinearity with other variables.

| Predictor variable | Pre-control source | Post-control source | Description |
|---|---|---|---|
| Upland Deciduous$^4$ | AVI | AVI | (Aw, Pb, Bw ≥ 70 % canopy cover), |
| Upland Mixedwood$^4$ | AVI | AVI | 40–60 % canopy cover, moisture = d or m |
| Lowland Deciduous$^4$ | AVI | AVI | (Aw, Pb, Bw ≥ 70 % canopy cover), |
| Lowland Mixedwood$^4$ | AVI | AVI | 40–60 % canopy cover, moisture = w or a |
| Upland Spruce | AVI | AVI | (Sb, Sw, Fb ≥ 70 % canopy cover), moisture = d or m |
| Lowland Spruce | AVI | AVI | (Sb, Sw, Fb ≥ 70 % canopy cover), moisture = w or a |
| Tamarack | AVI | AVI | Lt ≥ 70 % |
| Pine$^5$ | AVI | AVI | Pj ≥ 70 % |
| Upland Shrubs$^5$ | AVI | AVI | > 25 % shrub cover; < 6 % tree cover; moisture = d or m |
| Nonforest$^5$ | AVI | AVI | Areas with <6 % canopy |
| Open Wetland | AVI | AVI | < 6 % crown closure; moisture = w or a |
| Water | AVI | AVI | Standing or flowing water |
| Cutblock | ABMI$^1$ | ABMI$^3$ | Forest harvest areas |
| Seismic Line | UALF | ABMI$^3$ | Traditional, single petroleum exploration line |
| 3-D Seismic Line | UALF | ABMI$^3$ | 3-D seismic petroleum exploration line, deployed in a high-density hashtag pattern |
| Pipeline | ABMI$^1$ | ABMI$^2$ | Petroleum pipelines, typically wide and grass-covered |
| Road | ABMI$^1$ | ABMI$^3$ | Combination of road and rail (hard surface or vegetated verge) |
| Trail | ABMI$^1$ | ABMI$^3$ | Combination of trails and truck trails |
| Well Site | ABMI$^1$ | ABMI$^3$ | Petroleum extraction sites, including well and surrounding area |
| Block Feature$^5$ | ABMI$^1$ | ABMI$^3$ | Combination variable including borrow pits, dugouts, sumps, industrial sites, other disturbed vegetation |

### 3.2. *Effects of population reduction on drivers of wolf occurrence*

Before population reduction, wolf occurrence was best explained by anthropogenic linear features associated with movement subsidies at the 250-m scale: ($AIC_{cw} = 0.915$, deviance explained (DE) = 0.11) (Table 3, “movement ability model”). The prey habitat, exposure risk, and prey occurrence models that included other landscape features – forests and wetlands, cutblocks, well sites, and heterospecifics – explained comparatively little variability in wolf occurrence. Combined $AIC_w$ of these models = 0.085, which is analogous to saying there is an 8.5 % chance these models and associated variables best explained wolf occurrence.

After the onset of population reduction, wolf occurrence was associated predominantly with natural and anthropogenic landscape features associated with exposure risk at the 500-m scale ($AIC_{cw} = 0.986$, DE = 0.41) (Table 3). Open wetland, water, cutblocks, well sites, roads, pipelines, seismic lines, and 3-D seismic lines best explained wolf occurrence (Table 3, line 6, exposure risk model).

**Table 2**

Candidate models to explain wolf occurrence.

Candidate models to test the relative effect of preferred prey habitat, relative abundance of prey, movement ability and landcover associated with exposure risk on monthly wolf occurrence after the onset of wolf population reduction. Predicted direction of response is given as positive (+), negative (−), or unknown (u).

| Hypothesis – wolf occurrence best explained by: | Predictor variables |
|---|---|
| Prey habitat | Upland Deciduous/Mixedwood (+)<br>Lowland Deciduous/Mixedwood (+)<br>Upland Spruce (−)<br>Lowland Spruce (−)<br>Tamarack (u)<br>Open Wetland (+)<br>Water (u)<br>Cutblock (+)<br>Well Site (+) |
| Prey occurrence | Caribou (+)<br>Moose (+)<br>White-tailed deer (+) |
| Movement ability | Trail (+)<br>Road (−)<br>Pipeline (+)<br>Seismic Line (+)<br>3-D Seismic Line (−) |
| Exposure risk | Open Wetland (−)<br>Water (−)<br>Cutblock (−)<br>Well Site (−)<br>Road (−)<br>Pipeline (−)<br>Seismic Line (−)<br>3-D Seismic Line (−) |

Critically, the magnitude and/or direction of wolves’ relationships to anthropogenic features differed before and after culling (Fig. 4). Pre-cull, wolf occurrence increased with higher road density ($\beta = 0.370$ [0.119, 0.621]); post cull, wolf occurrence decreased with greater road density ($\beta = -0.546$ [−0.939, −0.153]). Pre-cull, wolf occurrence was neutral to seismic lines ($\beta = -0.106$ [−0.244, 0.032]) and pipelines ($\beta = -0.004$ [−0.123, 0.115]) (Fig. 4a), but post-cull, wolf occurrence strongly decreased with higher densities of these linear features (seismic $\beta = -0.568$ [−0.909, −0.227]; pipelines $\beta = -0.844$ [−1.261, −0.427]) (Fig. 4b).

Conversely, prior to the cull wolves were neutral to anthropogenic block features such as cutblocks ($\beta = 0.044$, SE = 0.048, $p = 0.366$) and well sites ($\beta = -0.048$, SE = 0.050, $p = 0.339$), as estimated in the unsupported “exposure risk” and “prey habitat” models, respectively. However, after the onset of culling, wolf occurrence increased (Fig. 4b) with increasing proportion of cutblocks ($\beta = 0.369$ [0.150, 0.588], $p < 0.001$) and well sites ($\beta = 0.519$ [0.268, 0.771], $p < 0.001$). Based on odds ratios, with each % increase in cutblocks in the landscape wolves were 1.44 times more likely to occur; with increasing proportion of well sites, wolves were 1.68 times more likely to occur.

In summary, the effect size of seismic lines on wolf occurrence was 5.4-fold greater post-cull; for pipelines, 211-fold greater post-cull; for cutblocks, 8.4-fold greater post-cull; and for well sites, 10.8-fold greater post-cull. Wolves were neutral, or showed a weak response, to other features before and after the cull (Fig. 4a,b).

## 4. Discussion

### 4.1. *Wolves habitat associations shifted following population reduction*

Wolf population control in the western Nearctic boreal forest triggered behavioural changes in the remaining population. Aerial gunning removed 92 wolves over three years, dropping relative abundance by 76 %, as indicated by camera-trap detections. Behavioural shifts were

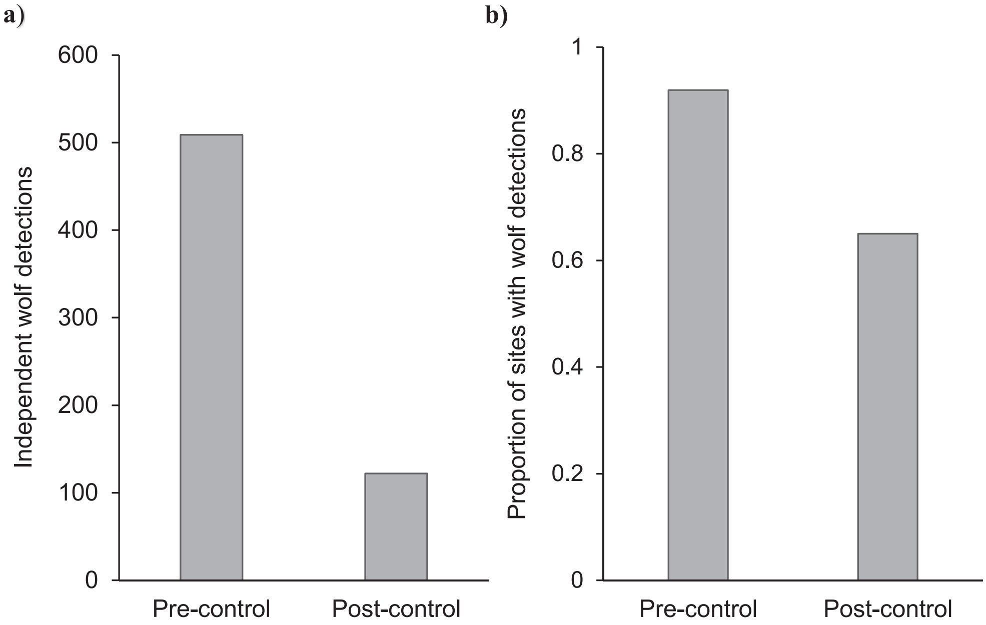

**Fig. 3.** Grey wolf relative abundance and distribution during the pre-control and post-control sampling period in the Christina Lake study area. Total number of independent wolf detections throughout the pre-control (November 2011 – September 2014) and post-control (November 2017 – September 2020) sampling periods, and (b) the proportion of sites in the pre-control and post-control sampling periods where wolves were independently detected.

**Table 3**

AICc table of pre-control and post-control candidate models of wolf occurrence.

AICc scores for pre-control and post-control candidate models of monthly wolf occurrence. The table includes AICc, model intercept, log-likelihood, delta (Δ) AICc and AICc weight for each model. Models are listed from most-supported to least-supported in each sampling period.

| Sampling period | Hypothesis | Intercept | df | log-lik | AICc | ΔAICc | AICcw |
|---|---|---|---|---|---|---|---|
| Pre-control | Movement ability | −1.839 | 6 | −183.795 | 381.1 | 0.00 | 0.915 |
| | Exposure risk | −1.857 | 9 | −182.755 | 387.0 | 5.85 | 0.049 |
| | Prey habitat | −1.947 | 10 | −181.694 | 387.7 | 6.58 | 0.034 |
| | Null | −1.773 | 1 | −195.508 | 393.1 | 11.96 | 0.002 |
| | Prey occurrence | −1.787 | 4 | −194.605 | 397.9 | 16.79 | 0.000 |
| Post-control | Exposure risk | −2.698 | 9 | −85.818 | 193.2 | 0.00 | 0.986 |
| | Movement ability | −2.662 | 6 | −94.113 | 201.8 | 8.58 | 0.014 |
| | Prey occurrence | −3.940 | 4 | −106.836 | 222.4 | 29.16 | 0.000 |
| | Null | −3.178 | 1 | −114.224 | 230.5 | 37.28 | 0.000 |
| | Prey habitat | −3.514 | 10 | −103.896 | 232.3 | 39.05 | 0.000 |

observed among survivors: pre-cull, wolf occurrence was positively associated with anthropogenic features offering movement subsidies that facilitate prey acquisition (sensu (Dickie et al., 2017; McKenzie et al., 2012)). Post-cull, wolves avoided those linear features, now associated with greater mortality risk. Wolves switched to anthropogenic block features – patches of early seral vegetation embedded in the forest matrix. Both linear and block features support ungulates (Dickie et al., 2020; Fisher and Burton, 2021; Tattersall et al., 2020b). There is no evidence that ungulates stop using linear features after wolf culls, so we attribute wolves' response as risk avoidance of linear features, replaced by a much stronger association with polygonal features for prey access. Previous research showed that wolves change diel activity behaviour in response to culls, with effects that ripple through to competitors and ungulates (Ethier et al., 2024; Frey et al., 2022). Here we show that predator control triggers different spatial-feature associations among the surviving wolf population. Consistent with our hypotheses, we contend these shifts signal a change in risk-reward value for widespread anthropogenic patches in the boreal matrix.

### 4.2. *Wolves avoided anthropogenic linear features following population reduction*

Before the onset of population reduction, wolf occurrence frequency was positively associated with the proportion of roads and seismic lines. Wolf use of these features is widely known in boreal and northern mountain systems (Boucher et al., 2022; Dickie et al., 2020; Dickie et al., 2017; Whittington et al., 2011; Whittington et al., 2005). Following the onset of population reduction, wolf occurrence was strongly and negatively associated with these features.

Aerial gunning uses a combination of a "Judas wolves" (radio- or GPS-collared animals that guide shooters to the pack) and snow-tracking to acquire targets. Long, open linear features lend themselves to aerial tracking and spotting wolves to shoot (D. Hervieux, pers. comm.). Our evidence suggests this new mortality risk shifts the perceived value of anthropogenic linear features for surviving wolves. Predators typically select habitat that decreases exposure risk to humans and, conversely, avoid habitat that increases exposure risk to humans in anthropogenic landscapes (Cristescu et al., 2013; Llaneza et al., 2016). However, predator associations with the landscape are not static, and can vary depending on their level of perceived risk relative to available resources (Cristescu et al., 2013; Llaneza et al., 2016; Llaneza et al., 2012).

This is the first examination of wolf spatial distribution before and after a cull, so analogues elsewhere in the world are sparse. In the Iberian peninsula, refuge from humans was the best predictor of wolf occurrence (Grilo et al., 2019). Similarities for other species exist; for instance, Scandinavian brown bears (*Ursus arctos*) shifted their resting

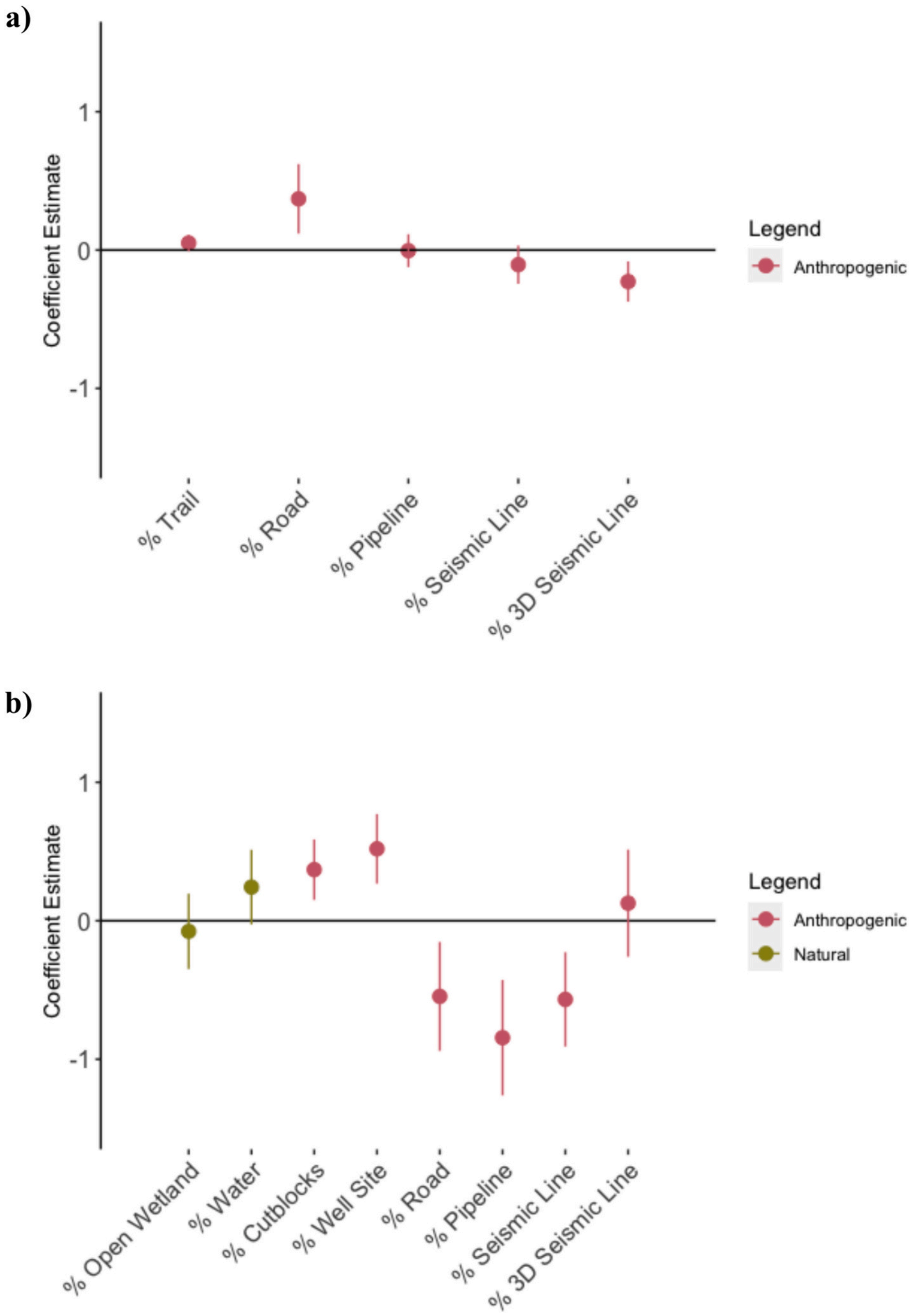

**Fig. 4.** Coefficient plots of top-ranked pre-control and post-control wolf occurrence models. Coefficient plots of top-ranked (a) pre-control and (b) post-control wolf occurrence models according to AICc scores. The top-ranked pre-control model was the movement ability model, which included the proportion of trails, roads, pipelines, seismic lines, and 3-D seismic lines as predictor variables. The top-ranked post-control model was the exposure risk model, which included the proportion of open wetland, water, cutblocks, well sites, roads, pipelines, seismic lines, and 3-D seismic lines as predictor variable.

site selection to sites with greater concealment and further from human settlements during the hunting season when detection risk by humans was highest (Ordiz et al., 2011); even moose hunting elicited a bear avoidance response (Brown et al., 2023).

### *4.3. Wolf occurrence is associated with anthropogenic block features following population reduction*

We predicted wolves would avoid all anthropogenic features associated with exposure risk after population reduction, but surviving wolves were negatively associated only with linear features. Contrary to our predictions, wolves were much more strongly associated with anthropogenic block features (cutblocks and well sites) post-cull than they were pre-cull. In retrospect this response makes sense, as aerial gunning follows linear flightlines along wolf-pack tracks, which follow linear features. In contrast block features are typically small (ca. 1 ha) and embedded in the forest matrix; moose and white-tailed deer select well sites and cutblocks due to their availability of early seral forage (Fisher et al., 2020; Francis et al., 2021; Latham et al., 2011b). Fisher and Ladle (2022) found that wolf occurrence frequency within anthropogenic block features was facilitated by the frequency of white-tailed deer occurrence. By selecting areas of high anthropogenic block feature density and avoiding areas with anthropogenic linear feature density, wolves are likely continuing to prioritize prey acquisition in these disturbed areas after population reduction. Moreover, local Indigenous knowledge from the boreal indicates wolves hunt (and moose are killed) primarily on the edges between forests and cutblocks or well sites (Fisher et al., 2021). That these reservoirs of prey remain and are heavily exploited post-cull poses questions about wolf rebound after the cessation of culling.

### *4.4. Implications for boreal mammal conservation*

Western boreal mammals must contend with rapid landscape change far outside historical or global analogs (Pickell et al., 2013; Pickell et al., 2015) and mammal species ranging in size from red squirrels (*Tamiasciurus hudsonicus*) to moose are affected (Fisher and Burton, 2018). Most profoundly affected are woodland caribou (Hebblewhite, 2017), and stemming their declines through wolf removals is a key conservation action. However culls address the symptom, not the cause: habitat restoration is ultimately required, and in several studies restoration treatments have reduced use of linear features by wolves and other boreal predators (Beirne et al., 2021; Keim et al., 2021; Tattersall et al., 2020b), hopefully reducing caribou encounters. Restoration has occurred in a small footprint in this study area, with some success (Dickie et al., 2021; Dickie et al., 2022). We contend that beyond this restored footprint, wolf avoidance of linear features after population reduction could further lead to decreased wolf-caribou encounter rates via potential reductions in wolf movement rates across the landscape. However, predator-prey spatiotemporal interactions are complex and change with linear feature characteristics (Beirne et al., 2021; Sun et al., 2021; Tattersall et al., 2020a); wolf density-dependent responses (Dickie et al., 2020) complicate this further. Effective conservation requires long-term monitoring of wolf space-use in a dedicated and robust design.

Wolf association with anthropogenic block features – themselves associated with higher densities of apparent competitors (i.e., moose and white-tailed deer) and which caribou avoid (James et al., 2004) – could facilitate wolf rebound. However again species co-occurrences and hence potential interactions vary with intensity of disturbance (Barnas et al., 2024; Fisher and Ladle, 2022) and so we strongly recommend future studies explicitly test whether predator control facilitates changes in (1) wolf movement rates and (2) spatiotemporal co-occurrence among wolves, caribou, and apparent competitors. Finally, the key question remains: how long will behaviors remain after culls are terminated? Both numerical and functional responses over time will require long-term monitoring of the mammal community after culling, which is currently nonexistent.

### *4.5. Caveats*

While we attributed anthropogenic and natural habitat types with lower canopy cover and vegetation height as being more likely associated with exposure risk to human persecution (Llaneza et al., 2016), we did not explicitly measure exposure risk between habitat types and, therefore, cannot with certainty attribute variation in selection between these features to risk avoidance. Quantification of exposure risk among habitat types using GPS coordinates of individual wolves killed by aerial shooting would be necessary to spatially attribute true risk. However, such data were not available.

Although we test a mechanism of anthropogenic-risk avoidance to explain wolf habitat selection in response to predator control, there are alternate mechanisms that we were not able to directly test. Firstly, density dependence is a known driver of wolf resource selection (Fuller et al., 2003; Kauffman et al., 2007), particularly in areas of high prey density (Cubaynes et al., 2014). Wolf population density estimates before and after predator control were not available and beyond the scope of this study. However density-dependence might be expected to increased selection for preferred linear features, due to reduced intraspecific competition for spatial resources (Cubaynes et al., 2014).

The potential for change in social stability may also be important. Wolves form social groups (packs), and population reduction disrupts wolf social stability with implications for demography (e.g. pack size, age structure, survival rates, genetic diversity, etc.) and behaviour (e.g. hunting skills, territory size, social behaviour, etc.) (Haber, 1996; Wallach et al., 2009). We recommend future studies attempt individual-level identification within the wolf population to generate a metric of social stability, ultimately allowing for differentiation between the influence of persecution risk and social dynamics on habitat selection in response to predator control.

Lastly, while it is possible that changes in wolf spatial associations could be attributed to changes in the availability of certain landscape features due to increasing industrial development within the study area between 2011 and 2020, we could not test for the relative impacts of predator control and landscape change in this study; we had before-after data but not control-impact data. We do not expect changes to the landscape throughout the study period to outweigh the effects of an extensive population reduction. When population reduction rates are high, environmental factors (Rich et al., 2013) and prey availability (Boitani, 2003; Fuller, 1989; Fuller et al., 2003) are weaker determinants of wolf abundance and distribution than population reduction (Bassing et al., 2019). Only when wolf populations are subjected to lower reduction rates (~35 %) do they respond more strongly to landscape change than population reduction (Bassing et al., 2019). However, targeted government-mandated wolf control programs in western Canada typically aim for a much higher population reduction rates (~95 %) (Bridger, 2019).

We recommend that wildlife managers conducting predator control invest in research that implements a before-after control-impact (BACI) study design to allow for empirical testing of the relative effects of predator control and other environmental factors on the wolf population, as well as the broader mammal community.

## 5. Conclusions

Lethal wolf control triggers behavioural shifts in survivors' diel activity behaviour (Frey et al., 2022) and in spatial behaviour, manifested in habitat selection and distribution. Predator control remains a primary strategy in the wildlife conservation toolkit, despite being criticized as a "shot in the dark" for lacking rigorous tests of community-level responses (Lennox et al., 2018; Treves et al., 2016). We suggest each cull should be an adaptive experiment with a purpose-built design that quantifies the population, spatial, and behavioural responses of the predator, the focal species to be conserved, and interacting species. Here we show initial evidence that during the first three years of a wolf cull, wolf distribution changed in ways that may aid caribou recovery, but which may facilitate wolf rebound. Other changes to the mammal community are likely however, and we strongly recommend that all such wildlife conservation actions implementing predator control invest in rigorous research to quantify expected – and unexpected – effects.

## CRediT authorship contribution statement

**Katherine Baillie-David:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John P. Volpe:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Conceptualization. **A. Cole Burton:** Writing – review & editing, Supervision, Resources, Investigation, Conceptualization. **Jason T. Fisher:** Writing – review & editing, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors have no competing statement of interest to declare.

## Data availability

Data will be made available at borealisdata.ca upon acceptance

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110677.

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