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Lethal wolf control elicits change in moose habitat selection in unexpected ways

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Abstract

Moose (*Alces alces*) and woodland caribou (*Ranger tarandus caribou*) are the 2 large prey species for wolves (*Canis lupus*) in the Nearctic boreal forest in North America. Caribou have declined, with widespread anthropogenic disturbance as the ultimate cause and wolf predation as the proximal cause. To conserve caribou the government of Alberta, Canada initiated a wolf control program to reduce predation rates on caribou populations and contribute to caribou population recovery. Predators play an important role in shaping the structure and function of ecosystems through top-down forces. We hypothesized that the strongest factors influencing moose occurrences would reflect changes in predation risk before and after the onset of wolf control. We weighed evidence for competing hypothesis by deploying cameras across a highly industrialized landscape in Alberta for 3 years after wolf control (2017–2020), capitalizing on 3 years of existing data before the onset of wolf control (2011–2014). We created generalized linear models representing competing hypotheses about moose response to natural and anthropogenic landscape features before and after wolf control, examining support for each in an information-theoretic framework. Prior to wolf control, the model containing landscape features providing security cover was best-supported, but this was scale-dependent. After wolf control, the model containing landscape features that offer increased forage opportunities was best-supported. Unexpectedly, the direction of

effect was often opposite to predictions, with moose avoiding some features thought to provide security and forage. We demonstrate that lethal predator control affects the spatial distribution of its primary prey species but in ways we do not fully comprehend, highlighting the need for a better understanding of community dynamics following wolf control.

Prior to widespread anthropogenic change, the North American western boreal forest supported a woodland caribou (*Rangifer tarandus caribou*)–moose (*Alces alces*)–wolf (*Canis lupus*) community. Wolves commonly preyed upon moose in naturally occurring disturbances and regenerating forests, such as burns, which provide early seral vegetation of high forage quality for moose (e.g., trembling aspen [*Populus tremuloides*], white spruce [*Picea glauca*]; James et al. 2004). Sympatric woodland caribou spatially separated themselves from wolves and moose habitat by occupying areas considered poor forage quality for moose (i.e., old growth forests or peatlands; Bergerud et al. 1984, Seip 1992, James et al. 2004). Extensive landscape modification via anthropogenic resource extraction practices (forestry and oil and gas) has transformed the woodland caribou–moose–wolf system in the western boreal forest (Hebblewhite and Fortin 2017). Anthropogenic disturbance has led to a heterogeneous landscape consisting of linear (e.g., seismic lines, roads) and polygonal features (e.g., forest cutblocks, petroleum well sites) interspersed between natural landscape cover (e.g., wetlands, deciduous, mixed wood, coniferous forests) outside the range of historical or contemporary natural variability (Delong and Tanner 1996, Lee and Boutin 2006, Pickell et al. 2015). These resource extraction activities remove mature boreal forests, which support caribou's lichen diet (Johnson et al. 2001). Simultaneously, resource extraction creates anthropogenic features that generate early seral vegetation communities offering high forage quality and quantity to moose (Wolff 1978). This forage also supports newly invaded white-tailed deer (*Odocoileus virginianus*; Fisher and Burton 2021), which are expanding their range because of human land use change and climate change (Dawe et al. 2014). This increased prey abundance has bolstered wolf populations (Latham et al. 2011, 2013), causing declines in woodland caribou populations via apparent competition (DeCesare et al. 2010, Latham et al. 2011, Boutin et al. 2012).

Landscape change is the ultimate source of woodland caribou declines (Wittmer et al. 2007, Hebblewhite and Fortin 2017); however, wolf predation is the proximal mechanism, so lethal wolf control is a caribou recovery strategy employed by wildlife managers (Boutin et al. 2012, Hervieux et al. 2014, Serrouya et al. 2019). Although researchers have investigated the numerical changes of prey populations following predator control (Hayes et al. 2003, Allen et al. 2014, Castle et al. 2021), there is limited research addressing changes in spatial distribution and habitat selection by prey in response to decreased predator density (but see Miner and Stein [1996] for an example). Landscape change coupled with predator population change is expected to incur behavioral responses in animals, such as habitat selection. Given that changes in prey spatial distribution could translate to changes in predator-encounter rates, and ultimately effects on threatened caribou populations via apparent competition (DeCesare et al. 2010, Ehlers et al. 2016, DeMars et al. 2019), understanding the spatial responses of prey to changing predator populations is imperative for conservation practitioners.

Moose are often used as a model herbivore to test key ecological theories about behaviors such as habitat selection (Belovsky 1978, Mabille et al. 2012, Serrouya et al. 2019, Francis et al. 2021, Boucher et al. 2022). Under optimal foraging theory, the time-minimization approach predicts that an animal's fitness does not increase after net energy gained meets its fixed requirement, and that minimizing time spent foraging allows maximization of other

activities including reproduction, thermoregulation, and predator avoidance (Kie 1999). In contrast, the energy-maximization approach predicts that an animal's overall fitness is positively correlated with time spent foraging. Although there is some evidence that moose behave as energy maximizers (Belovsky 1978, 1981), these models do not consider risk of predation on moose foraging strategies, despite extensive evidence that predation risk and the landscape of fear may impose behavioral and physiological costs, which reduce survival and fecundity (Sivy et al. 2017, Kohl et al. 2018). Thus, landscapes with high predator density would further modify forage behavior toward a time-minimization strategy (Kie 1999, Bergman et al. 2001). Changes in moose habitat selection and diets have forced moose into using suboptimal resources in response to predation risk (Edwards 1983), but it is not clear if with decreased predation risk the reverse shift may occur.

Mammal community research projects were being conducted in a highly industrialized boreal forest landscape in the Canadian oil sands (Fisher and Burton 2018, Burgar et al. 2019) when a government-mandated wolf control program was implemented, providing opportunities for before-and-after experiments on the effects of wolf control on behavior in mammal communities. A first analysis showed widespread shifts in diel activities of wolves, competitors, and prey following wolf control (Frey et al. 2022). But the spatial response by these species had not been examined; an observed cascading effect of wolf control onto its sympatric prey would illuminate whether there are unintended consequences of this management practice.

The objective of this study was to contrast hypotheses explaining habitat selection by moose prior to and following lethal wolf control using an information-theoretic approach. Assuming moose use a time-minimization strategy in this predator-dense landscape (Burgar et al. 2019), we hypothesized that before wolf control moose prioritized security by selecting habitat characterized by lower forage quality and quantity but increased canopy and visual cover such as forests and edge habitat. Post-wolf control, we hypothesized moose would forgo security to select more strongly for forage by choosing habitat characterized by higher foraging potential but also increased predator vulnerability such as open, disturbed areas like cutblocks (i.e., clearcuts) and burns with abundant early seral vegetation.

STUDY AREA

The Christina Lake study area is a 3,500-km^2 expanse of western boreal forest approximately 350 km northeast of Edmonton, Alberta, Canada, within Treaty 6 territory (Figure 1). Located at approximately 556 m above sea level, the landscape has a relatively uniform flat topography, with a heterogenous mosaic of coniferous, mixed wood, and deciduous forests along with wetlands, bogs, fens, lakes, and rivers. The fauna includes wolves, cougars (*Puma concolor*), black bears (*Ursus americanus*), moose, white-tailed deer, and many other species of mammals. Many bird species are also present in the study area, but we do not consider them in this study. We conducted this study from October 2011 to 2014, and from October 2017 to 2020 (see methods below). The Christina Lake study area experiences 4 distinct seasons throughout the year: summer, autumn, winter, and spring. Local weather varies within seasons, but generally follows similar climate trends of northern Alberta with hot summers and cold winters. The Christina Lake study area has been the subject of extensive forestry and oil and gas activity, which has manifested as an anthropogenic disturbance regime composed of seismic exploration lines (Dabros et al. 2018), transmission lines, pipelines, roads, well sites, industrial camps, and cutblocks. The Cold Lake and East Side Athabasca River caribou ranges intersect within the Christina Lake study area and both herds are at risk of extirpation. The Government of Alberta initiated lethal wolf population control in the winter of 2016–2017 within the Cold Lake and East Side Athabasca River caribou ranges with the objective to reach wolf population levels that allow caribou population stability or growth. Wolves were removed via aerial gunning from helicopters in the winter when aerial snow tracking is possible (Bridger 2019). This method was selected for wolf control because of its efficiency and because it reduces the risk of bycatch (Bridger 2019); the government target for removal is 95% of the population. Wolves (*n* = 92) were removed from Cold Lake and East Side Athabasca River caribou ranges between 2017 and 2020 (30, 9, 20, and 33 in each year, respectively; D. Hervieux, Government of Alberta, personal
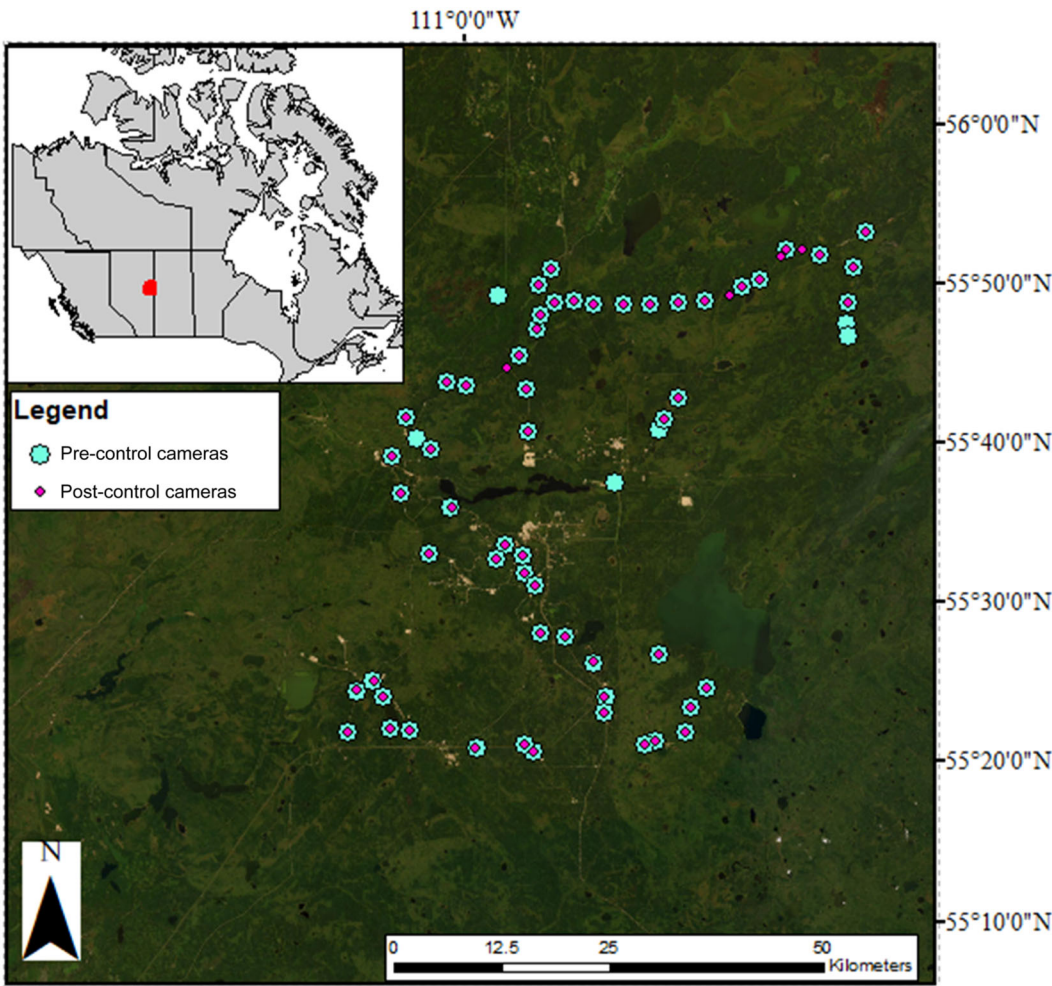
FIGURE 1 We deployed an array of 62 (pre-control) and 60 (post-control) motion-sensitive cameras across the 3,500-km^2 study area in northeastern Alberta, Canada (red square, inset). We examined detections of moose and wolves before (Oct 2011–2014) and after (Oct 2017–2020) wolf control using camera data from the Christina Lake study area.

communication), which reduced wolf relative abundance (detections) by 76% (Frey et al. 2022), with an as-yet unknown reduction in absolute wolf numbers.

METHODS

Mammal sampling

We had originally deployed a motion-sensitive camera array (Burton et al. 2015) throughout the study area in October 2011, 3 years before the wolf control program began, to understand mammals' responses to anthropogenic disturbance in northeastern Alberta. We used a constrained stratified random design to capture the heterogeneous land cover types across our study area (Fisher and Burton 2018, Wittische et al. 2021, Fisher and Ladle 2022). We divided the landscape

into 1-km^2 cell grids in ArcGIS 10.2 Spatial Analyst (Esri, Redlands, CA, USA) and randomly selected grid cells (constrained by site access by field technicians and placed a minimum of 2 km apart) from within 4 strata defined by canopy cover, tree species, and topography. Within this subset of cells, we deployed a single unlured Reconyx PC900 Hyperfire (Holmen, WI, USA) infrared remote digital camera on a tree facing an active game trail to maximize detection probability of wildlife. We set cameras to high sensitivity and no delay between triggers. Prior to the onset of wolf population control, cameras operated across 62 sites from October 2011 to October 2014. After the onset of wolf population control (winter 2016–2017), we re-deployed 60 cameras as close as possible to the original locations from October 2017 to October 2020. Camera locations were nearly identical, the average minimum distance to the nearest camera pre-control was 1,264 m and post-control was 1,086 m (Figure 1). Cameras were deployed by different field crews but followed the same protocols.

We retrieved data from cameras semi-annually and analyzed images for species detections using Timelapse 2.0 software (Greenberg et al. 2019). We considered detections of moose as independent when separated by >30 minutes, a commonly used threshold in camera-based wildlife studies (Burton et al. 2015, Granados et al. 2023). For example, if a moose was detected at a camera at 1015, and again at 1030, these would not be considered independent (Figure 2). As a measure of predator site-use, we quantified wolf independent detections using the same methods as moose. We recorded the number of days a camera was active at a site to control for sampling effort in models (Figure S1, available in Supporting Information).
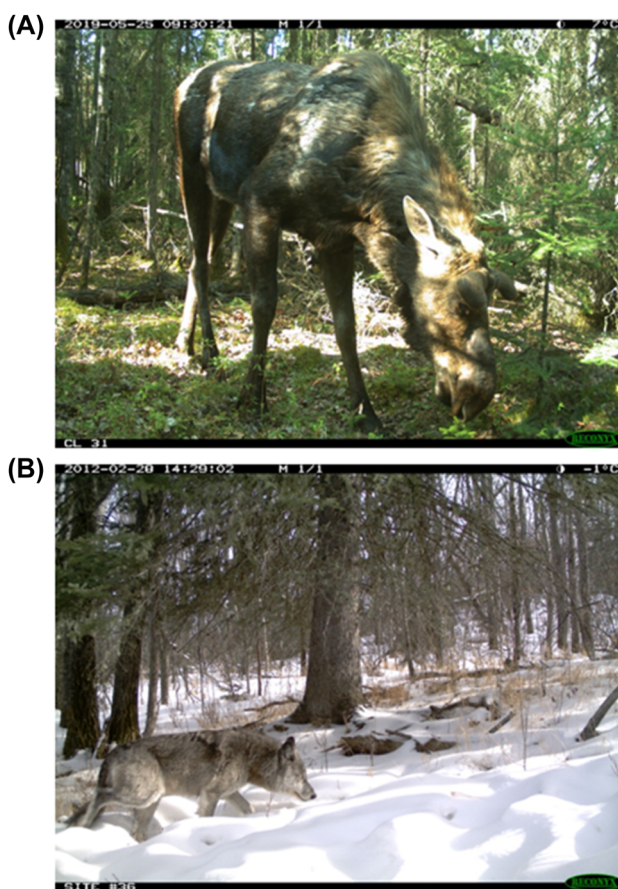

FIGURE 2 We identified moose and wolf detections from motion-sensitive camera images in the boreal forest in the Christina Lake study area of Alberta, Canada, from October 2011–2014 and October 2017–2020 and binned data into independent detection metrics for statistical analysis.

Natural and anthropogenic landscape variables

To consider the response of moose to local camera site conditions and large landscape patterns, we quantified the percentage of natural and anthropogenic land cover variables within a 250-m and 1,000-m radius buffering each camera following the scale-dependent analysis by Fisher and Burton (2018). We chose these scales to evaluate influences of land cover variables on moose in the immediate vicinity of cameras (250 m), and to examine influences at a larger spatial scale (1,000 m). We quantified 12 natural land cover classes (Table 1) using Alberta vegetation inventory (Alberta Sustainable Resource Development 2005), including upland deciduous, upland shrubs, water, nonforested areas, lowland deciduous, upland mixed wood, lowland mixed wood, upland spruce, lowland spruce, pine, tamarack, and open wetlands (Figure S2, available in Supporting Information). Visual inspection of histograms showed low variability in lowland deciduous land cover; thus, we grouped lowland and upland deciduous into a single variable.

For each camera site, within the same 250-m and 1,000-m radius buffer, we extracted the percentage cover of 9 anthropogenic landscape features using the Alberta Biodiversity Monitoring Institute's Human Footprint Inventory. We quantified cutblocks, pipelines, transmission lines, well sites, other block features, roads, trails, seismic lines, and 3D seismic lines (Figure S3, available in Supporting Information). Given the intensity of anthropogenic development within our study area, we accounted for differences in spatial data between the pre- and post-control timeframes by calculating the amount of anthropogenic land cover classes from spatial data collected in 2010 and 2016 for pre- and post-control, respectively (Alberta Biodiversity Monitoring Institute 2010, 2016). Similar to above, we grouped pipelines and transmission lines into a new variable (large linear features) because of the low prevalence of each (see Table S1, available in Supporting Information, for detailed variable descriptions). Prior to model construction, we examined Pearson's correlation coefficients between all variables and did not observe any correlations above $r = 0.7$ (Figure S4, available in Supporting Information).

Statistical analysis

We modeled pre-control and post-control independent detections of moose at each spatial scale to test whether habitat associations differed before and after the onset of wolf population control and determined which landscape features best explained moose distribution. We used generalized linear models, assuming a Poisson distribution for counts of independent detections with a log link function. We considered a non-detection to represent a true zero; thus, we considered the zeros in each site's repeat detection data to be due to temporary emigration, a part of the site-choice state process (Efford and Dawson 2012, Neilson et al. 2018, Stewart et al. 2018), rather than a false absence derived from the observation process (MacKenzie et al. 2017).

We built 5 competing models for pre-control and post-control periods based on our hypotheses of the primary influences of moose occurrence (Table 1). The security model represents moose selecting intact forest stands, risk-averse habitat that provides cover and thermoregulation but lower forage abundance (Laforge et al. 2016, DeMars et al. 2019, Francis et al. 2021, Routh and Nielsen 2021, Boucher et al. 2022). Following this, we expected positive estimates for the fixed effects in this model representing dense mature forest offering visual security: lowland mixed wood, upland mixed wood, upland spruce, lowland spruce, and tamarack. We also included controlling variables for water, open wetlands, independent detections of wolves at the site, and the number of days a camera was active. The forage model represents moose habitat selection influenced by areas with anthropogenic, early-seral forage subsidies (Finnegan et al. 2018, 2019; MacDonald et al. 2020; McKay and Finnegan 2022) that carry increased risk of predation (McKenzie et al. 2012, Dickie et al. 2017, Boucher et al. 2022). We expected positive estimates for the fixed effects in this model representing potential food subsidies including natural forest forage from deciduous, upland shrubs, and nonforest vegetation but also anthropogenic features offering subsidies from cutblocks, other block features, well sites, roads, large lines, trails, seismic lines, and 3D seismic lines. This model also included the same controlling

TABLE 1 Candidate models compete the relative effect of security habitat, forage habitat, and forage habitat without linear features on monthly moose occurrence before (Oct 2011–Oct 2014) and after (Oct 2017–Oct 2020) wolf control in the Christina Lake study area, Alberta, Canada. This study examined detections of moose and wolves using camera data and predictors were measured at 2 scales: 250- and 1,000-m buffer around camera locations.

Hypothesis – moose detections best explained by:	Predictor variables
Forage model	Deciduous (%)
	Upland shrubs (%)
	Nonforest (%)
	Cutblock (%)
	Block features (%)
	Well site (%)
	Road (%)
	Large lines (%)
	Trail (%)
	Seismic line (%)
	3-D seismic line (%)
	Water (%)
	Open wetland (%)
	Wolf presence (independent detections)
	Camera days (number of days)
Forage without linear features	Deciduous (%)
	Upland shrubs (%)
	Nonforest (%)
	Cutblock (%)
	Block features (%)
	Well site (%)
	3-D seismic line (%)
	Water (%)
	Open wetland (%)
	Wolf presence (independent detections)
	Camera days (number of days)
Security model	Lowland mixed wood (%)
	Upland mixed wood (%)
	Upland spruce (%)
	Lowland spruce (%)
	Tamarack (%)
	Water (%)
	Open wetland (%)
	Wolf presence (independent detections)
	Camera days (number of days)
Controlling variables model	Water (%)
	Open wetland (%)
	Wolf presence (independent detections)
	Camera days (number of days)
Null model	—

variables as the security model above. We built the third model to represent forage including natural forest cover from deciduous, upland shrubs, and nonforest vegetation but also polygonal features for cutblocks, other block features, well sites, and 3D seismic lines. We used the same controlling variables as above. This model excluded linear features to investigate if moose responded differently to linear features than polygonal, given that wolves capitalize on linear features to increase travel speed and prey encounters (Serrouya et al. 2020; Dickie et al. 2021, 2023). We included a

controlling variables model, which only included water, open wetlands, independent detections of wolves at the site, and the number of days a camera was active. Lastly, we included a null model (intercept only) as an alternative to our hypothesized models. We assessed collinearity among predictor variables by calculating variance inflation factors and kept variable sets where variance inflation factors were <3 (Zuur et al. 2010). We jointly scaled pre-control and post-control predictor variables to facilitate model convergence and allow for comparisons of coefficient estimates before and after wolf population control.

We fit all models with maximum likelihood using log link function. We evaluated empirical support for each model and its corresponding hypothesis using the Akaike's Information Criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002) and model diagnostics and model validation according to Zuur et al. (2007). We report beta coefficients (±95% CIs) from best-supported models in each period and scale. We report measures of dispersion (ĉ) for the top model in each treatment and scale. We investigated for spatial autocorrelation in top models for each treatment period and spatial scale by examining spatial patterns of moose detections, simulated residuals and Moran's I using the DHARMa package (Hartig and Hartig 2017). We performed all analyses with R statistical software version 4.2.0 (R Core Team 2017), using packages dplyr for general data management (Wickham et al. 2015), ggplot2 for data visualization (Wickham 2016), lubridate for datetime data (Grolemund and Wickham 2011), and glmmTMB for model construction (Brooks et al. 2017, Magnusson et al. 2017).

RESULTS

Relative abundance of moose and wolves before and after wolf control

As expected, wolf occurrence changed markedly pre- and post-control: the mean number of independent wolf detections in the pre-control period was 8.2 ± 8.2 (range = 0–37), and in the post-control period was 2.2 ± 3.6 (range = 0–20; Figure 3). Moose occurrence did not markedly change pre- and post-control; the mean number of independent moose detections in the pre-control period was 1.4 ± 2.3 (range = 0–13), and in the post-control period was 2.7 ± 3.5 (range = 0–13). We reviewed camera data from 123,574 camera days, and camera operability was broadly similar between the 2 treatment periods. Mean number of days of operation for pre-control cameras was 1,001 ± 180 days (range = 91–1,092) and for post-control cameras was 1,025 ± 123 days (range = 533–1,089). We detected no obvious trend in moose detections throughout each year; however, wolf detections did appear to increase throughout the year (Figure S5, available in Supporting Information). When examining detections separately for each year, we detected no obvious patterns (Figure S6, available in Supporting Information). We also did not observe any clear patterns in the spatial distribution of independent moose detections (Figure S7, available in Supporting Information).

Scale-dependent moose habitat associations change following wolf control

Prior to wolf control, moose detections were best explained by the model containing landscape features associated with dense forest and hence visual security at the larger (1,000-m radius) landscape scale (AIC$_c$ weight = 1; Table 2). Ostensibly this supported our hypothesis that habitats associated with security from predators best explain moose detections. Contrary to our predictions, the model revealed positive effects for tamarack (β = 0.21 ± 0.06) and negative effects for lowland mixed wood (β = −0.22 ± 0.11) and lowland spruce (β = −0.97 ± 0.19), suggesting unexpected avoidance of habitats thought to be associated with security and cover (Figure 4A; Figure S10, available in Supporting Information).

Following wolf control, moose detections were best explained by the model containing landscape features associated with disturbance (young forests) providing forage, at the 1,000-m scale (AIC$_c$ weight = 0.483; Table 2). While we expected positive estimates of coefficients associated with forage habitat, the model revealed a positive effect for large lines (β = 0.33 ± 0.12), and negative effects for upland shrubs (β = −0.25 ± 0.11), nonforest
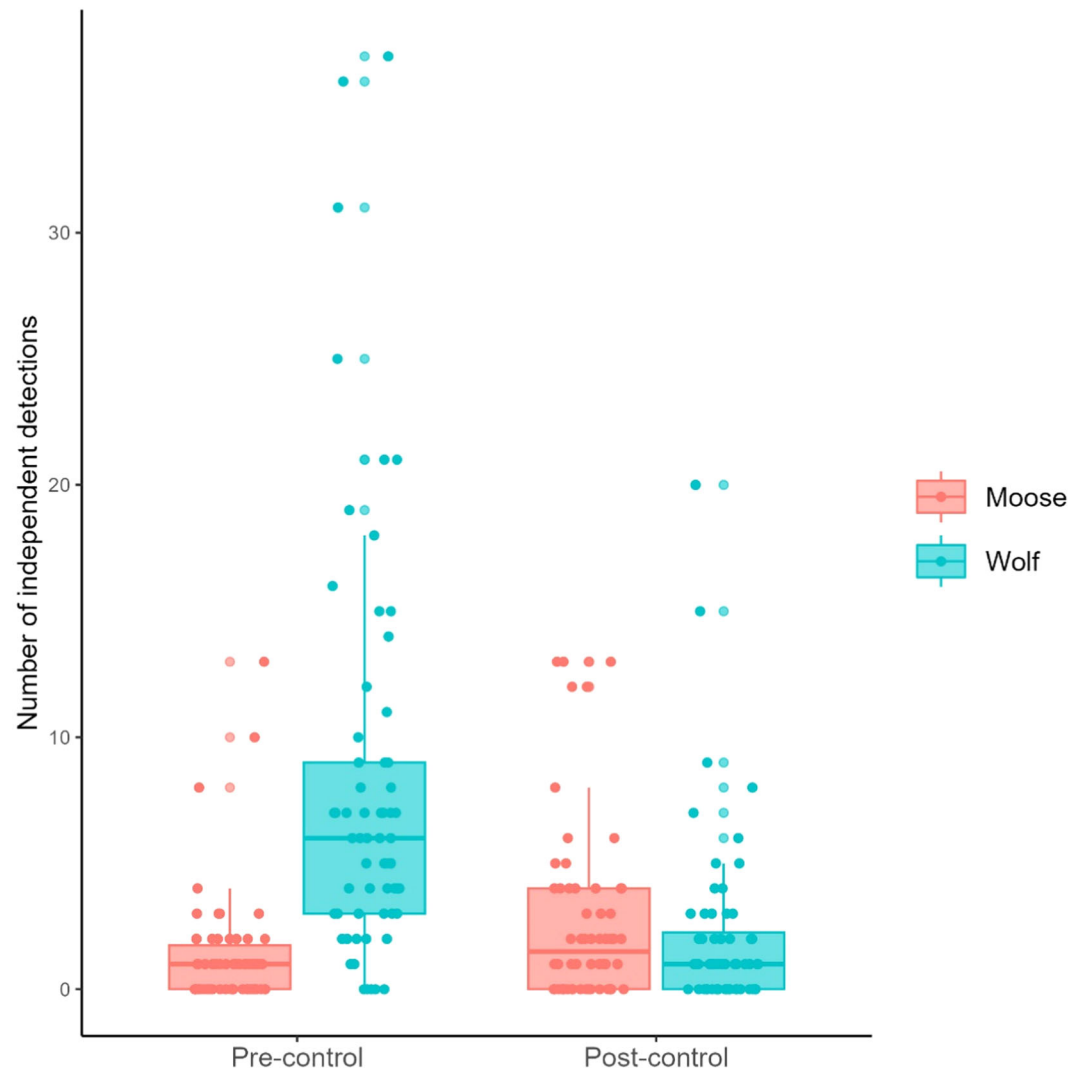
FIGURE 3 Summary of moose and wolf independent detections per camera in the pre- (Oct 2011–Oct 2014) and post-control (Oct 2017–Oct 2020) period in the Christina Lake study area of Alberta, Canada.

($\beta = -0.31 \pm 0.13$), roads ($\beta = -0.79 \pm 0.29$), seismic lines ($\beta = -0.65 \pm 0.19$), and 3D seismic lines ($\beta = -0.37 \pm 0.14$; Figure 4B; Figure S11, available in Supporting Information). The next best supported models were the controlling variables model ($\Delta AIC_c = 1.48$, AIC_c weight = 0.231) and the null model ($\Delta AIC_c = 2.18$, AIC_c weight = 0.162); both had considerably lower model weight and we do not consider them here.

At the smaller 250-m scale, prior to wolf control the null model was most supported (AIC_c weight = 0.85; Table 2). Following wolf control, the most supported model was the forage model (AIC_c weight = 1). In this model there were positive effects for forage habitat in deciduous cover types ($\beta = 0.24 \pm 0.09$), well sites ($\beta = 0.16 \pm 0.06$), and large lines ($\beta = 0.25 \pm 0.05$; Figure 5; Table S2 and Figure S9, available in Supporting Information).

Variance inflation factors in the models were <3; thus, all variables were retained in each candidate model. We detected overdispersion in the top models in both treatment periods and scales (Table S3, available in Supporting Information). There was evidence of spatial autocorrelation in the null model in the pre-treatment period at 250 m, the remaining top models with explanatory variables of interest had no evidence of spatial autocorrelation:

TABLE 2 Akaike's Information Criterion corrected for small sample size (AIC_c) scores of pre-wolf control (Oct 2011–Oct 2014) and post-wolf control (Oct 2017–Oct 2020) candidate models of independent moose detections in the Christina Lake study area, Alberta, Canada. We present the number of parameters (K), log-likelihood (logLik), difference in AIC_c scores between the current model and the best supported model (ΔAIC_c), and model weight or relatively likelihood of a model (w_i).

Scale	Sampling period	Hypothesis	K	logLik	AIC_c	ΔAIC_c	w_i
250 m	Pre-control	Null model	1	−122.33	246.73	0.00	0.85
		Controlling variables model	5	−120.01	251.08	4.35	0.10
		Forage without linear features model	12	−111.09	252.55	5.82	0.05
		Security model	10	−116.70	257.71	10.98	0.00
		Forage model	16	−109.31	262.71	15.98	0.00
	Post-control	Forage model	16	−142.00	328.66	0.00	1
		Forage without linear features model	12	−159.19	349.01	20.35	0
		Security model	10	−164.93	354.34	25.69	0
		Controlling variables model	5	−173.07	357.24	28.59	0
		Null model	1	−178.59	359.25	30.59	0
1,000 m	Pre-control	Security model	10	−93.33	210.98	0.00	1
		Forage without linear features model	12	−105.25	240.86	29.88	0
		Null model	1	−122.33	246.73	35.76	0
		Controlling variables model	5	−118.23	247.53	36.56	0
		Forage model	16	−102.26	248.62	37.64	0
	Post-control	Forage model	16	−156.21	357.06	0.00	0.48
		Controlling variables model	5	−173.72	358.55	1.48	0.23
		Null model	1	−178.59	359.25	2.18	0.16
		Security model	10	−167.66	359.81	2.75	0.12
		Forage without linear features model	12	−168.78	368.19	11.12	0.00

pre-control 250-m null Moran's I = 0.055, $P < 0.01$; pre-control 1,000-m security model Moran's I = 0.014, $P < 0.30$; post-control 250-m forage model Moran's I = 0.017, $P < 0.275$; post-control 1, 000-m forage model: Moran's I = −0.025, $P < 0.80$, and simulated scaled residuals revealed no clear pattern (Figure S8, available in Supporting Information).

DISCUSSION

Lethal wolf control is expected to affect predator–prey dynamics by modifying perceived and actual risk across a landscape, which in turn alters antipredator behavior in prey species. Our results suggest that the landscape of fear (Laundré et al. 2010) present in a wolf-dominated northwestern Nearctic boreal forest changes after wolf populations are substantially reduced. Our hypotheses that prior to wolf control, models containing landscape features hypothesized to
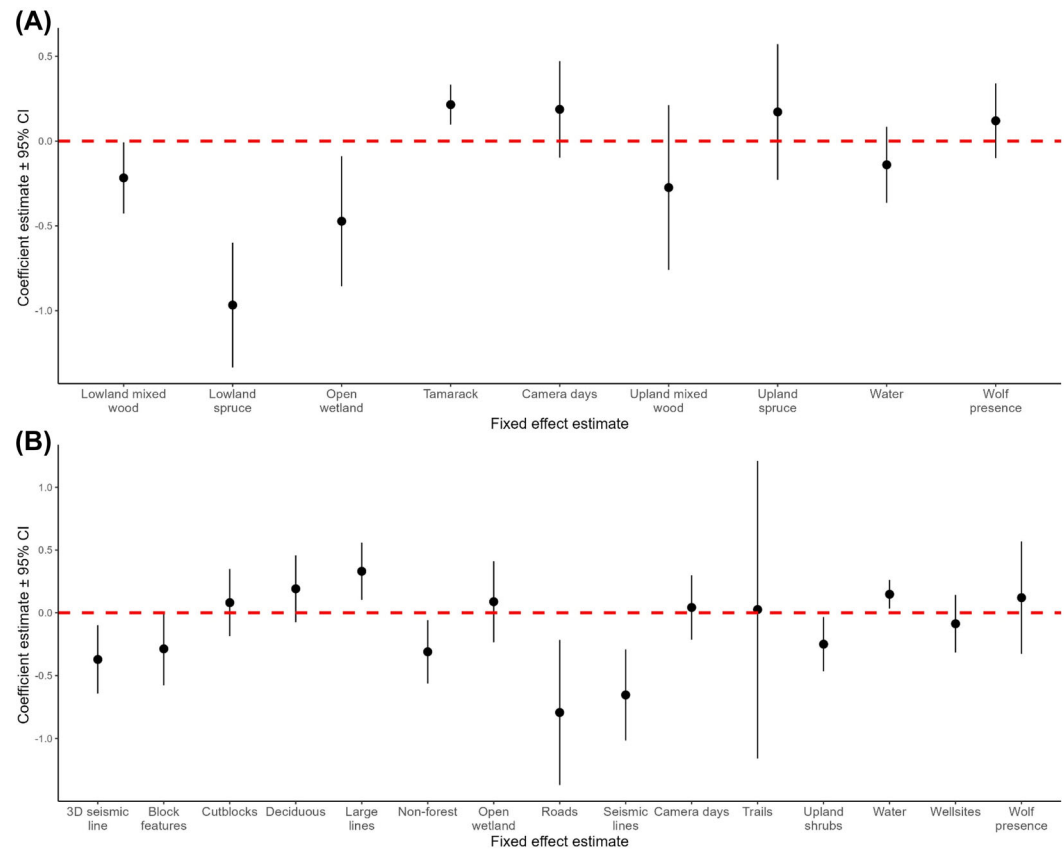
FIGURE 4 Estimated coefficients ± 95% confidence intervals of factors predicted to affect moose occurrence from A) the security model pre-control (Oct 2011–2014) and B) the forage model post-control (Oct 2017–2020). Models are constructed from variables extracted at 1,000-m-radius buffers around cameras. We examined detections of moose and wolves before and after wolf control using camera data from the Christina Lake study area of Alberta, Canada.

provide visual security from predators was supported and best explained moose distribution and suggest moose acted according to the time-minimization mechanism of optimal foraging theory. Coefficient estimates from the larger scale (1,000-m buffer) suggest moose, unexpectedly, actually avoided dense mature forests hypothesized to provide security. After wolf control, models containing anthropogenic landscape features hypothesized to provide forage subsidy best explained moose distribution and suggest moose acted according to an energy-maximization strategy, spending more time in riskier habitats with greater forage availability. This was not consistent, as we also observed negative associations with some landscape features hypothesized to provide forage subsidies (e.g., seismic lines). This switch in the initial pre-control period was scale-dependent; at small scales (250 m) moose in the pre-cull period was best explained by a null model rather than our hypothesized models of security or forage, whereas at a larger scale (1,000 m) in the pre-control period moose detections were explained by habitats related to security features.

Risk-averse habitat and changes in the landscape of fear

The presence of predators often leads to a behavioral trade-off between food acquisition and predator avoidance, leading to shifts in prey distributions to habitat with lower forage quality and quantity but increased cover
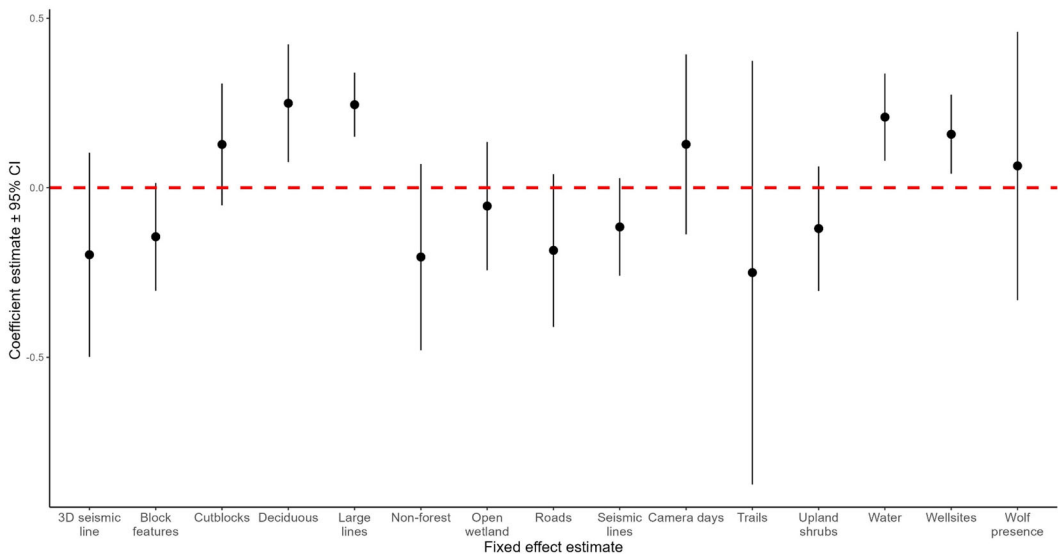
FIGURE 5 Estimated coefficients ± 95% confidence intervals of factors predicted to affect moose occurrence from the forage model post-control (Oct 2017–2020). The model is constructed from variables extracted at 250-m-radius buffers around cameras. We examined detections of moose and wolves before and after wolf control using camera data from the Christina Lake study area of Alberta, Canada.

(Sih 1980, Holomuzki 1986, McNamara and Houston 1986, Lima and Dill 1990, Abrams 1992). Our hypothesis that in a pre-wolf control landscape, moose occurrence is best explained by landscape features hypothesized to provide risk-averse habitat was supported. In contrast, previous researchers reported that at the individual level, female moose will forgo risk-averse habitat selection and prioritize forage instead, but this was seasonally dependent (Francis et al. 2021). We did not consider sex of moose, or season in our models; thus, we are unable to examine population-level effects of these factors. Nor were we able to account for individual variability in moose habitat selection. The inconsistency in response across forest features suggests that while some support for visual security may be observed, there are other unmeasured factors at play dictating moose habitat selection in this landscape.

Prior to wolf control there was more support for models associated with security land cover types, but this switched to more support for models with forage land cover following wolf control. Predators use anthropogenic linear features as travel corridors, which facilitates greater prey acquisition (McKenzie et al. 2012, Dickie et al. 2017, Boucher et al. 2022). Previous researchers reported that moose avoid these risky features pre-control (Fisher and Burton 2018, Fisher and Ladle 2022). While we predicted the landscape of fear would dissipate following wolf control, in the post-control landscape moose were negatively associated with several linear features (Figure 4), which was unexpected.

The partial signal for a behavioral shift by moose after wolf control is founded in landscape of fear theory. The reintroduction of wolves in Yellowstone National Park, Wyoming, USA, is a prime example of communities shaped by top-down control. In this community, elk (Cervus canadensis) used less open areas in the summer but more open areas in the winter than they did before the reintroduction of wolves (Mao et al. 2005). Likewise, moose habitat selection changes seasonally (Ditmer et al. 2018); although we did not account for seasonality in the present study, moose may be selecting anthropogenic features for forage in summer and intact coniferous forage for thermal refuge in late winter, which could parse apart shifts in habitat selection behavior following wolf removal.

Another possibility to consider is that the shift in moose habitat selection is due to density-dependent habitat selection, as predicted under ideal free distribution theory (Fretwell 1969, 1972; Smith et al. 2023). In the case where wolf control led to moose increases, competition increases, and moose habitat selection would shift to

accommodate the loss of resources per patch to those competitors (Avgar et al. 2020). We did not see a signal of moose population increases and the time lag (1–3 years after control) is quite short for this long-lived species to respond to lower predator numbers. Moreover, the circumstances under which ideal free distribution may or may not manifest are unclear (Kacelnik et al. 1992, Kennedy and Gray 1993, Křivan et al. 2008). It is possible both landscape of fear and density-dependent selection are at play, but more research is required to parse this apart.

Ultimately, some (albeit inconsistent) evidence exists that moose were more risk-averse in a high-density (Burgar et al. 2019) wolf landscape; after the onset of wolf control, moose tended to behave as energy-maximizers by prioritizing natural and anthropogenic forage subsidies (as is seen in deer; Darlington et al. 2022), while still avoiding linear features associated with predator movements A partially diminished landscape of fear following wolf cull no longer restricts moose to habitats that offer security, and moose use some landscape features previously considered risky, while others remain strongly avoided despite their abundant available forage (Finnegan et al. 2023).

Caveats and limitations

Our study consists of only 3 years of data following the onset of wolf control. If moose change their habitat selection in response to alleviated predation risk, this may take longer to manifest. Moreover, although wolves are a primary predator of moose, other predator species (e.g., black bears, cougars) and human hunters are present in the study area that may predate upon moose but were unaccounted for within our analyses. Black bears did not shift habitat use following wolf control; instead, occurrence was best predicted by natural land cover but not prey availability or anthropogenic features (Baillie-David 2022). Furthermore, occurrence of other non-apex predators, such as coyote (Canis latrans) and lynx (Lynx canadensis), shifted from being explained by intraguild competitor occurrence pre-control to prey availability in a post-control system (Baillie-David 2022). Although coyote and lynx are not primary predators of moose (Benson and Patterson 2013), they may prey upon vulnerable moose such as neonates.

We did not account for fine-scale variation in spatial features that could lead to differences in moose occurrence. For example, moose selection of cutblocks is dependent on time since harvest because of changes in forage biomass and predation risk over time (Mumma et al. 2021), but we did not include cutblock age class in our models. Furthermore, we did not examine spatial configuration of forage features (e.g., cutblocks) and their proximity to natural landscape features that provide cover, which could have influenced moose response to anthropogenic features. Future research could also examine the role of plant productivity, as measured by normalized difference vegetation index or enhanced vegetation index as productivity has been observed to be associated with moose habitat selection (Lone et al. 2014, Burton et al. 2022). We elected not to include either of these indices in the present approach, as we were primarily interested in habitat composition related to the proportion of land cover types and features hypothesized to provide security or forage subsides. Further, we did not explore temporal changes in wolf abundance throughout the year (Figure S5), but this may be of interest for future research given the potential for increased predator population growth rate in years following removal effort (Knowlton et al. 1999). We chose to model treatment periods separately rather than including an interaction term for treatment period. While we believe this was an appropriate decision to reduce model complexity in favor of a more straightforward interpretation, decisions made by different analysts in ecological sciences can yield different results (Gould et al. 2023). Future examinations featuring more complex modeling approaches should be considered.

Restoration of linear features has been implemented throughout parts of the western boreal forest to reduce travel efficiency of predators, to ultimately reduce caribou mortality (Dickie et al. 2021). Both moose and wolves are less likely to be near linear features that are restored, with this response depending on intensity of restoration (Dickie et al. 2021). Likewise linear feature restoration affected use rates by predators and prey in nearby landscapes (Tattersall et al. 2020a, 2020b; Beirne et al. 2021). While we did not account for linear feature restoration between pre- and post-control, it is possible that the lack of selection for seismic lines in our forage model post-cull is due to the combined effects of contemporary linear feature restoration and the wolf cull, and moose have not yet formed an optimization strategy to compounding anthropogenic interventions.

MANAGEMENT IMPLICATIONS

Moose management plans and strategies for landscape restoration may have to consider if new patterns of moose selection emerges over time, necessitating long-term monitoring of wildlife communities post-wolf cull. Wolf control has often been risky and we were fortunate in this before-after experiment, but it was not planned, and funding ended after only 3 years. Wildlife management must consider responses of interacting species following predator control; planned research and long-term monitoring is required to fully understand its effects on the wider mammal community and allow for effective conservation management.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Research was reviewed and approved by InnoTech Alberta's Animal Care Committee operating under the Canadian Council on Animal Care (CCAC). Research was permitted by the Government of Alberta, Ministry of Environment and Parks, Fish and Wildlife Division, Collection License 49143 and Permit 20-335. The research team was not involved in the lethal control of wolves, which was conducted solely by the Government of Alberta and its agents operating as the legally designated authority under Alberta's Wildlife Act.

DATA AVAILABILITY STATEMENT

All data and associated code are available on the Borealis data depository at https://doi.org/10.5683/SP3/SJEYOV.

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SUPPORTING INFORMATION

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