

Research Article

Forest and fire drive moose (*dené*) detections near their northern range limit

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One way to understand species range shifts in response to anthropogenic climate change is to study populations living at the limit of climate and resource suitability. Moose *Alces alces* (*dené* in Dënesų́łné) generally require forest–wetland landscape complexes but are increasingly seen across the forest–tundra transition at their northern range limit. To quantify the drivers of moose detections near this northern range limit we used camera trap data across Thaidene Nëné Indigenous Protected Area, Canada. We used a generalised linear mixed modelling approach to examine how moose detections related to land cover classes, post-fire age, fire severity, and detection rates of competitor and predator species. Only 1.6% of moose detections were on tundra, and all tundra detections were during the snow-free period. In summer, moose were detected most frequently in areas >20 years post-fire. In winter moose were detected most in mixed forest and rugged terrain. Moose rarely co-occurred with predators, and neither predator nor competitor models provided the most parsimonious explanation of moose detections in either season. Consistent with range-centric moose knowledge, forested areas provide important habitat for moose near their northern range limit, particularly in the winter. With continued climate-induced changes across Canada's treeline, moose habitat will continue to change, likely affecting northern moose in complex ways.

Keywords: *Alces alces*, leading edge, range expansion, resource selection, tundra

Dënesų́łné, the traditional language of the Łutsël K'é Dene First Nation, is used throughout the text for species names as a form of Indigenous language revitalization.

Introduction

Anthropogenic climate change is dramatically changing ecosystems, which is amplifying shifts in many species' distributions (Hickling et al. 2006, Chen et al. 2011,



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Harvey et al. 2023, Lawlor et al. 2024). Generally, species are contracting at the trailing, or warm, edge and expanding at the leading, or cold, edge of their range (Hitch and Leberg 2007, Pacifici et al. 2020, Péliissié et al. 2022). Impacts from these shifts can substantially alter ecological communities and impact species' ability to coexist often leading to conservation concerns (Holt 2013, Zarzychny et al. 2024). These concerns are generally highest in areas with limited niche redundancy like the Arctic (Valladares et al. 2015) where new species compete with preexisting ones (Callaghan et al. 2004, Descamps and Strøm 2021). A better understanding about range shifts, and the limits that exist, can provide insights into the dynamism of species distributions and help to predict future change (Gaston 2009).

Range limits are determined by temporal and spatial abiotic and biotic factors that allow a species to persist (Bridle and Hoffmann 2022), but the combination of the most important factors for each species can be difficult to identify (Sexton et al. 2009, Godsoe et al. 2017, Connallon and Sgrò 2018, Chen et al. 2024). Abiotic factors include climate variables like temperature, rainfall, snow depth, and soil moisture, physical barriers like elevation and water depth, and resource availability variables like water, shelter and certain forage species (Thomas 2010, Sirén et al. 2021). Biotic factors also play an important role, with predation, competition, mutualism and parasitism further limiting or extending a species range (Pigot and Tobias 2013, Alexander et al. 2022). To understand how both abiotic and biotic factors contribute to a species range an integrated approach involving individuals near the species range edge is required (Sirén and Morelli 2020, O'Brien et al. 2022).

Edge populations generally experience more frequent and stronger limiting factors (Brown et al. 1996, Cahill et al. 2014, Slaton 2015). To respond to these additional pressures populations have adaptive strategies and tradeoffs that differ from populations living at the centre of the species range (Sexton et al. 2009, Parmesan and Singer 2022). Strategies include a shift in diet, altered movement behaviours, and differing habitat selection (Hebblewhite and Merrill 2009, Wattles et al. 2018, Stewart et al. 2022, Willi and Van Buskirk 2022), combined with changes to predation and competition (Sirén et al. 2023), and can allow a species to persist past their usual ecological niche. Limiting factors on edge populations can change temporally; with the impact and magnitude of these factors changing between seasons, including extreme weather conditions and density of predators and competitors (Bartoń and Zalewski 2007, Joly et al. 2016, Butler et al. 2023).

One species with dynamic range shifts is the moose *Alces alces* (denié), a large northern ungulate that lives mostly in the circumpolar boreal forest (Darimont et al. 2005, Timmermann and Rodgers 2017, Jensen et al. 2018, Meiri et al. 2020, Teitelbaum et al. 2021). At a range-wide scale, it is theorized that moose are mostly limited by cover and resource availability at the leading edge, and climate at the trailing edge (Karns 2007). Moose often select habitats with more deciduous shrub forage, particularly near bodies

of water and wetlands (Maier et al. 2005, Laforge et al. 2016) and prefer conifer forests for thermal protection in both winter and summer (Timmermann and McNicol 1988, Wattles et al. 2018). Moose in the boreal forest are one of the first large mammals to return after fire, particularly favouring habitats 11–25 years old post-fire (Fisher and Wilkinson 2005, Brown et al. 2018, Mumma et al. 2024). Moose also avoid areas with higher predator densities, particularly wolves *Canis lupus* and bears *Ursus* spp. (Van Ballenberghe and Ballard 1994, Dussault et al. 2005). While known to be relatively cold-tolerant (Sullender et al. 2025), moose at their northern range are exposed to climatic factors that could limit their distribution, including deep snow making access to forage difficult (Dussault et al. 2005, Sexton et al. 2009, Joly et al. 2016) and extreme cold temperatures >30°C (Renecker and Hudson 1986). More recently, moose have been documented on tundra (Moskvitina et al. 2011, Jensen et al. 2020), hypothesized to be associated with warming and increased shrubification (Tape et al. 2016). An ecological study quantifying multiple factors associated with moose detections near their range limits would help elucidate the key biotic and abiotic drivers of this species as the north keeps changing.

To quantify factors predicting moose detections near their northern range limit, we employed an existing multi-species camera trap array overlaying the transition of boreal forest and tundra in northern Canada. We paired these data with remotely sensed information on land use and fire features. Moose have been sighted in both ecozones but are more abundant in the boreal across this landscape. Given the pronounced differences in vegetation communities from taiga-tundra and the importance of woody species for moose browse and cover, we hypothesized that abiotic conditions best predict moose detections; the composition of land cover, including the distribution of fire-impacted areas, would have a stronger impact on moose distribution when compared to the detection of co-occurring predators and competitors (i.e. biotic factors). Quantifying the relative importance of ecological factors on moose detections will provide insight into future potential range shifts and associated wildlife management priorities near the northern edge of this species circumpolar range.

Material and methods

Study area

Thaidene Nënë is an Indigenous Protected Area in the Northwest Territories, Canada (26 000 km², Fig. 1, Łutsël K'édene First Nation et al. 2026). In the forested area, the habitat of Thaidene Nënë is largely dominated by black and white spruce, *Picea mariana* and *P. glauca*, with sections of exposed bedrock. Trees become less common past the treeline and landscape becomes dominated by small shrubs, including dwarf birch *Betula glandulosa*, sedges *Carex* spp., and ground cover species, including labrador tea *Rhododendron tomentosum*, mountain cranberry *Vaccinium vitis-idaea*, billberry

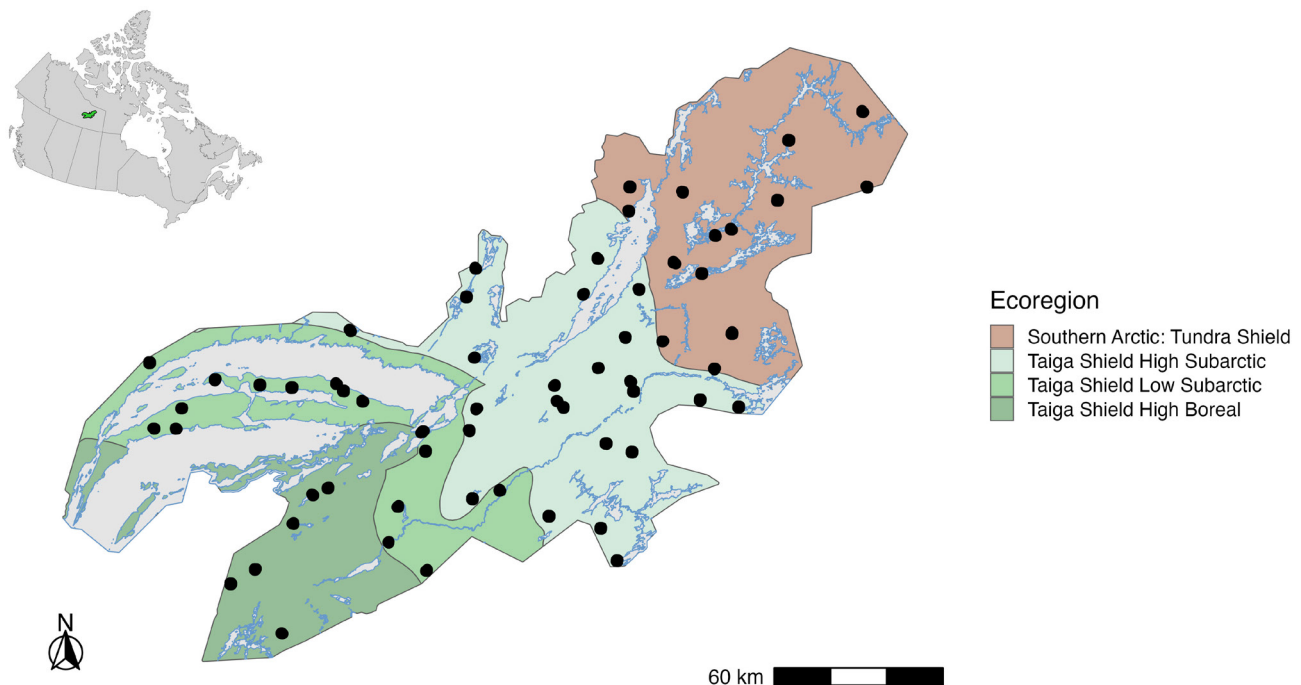


Figure 1. Between 2021–2022, 307 camera traps were deployed across 60 sites (black dots) in Thaidene Nënë Indigenous Protected Area, Canada. This region straddles the boreal forest and tundra and is divided into four separate ecoregions.

Vaccinium uliginosum, cloudberry *Rubus chamaemorus*, crowberry *Empetrum nigrum* and alpine bearberry *Arctous alpina* (Ecosystem Classification Group 2012). Thaidene Nënë is largely impacted by fire, with 26% burned in the past 50 years. Of this burned area, 9.2% is < 10 years old, 5.3% is 11–20 years old, 7.4% is 21–30 years old, 0.4% is 31–40 years old, and 3.6% is 41–50 years old. Most unburned area is on the tundra. The average annual temperature for the region is -3 to -9°C , with the average temperature in the warmest month (July) at 11°C and the coldest month (January) at -30°C (Ecosystem Classification Group 2008, 2012).

Moose densities in Thaidene Nënë are not known but in nearby regions there were 2 and 5 moose per 100 km^2 in the taiga shield and taiga plains, respectively (Cluff 2005, Haas 2014). There are no current estimates of moose density for the tundra. Thaidene Nënë lies near the northeastern most edge of moose range in the Northwest Territories, Canada (Government of the Northwest Territories 2025). The main predators of moose are grey wolves *Canis lupus* (nuni; Mech 1966), grizzly bears *Ursus arctos horribilis* (sas cho), American black bears *Ursus americanus* (sas delzën; Van Ballenberghe and Ballard 1994, Bertram and Vivion 2002, Garneau et al. 2008), and humans *Homo sapiens* (dené; Coady 1980, Carrière 2012). The two other ungulate species in Thaidene Nënë are muskoxen *Ovibos moschatus* (yutthéjéré) and barren-ground caribou *Rangifer tarandus groenlandicus* (ʔetthén).

Camera trapping

We quantified moose detections using data collected by a multi-species monitoring project across Thaidene Nënë. In 2021, the Łutsël K'é First Nation's Ni Hat'ni Dene

Guardians, Government of the Northwest Territories, Parks Canada Agency, Canadian Wildlife Service, University of British Columbia and Wilfrid Laurier University partnered to deploy 307 cameras across 60 sites in Thaidene Nënë (Beirne et al. 2022a) under the Northwest Territories Biodiversity Monitoring Program initiative (NWTBMP; Environment and Climate Change, Government of the Northwest Territories 2026). At most sites, five single-camera stations were deployed, with an average distance of 524 m (SD = 186 m) between cameras and 98 km (SD = 55 km) between sites. The nested sampling design was intended to be representative of habitats within Thaidene Nënë and support territorial and national monitoring initiatives, while increasing detectability at each site and minimizing auditory overlap between stations for audio recorders paired with the cameras (Wilgenburg et al. 2020, Beirne et al. 2022a). This resulted in six sites in the taiga shield high boreal, 16 sites in the taiga shield low subarctic, 24 sites in the taiga shield high subarctic, and 14 sites in the southern arctic (Fig. 1, Ecosystem Classification Group 2008, 2012). We used Reconyx Hyperfire 2 HF2X cameras (Reconyx). Cameras were operational from approximately August 2021 to September 2022, with an average of 348 (± 39 SD) recorded days per camera. This excluded days when cameras did not capture the initial field of view, which was primarily when they were obstructed by snow.

Details on camera deployment and image processing are documented elsewhere (Beirne et al. 2022a, Jolin 2025). Briefly, we followed protocols developed by other monitoring programs (Alberta Biodiversity Monitoring Institute 2021, DeWitt and Cocksedge 2023), where cameras took

three images per trigger, with no delay between triggers. Cameras were set at one meter high, angled slightly down with the aim for the motion sensor to be triggered approximately 80 cm off the ground, 5 m away from the camera. The stations were not baited. Wildlife species were identified in each motion-triggered photo using the online photo-tagging system WildTrax (Alberta Biodiversity Monitoring Institute 2026), which utilises a machine learning algorithm called Megadetector (Microsoft AI for Good 2026). A confidence threshold of 0.15 was used to filter images with animals to minimize false negatives (Leorna and Brinkman 2022) and is consistent with a previous NWTBMP study (Stewart et al. 2025). These images were then manually identified to species by six trained technicians.

Species variables

All statistical analyses are conducted in R ver. 4.5.2 (www.r-project.org) and data exploration was conducted as in Zuur et al. (2010); values are presented as mean $\pm$ SE unless otherwise noted. To advance the reproducibility of this work analyses and workflow are hosted on GitHub (https://github.com/claudia-nwt/moose_tdn). Species detection rates were calculated using the 'wildRtrax' package ver. 1.5 (Becker 2025). Detection rates were defined and calculated as the number of independent detections per month, when there was more than 30 min between subsequent motion-triggered photos of the same species, a commonly used approach for large mammals (Wearn and Glover-Kapfer 2017, Frey et al. 2020, Beirne et al. 2022b, Fisher et al. 2023). Moose detection rates were used for the whole sampling period (annual) and also separated into snow-on-ground and snow-off-ground seasons: eight winter months (October to May), and four summer months (June to September, Fig. 2). Due to

sample size limitations of moose detections, it was not possible to separate our data into additional biological seasons (e.g. calving in spring and rut in the fall) as is common in other studies (Francis et al. 2021, Koetke et al. 2023).

Landscape variables

Landscape variables were calculated using the 'terra' R package ver.1.8 (Hijmans 2025) and included: 1) proportion of each land cover class; 2) number of land cover classes (a measure of heterogeneity); 3) proportion of each fire age class; 4) average fire severity; 5) distance from camera to nearest major body of water (m); and 6) terrain ruggedness index (Table 1).

Land Cover of Canada (ver. 2) was used as it includes a class for wetlands (Canada Centre for Remote Sensing et al. 2022), which is considered an important habitat for moose (Wattles et al. 2018, Janík et al. 2021, Teitelbaum et al. 2021), and was collected from a similar time period as camera deployment (2020). Landscape variables were calculated within a 3 km buffer around each camera station. This buffer size is based on the average home range for northern moose (Cederlund and Sand 1994, Hundertmark 2007, Francis et al. 2021), which we expected to be influential for moose detections (Maier et al. 2005) as it represents the second order habitat selection (Johnson 1980). Similar land cover categories were merged to ensure average land cover proportions across camera sites were large enough to be relevant for modeling ($>10\%$) and otherwise rare land cover classes ($<1\%$ of the study area; urban and built up, sub-polar or polar barren-lichen-moss, and temperate or sub-polar broadleaf deciduous forest) were excluded from further analysis (Table 1; sensu Maxie et al. 2010, Sahraoui et al. 2017).

Fire characteristics were calculated for fire age and size from the National Burned Area Composite (Canadian Forest

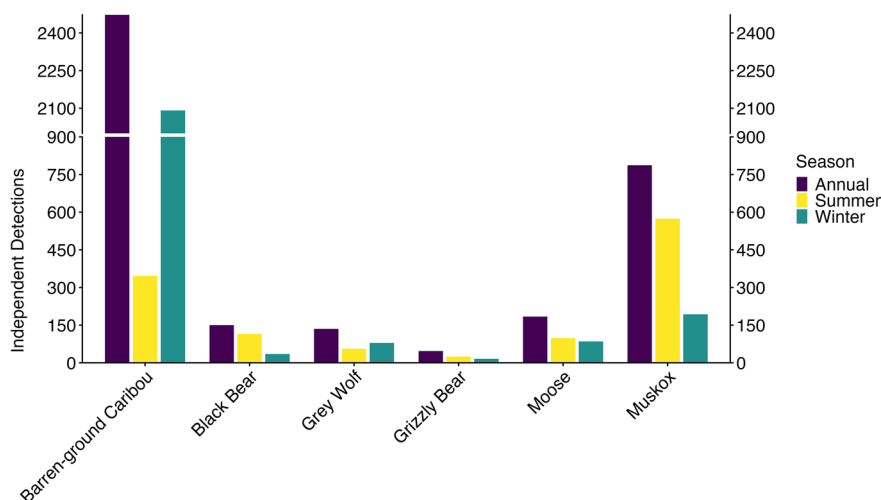


Figure 2. Independent detections of moose, grey wolves, black bears, grizzly bears, muskox and barren-ground caribou between 2021–22 in Thaidene Nēné Indigenous Protected Area, Canada, including summer (June to September), winter (October to May) and annual totals. Note that the axis for independent detections is broken between 900 and 2000 to accommodate much higher barren-ground caribou independent detections than other species. Detections were similar by season for moose but higher in the summer than in the winter for all other species except barren-ground caribou and grey wolf.

Table 1. Description of fixed effects in generalized linear mixed effect models representing hypotheses to explain moose detections between 2021–22 in Thaidene Nënë Indigenous Protected Area, Canada. Predicted directions are positive (+), negative (–) or neutral (~).

Hypothesis categories	Variable name (abbreviation)	Description of variable	Predicted direction of effect
Core model	Distance to water	Distance from camera to the edge of a nearest major body of water (lake or river).	–
	Terrain ruggedness index	An index measuring elevation difference around the camera.	–
Land cover	Conifer forest (CONFOR)	Proportion of merged temperate or sub-polar needleleaf forest and sub-polar taiga needleleaf forest land cover class within a 3 km buffer around each camera.	+
	Mixed forest (MIXFOR)	Proportion of mixed forest land cover class within a 3 km buffer around each camera.	+
	Grassland (GRASS)	Proportion of merged temperate or sub-polar grassland and sub-polar and polar grassland-lichen-moss land cover class within a 3 km buffer around each camera.	–
	Shrubland (SHRUB)	Proportion of merged temperate or sub-polar shrubland and sub-polar and polar shrubland-lichen-moss land cover class within a 3 km buffer around each camera.	–
	Barrenland (BARREN)	Proportion of barrenland land cover class within a 3 km buffer around each camera.	–
	Water (WATER)	Proportion of water class within a 3 km buffer around each camera	–
	Wetland (WETLA)	Proportion of wetland land cover class within a 3 km buffer around each camera.	+
Fire	Heterogeneity(HETERO)	Number of land cover classes within a 3 km buffer around each camera.	+
	Age <10 years old (FAGE<10)	Proportion of 3 km buffer impacted by fires that occurred <10 years since camera deployment.	–
	Age 11–20 years old (FAGE<20)	Proportion of 3 km buffer impacted by fire was 11 to 20 years since camera deployment.	+
	Age 21–30 years old (FAGE<30)	Proportion of 3 km buffer impacted by fire was 21 to 30 years since camera deployment.	+
	Age 31–40 years old (FAGE<40)	Proportion of 3 km buffer impacted by fire was 31 to 40 years since camera deployment.	–
	Age 41–50 years old (FAGE<50)	Proportion of 3 km buffer impacted by fire was 41 to 50 years since camera deployment.	–
	No Fire in 50 years (FAGE>50)	Proportion of 3 km buffer with no recorded fire in 50 years since camera deployment.	–
Biotics	Fire Severity (FSEVER)	Average annual change magnitude value as the differenced Normalized Burn Ratio (dNBR) within the 3 km buffer impacted by fire.	–
	Wolf (WOLF) detections	Number of independent grey wolf detections per month.	–
	Black bear (BBEAR) detections	Number of independent black bear detections per month.	–
	Grizzly bear (GBEAR) detections	Number of independent grizzly bear detections per month.	–
	Barren-ground caribou (BGCAR) detections	Number of independent barren-ground caribou detections per month.	~
	Muskox (MUSK) detections	Number of independent muskox detections per month.	~

Service 2025), which has data from 1972 to present day. Fire age was split into decades based on expected forest succession patterns and previous studies (Fisher and Wilkinson 2005, DeMars et al. 2019, Stewart et al. 2023). The 31–40 years fire age category was not common in the study area, making up only 1.6% of all fires, and was not present in camera buffers so was not included in the analysis. Average fire severity within each buffer was calculated using the differenced normalized burn ratio (dNBR) from the National Terrestrial Ecosystem Monitoring System covering years 1985 to 2020 (Hermosilla et al. 2016).

We also calculated two other landscape variables that are included as abiotic predictor variables (Gunn et al. 2011, Leblond et al. 2016, Estevo et al. 2022). Distance to the nearest water body (major lake or river) was calculated using water polygons from the 2011 Census dataset (Government of Canada 2011). Average terrain ruggedness index was calculated using the standard method of mean difference in elevation between the camera and its surrounding 8 raster cells (Horn 1981, Riley et al. 1999). The Arctic Digital Elevation Model (DEM) dataset was used for elevation at a 500 m resolution, ver. 4.1 (Porter et al. 2023).

Statistical analysis

We examined the drivers of moose detections at the northern extent of their range using negative binomial generalized linear mixed models (GLMMs). To minimize errors and violations of model assumptions, best practices were followed for linear models and proportional covariates (Zuur and Ieno 2016, Valle et al. 2024) using the ‘performance’ ver. 0.15.2 (Lüdecke et al. 2021) and ‘DHARMA’ ver. 0.4.7 (Hartig 2024) R packages. After reviewing variables for outliers, one camera near a wolf den with high wolf detections was removed from further analysis to mitigate potential bias. Correlation coefficients and variance inflation factors (VIF) were used to test for correlation and collinearity of variables. Variables were retained in the same model with a correlation coefficient < 0.6 and $VIF < 3$. Fire size was ultimately not included as it was highly correlated with fire ages ($VIF = 3.67$).

We developed three suites of model sets representing different hypothesized drivers of moose detections, including land cover, fire, and species co-occurrences (Table 1). In all models the response variable was the number of monthly independent moose detections during the study period. All predictor variables were centered and scaled. As we were using proportional covariates for land cover and fire age (Valle et al. 2024), we used shrubland and no fire recorded in the previous 50 years as reference categories in their respective models. As is standard for camera trapping research a log-transformed offset of the number of active camera days was used to control for differences in effort across months (sensu Cano-Martínez et al. 2024, Curveira-Santos et al. 2024, Jachowski et al. 2024). Additionally, each model included 1) a core set of variables shown elsewhere to be important in predicting moose detections – terrain ruggedness index and the distance of the camera to the nearest body of water (Timmermann and McNicol 1988, Joly et al. 2016), and 2) a random effect of site to control for camera clustering. Separate models were run for the entire dataset (annual) as well as for summer and winter months to investigate seasonal drivers, resulting in 33 total models across three (annual, and two seasonal) suites.

Models were compared using Akaike information criterion with a correction for small sample sizes (AICc; Burnham and Anderson 2002) using the R package ‘MuMIn’ ver. 1.48.11 (Bartoni 2024). The most parsimonious model was identified as the one with the lowest AICc, and all models with a delta AICc value of < 2 were considered analogous. Once the most parsimonious model was determined for each model suite, these models were then compared against each other and the null and global models. Beta co-efficients were then compared within the most parsimonious model to further assess the likely ecological impact of each predictor and its significance. For a goodness of fit of the most parsimonious model, conditional R^2 (fixed and random effects) and marginal R^2 (random effects only) were calculated (Nakashima et al. 2018) using the R package ‘performance’ ver. 0.15.2 (Lüdecke et al. 2021).

Results

Seasonal detections of moose varied little, unlike other species

Between 2021 and 2022 camera traps captured 1 816 549 images over 106 853 camera days. Throughout this period there were 184 independent detections of moose, with similar detections by season (summer = 98, winter = 85; Fig. 2) and moose were detected throughout the protected area in all ecoregions (Supporting information). Annual independent detections of moose predators and competitors included: 135 grey wolves, 150 black bears, 47 grizzly bears, 1436 muskoxen and 2471 barren-ground caribou. Unlike with moose, independent detections of predators and competitors of moose varied by season with grey wolves and barren-ground caribou detected more often in the winter, and black bears, grizzly bears and muskox detected more often in the summer (Fig. 2). Grey wolves and muskox were detected in all ecoregions throughout the protected area, whereas black bears were only observed within the forested taiga shield ecoregions, and grizzly bears and barren-ground caribou were only observed in the southern Arctic and high subarctic of the taiga shield (Supporting information).

Importance of fire and land cover on moose detections changes with season

The most parsimonious model of moose detections changed between seasons. In the summer, the fire model set best explained moose detection rates, with the land cover model set nearly as parsimonious ($\Delta AIC = 2.39$, Table 2, Supporting information). Conversely, in winter, the land cover model best explained moose detections and the fire model set was nearly as parsimonious ($\Delta AIC = 1.52$, Table 2, Supporting information). For annual models, again land cover best explained moose detections but the fire model set was less parsimonious ($\Delta AIC = 4.16$, Table 2, Supporting information). Regardless of season, models with predator and competitor detection rates as predictor variables were comparatively poor at explaining moose detections (summer $\Delta AIC = 6.49$, winter $\Delta AIC = 8.21$, annual $\Delta AIC = 7.20$, Table 2).

The most parsimonious model for summer included only fire age. The model suggested moose detection rates were highest and significant for cameras in burns > 20 years old (21–30 years, $\hat{\phi} = 0.62 \pm 0.22$; 41–50 years, $\hat{\phi} = 0.47 \pm 0.18$ SE; Fig. 3). Modeled moose detection rates predicted by the summer model were 2–4 times higher for cameras surrounded by older burns (Fig. 4).

The most parsimonious model in winter and annually included all land cover classes. In winter, mixed forests ($\hat{\phi} = 0.55$, ± 0.24 SE) and ruggedness ($\hat{\phi} = 0.34$, ± 0.16 SE) significantly explained moose detection rates, whereas conifer did not ($\hat{\phi} = 0.06$, ± 0.28 SE, Fig. 3), even though conifer was a more dominant land cover class (Supporting information). At the annual temporal scale, mixed forest ($\hat{\phi} = 0.50 \pm 0.19$ SE) and barrenland ($\hat{\phi} = -0.95 \pm 0.45$ SE; Fig. 3) significantly predicted moose detection rates

Table 2. Top model results of three competing hypotheses, null model, and global model for describing moose detections near the northern edge of their range between 2021–22 in Thaidene Nënë Indigenous Protected Area, Canada. All models include the core model consisting of the variables distance to the nearest body of water and terrain ruggedness, as well as a random factor for site. R^2_m is the marginal R-squared (random effects variance only) and R^2_c is the conditional R-squared (fixed and random effects variance). The fire model set best explained moose detections in summer, and land cover best explained moose detections in winter and annually.

Season	Model set	Model name	Variables	df	logLik	AICc	Delta	R^2_m	R^2_c
Summer	Fire	1 - Age	FAGE<10+FAGE<20+FAGE<30+FAGE<50+core model	9	-292.25	602.64	0.00	0.13	0.29
	Land cover	1 - Forest	CONFOR+MIXFOR++HETERO+core model	8	-294.46	605.03	2.39	0.10	0.28
	Null	Null	Core model	5	-298.88	607.81	5.17	0.06	0.29
	Biotic	2 - Direct competition	MUSK+BGCAR+core model	7	-297.52	609.12	6.49	0.06	0.29
	Global	Global	CONFOR+MIXFOR+GRASS+WETLA+BARREN+WATER+HETERO+FAGE<10+FAGE<20+FAGE<30+FAGE<50+FSEVER+WOLF+BBEAR+GBEAR+MUSK+BGCAR+core model	22	-282.79	610.36	7.72	0.23	0.32
Winter	Land cover	4 - All landcover	CONFOR+MIXFOR+GRASS+WETLA+BARREN+WATER+HETERO+core model	12	-283.16	590.47	0.00	0.30	0.43
	Fire	2 - Severity	FSEVER+core model	6	-289.97	591.99	1.52	0.13	0.33
	Null	Null	Core model	5	-292.87	595.77	5.30	0.07	0.29
	Biotic	1 - Predation	WOLF+BBEAR+GBEAR+core model	8	-291.31	598.68	8.21	0.92	0.94
	Global	Global	CONFOR+MIXFOR+GRASS+WETLA+BARREN+WATER+HETERO+FAGE<10+FAGE<20+FAGE<30+FAGE<50+FSEVER+WOLF+BBEAR+GBEAR+MUSK+BGCAR+core model	22	-281.08	606.66	16.19	0.89	0.91
Annual	Land cover	4 - All landcover	CONFOR+MIXFOR+GRASS+WETLA+BARREN+WATER+HETERO+core model	12	-580.93	1185.96	0.00	0.23	0.35
	Fire	1 - Age	FAGE<10+FAGE<20+FAGE<30+FAGE<50+core model	9	-586.03	1190.12	4.16	0.10	0.25
	Biotic	2 - Direct competition	MUSK+BGCAR+core model	7	-589.56	1193.15	7.20	0.08	0.27
	Null	Null	Core model	5	-592.70	1195.41	9.45	0.05	0.25
	Global	Global	CONFOR+MIXFOR+GRASS+WETLA+BARREN+WATER+HETERO+FAGE<10+FAGE<20+FAGE<30+FAGE<50+FSEVER+WOLF+BBEAR+GBEAR+MUSK+BGCAR+core model	22	-576.07	1196.44	10.48	0.23	0.34

and conifer again did not ($\hat{\delta}=0.18$, ± 0.21 SE, Fig. 3). Cameras surrounded by more mixed forest are predicted to have 2 times higher modeled moose detection rates (Fig. 4). Wetland did not significantly predict moose detection rates at either temporal scale (winter: $\hat{\delta}=-0.75$ ± 0.47 SE; annual: $\hat{\delta}=-0.11$ ± 0.22 SE).

Moose rarely observed on the tundra

Moose were rarely detected on the tundra in Thaidene Nënë. However, it is important to note there was one detection (site 3 on Fig. 5) in the Handbury Plain Low Arctic south Ecoregion where moose had been previously recorded as

absent (Ecosystem Classification Group 2012, Government of the Northwest Territories 2025). Moose were detected on the tundra at three cameras across three different sites, with the site furthest north (site 3 on Fig. 5) over 90 km from the nearest border with the taiga shield forest (or treeline). All detections were between June and October, prior to snow fall.

Discussion

Landscape features are the primary driver of moose within this study, with fire age and land cover classes explaining

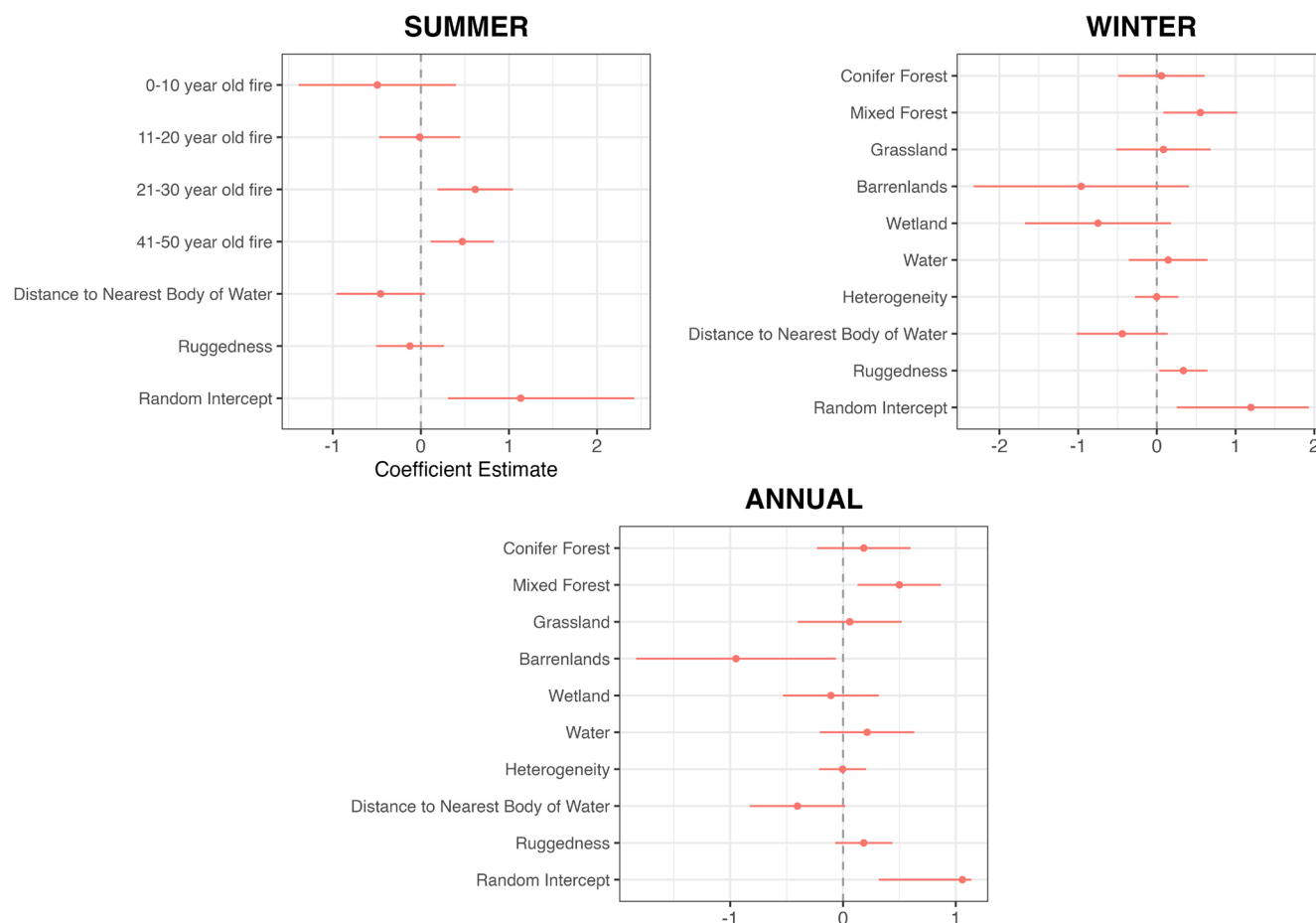


Figure 3. Beta coefficients with 95% confidence intervals for the most parsimonious model describing moose detections between 2021–2022 in Thaidene Nënë Indigenous Protected Area, Canada in summer (June to September), winter (October to May) and annually. Site was a random factor in each model. Moose detections had a positive association with burns >20 years old in summer, a positive association with mixed forest and ruggedness in winter, and a positive association with mixed forest and a negative association with barrenlands annually.

most moose detections across seasons. In alignment with our hypothesis, we did not find strong evidence to suggest that competitor or predator co-occurrence drive moose detections near these northern range limits. While predators have been documented to have strong limiting effects on moose occurrence elsewhere in the boreal forest (Van Ballenberghe and Ballard 1994, Dussault et al. 2005, Garneau et al. 2008, Boone et al. 2025, DeCesare et al. 2025), moose detections at their northern range limit in this study was best supported by landscape features.

For barren-ground caribou in our study area, co-occurrence of predators was an important seasonal predictor of detections (Jolin 2025). This may reflect the importance of caribou as primary prey species for wolves in the subarctic, despite predators being important for moose elsewhere (Gasaway et al. 1992, Van Ballenberghe and Ballard 1994). Our study also did not quantify strong evidence of the potential for competition between moose and other ungulates, with barren-ground caribou and muskox detections being poor predictors of moose detections. While this is the first study

that assesses the potential for competition between moose and other far north ungulates, opportunities for competition between these species may be less strong – although still potentially present – than the importance of landscape features for moose as moose occupy unique habitats compared to other ungulates (Christopherson et al. 2019, DeMars et al. 2019). Longer term camera, or movement, studies would aid in documenting pronounced trends in predation or resource-dependent competition. However, these results do highlight the relative importance of abiotic bottom-up processes like fire and land cover on moose detections, when compared to biotic species interactions like co-occurrence of predators and ungulate competitors.

The composition of land cover, including fire impacted areas, is important for moose at the leading edge of their range. In summer, moose were frequently detected in older fire age classes (>20 years), contrasting with previous studies on moose at lower latitudes, where moose were found to select for younger burns 10–25 years old (Brown et al. 2018, Mumma et al. 2024). Part of this discrepancy may be

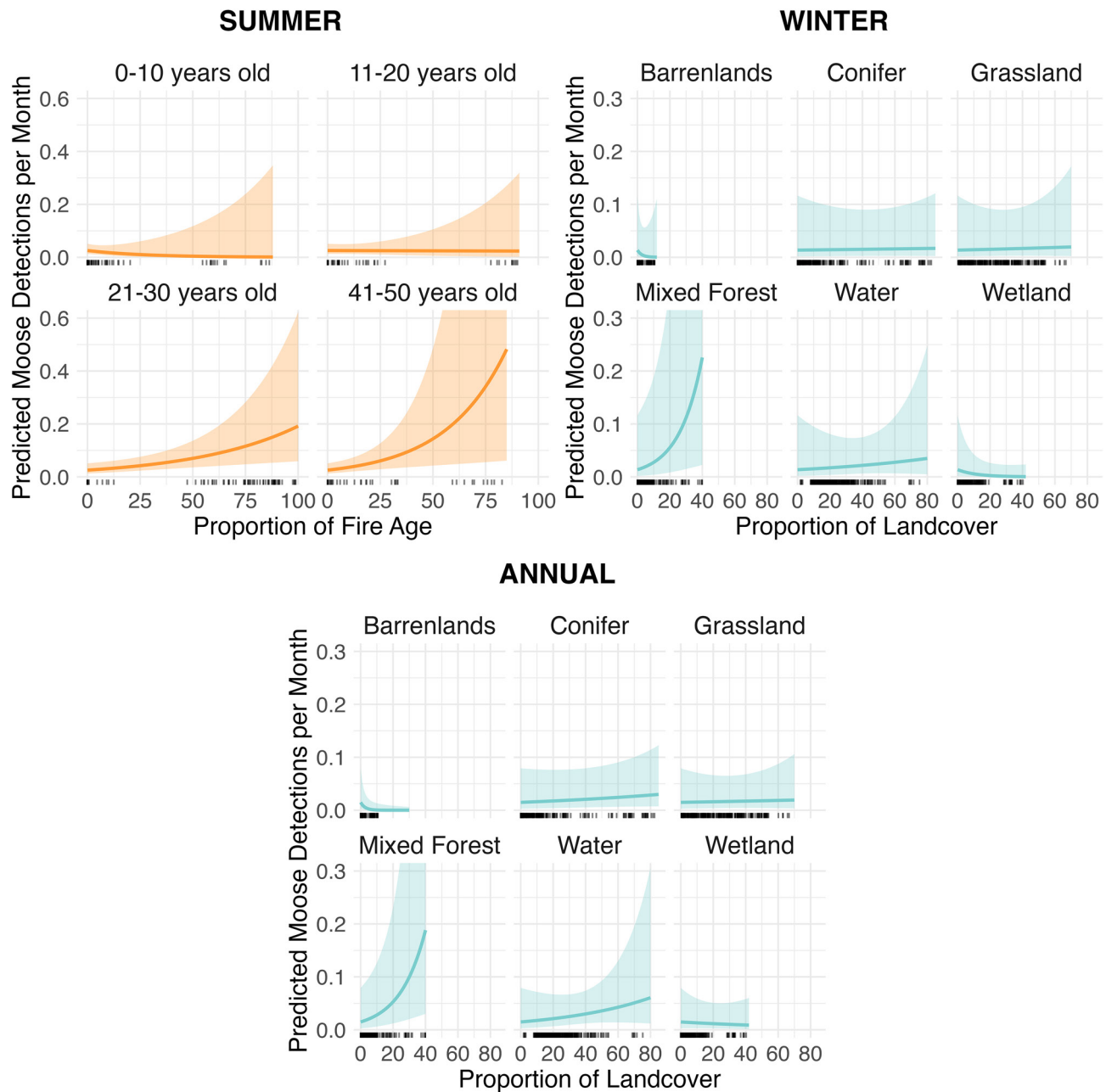


Figure 4. Model predictions derived from the most parsimonious model of monthly moose detection rates between 2021–2022 in Thaidene Nēné Indigenous Protected Area, Canada, in summer (June to September), winter (October to May) and annually. In summer, fire age was the best predictor of moose detections, whereas in winter and annually, land cover was the best predictor of moose detections. Ticks at the bottom of each figure represent the observed proportions of land cover or fire age classes around cameras.

due to slower vegetation regeneration rates at northern latitudes (Lieth 1975, Gillman et al. 2015). Regenerating forage species may take longer to reach optimal browse heights for moose, leading to a selection of older fire age classes. In winter, land cover variables were better predictors of moose detection, with moose detected more often in areas with more mixed forest but not coniferous forest (Fig. 3, Supporting information). Coniferous forests are the dominant land cover across the North American moose range and have been hypothesized to be important sources of thermal protection

(Hodder et al. 2013, Wattles et al. 2018). Trees size and shape are similarly limited by the slower vegetative regeneration rates and sun availability at northern latitudes (Kuuluvainen 1992, Lindh et al. 2018). These smaller, more stunted trees likely do not provide the same thermal protection as those in more central parts of moose range. Additionally, mixed forests may provide both thermal protection and deciduous vegetation, a preferred forage for moose (Weixelman et al. 1998, Maier et al. 2005). Given deciduous forests are rare in the study area and in the region (Ecosystem Classification

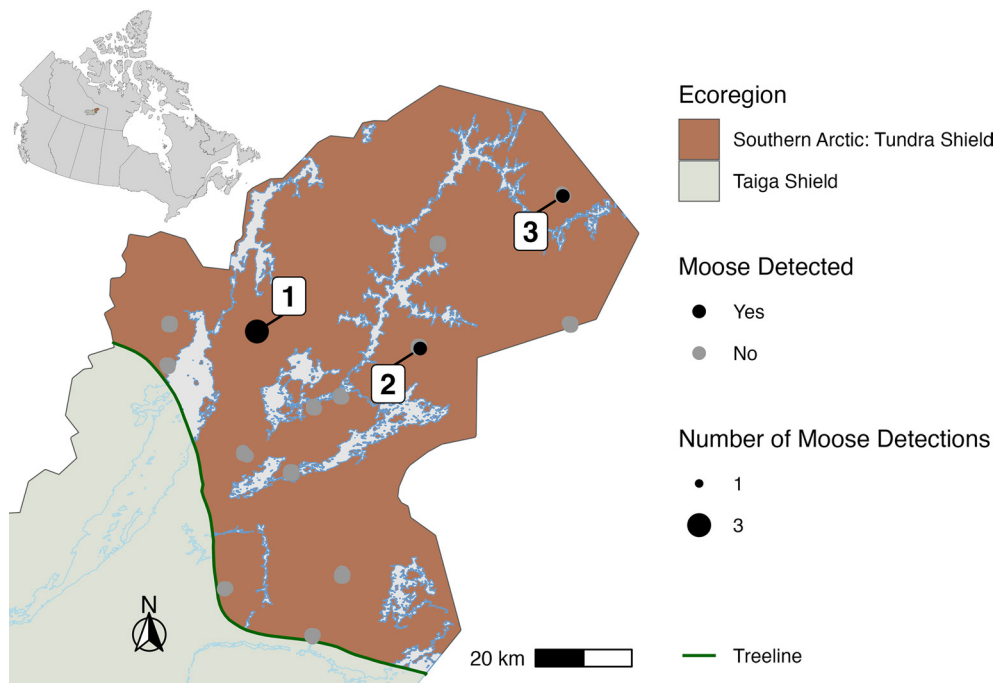


Figure 5. Moose were detected at 3 of 14 sites on the tundra of this study in Thaidene Nënë Indigenous Protected Area (2021–2022). Moose were only detected on the tundra between snow-free periods of June and October, and the furthest detection (site 3) was at a site 90 km from the treeline.

Group 2008, 2012), but expected to become more dominant with climate change (Baltzer et al. 2021, Barros et al. 2023, Stewart et al. 2023), mixed forest habitat could be particularly important for moose near the edge of their range. The importance of forested habitat is further emphasised by the comparatively few moose detections on the tundra, particularly in winter. Regardless of the drivers, forested land covers, particularly those from older burns, appear to be important for moose distribution near the leading edge of their range.

The results of this study have mixed implications for the effect of climate change on northern moose. Increases in fire extent, frequency, and intensity are expected in the next century (Kelly et al. 2013, Wang et al. 2020, Gaboriau et al. 2023, Nesbitt et al. 2025), which would impact the structure and composition of vegetation in the subarctic, including the dominance and distribution of tree species like black spruce (Whitman et al. 2019, Baltzer et al. 2021). These changes may impact the availability of older post-fire vegetation that moose were frequently associated with in this study during the summer. Climate change is also increasing shrub density throughout the tundra of the circumpolar Arctic. This shrubification has been linked to the expansion of boreal wildlife species onto the tundra, including moose (Elmhagen et al. 2015, Tape et al. 2016, 2018, Wheeler et al. 2018, Speed et al. 2021). While shrubification may benefit moose, continued range expansion onto the tundra may be limited by winter conditions and the slower expansion of the boreal forest transition zone (Sirois and Shugart 1993, Dial et al. 2016, Speed et al. 2021). Models from this study

could be incorporated into a predictive multi-model framework (sensu Micheletti et al. 2021, Stewart et al. 2023) to forecast complex and competing impacts of climate change on moose habitat.

Several limitations affected our study inferences. Our data was collected over one year, when a longer temporal study would better quantify the annual and seasonal impact of predators and competitors on moose (Holt and Barfield 2003, Burton et al. 2022, Steenweg et al. 2023). Similarly, while our study provides a snapshot of moose habitat use near the northern extent of their range, a deeper understanding of habitat selection at multiple scales would provide a clearer picture of novel habitat requirements. For example Granados et al. (2023) looked at multiple spatial scales with camera data and found different habitat responses to recreation and land uses for a number of predator and prey species, including moose. In winter, many cameras were covered in snow, with only an average of 18 days (± 10 days) active recording days per month in both December and January, particularly on the tundra. Focusing on camera setup methods to prevent wind-blown snow from covering the camera lens may help increase tundra-specific moose detections in winter. Finally, although snow depth in our study area is anticipated to be lower than other areas of the moose range (Meteorological Service of Canada, Environment Canada 2009), adequate landscape scale remotely sensed, or empirical, data was not available for snow cover across our study region. Snow depth is expected to be an important limiting factor in moose presence (Kelsall and Telfer

1974, LeResche et al. 1974, Dussault et al. 2005), and is changing with climate change (Bigalke and Walsh 2022, Eythorsson et al. 2023); quantifying moose–snow relationships at the leading edge of their range may be important for understanding future moose presence on the tundra.

The results of this study suggest that moose populations near the northern edge of their range are more limited by habitat characteristics than interspecific interactions, which differs from other ungulates in the study area, and moose populations at more southern latitudes. The implications of climate change on moose range limits are difficult to predict, as mixed-forest habitats that moose use may expand northwards leading to more habitat, but the availability of older post-fire age classes with optimal foraging conditions may decline. These results highlight the relative importance of bottom-up processes, as compared to top-down processes, in determining the leading edge of this species' range and underscores the importance of abiotic impacts, such as climate change, in determining this species' distribution.

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Author contributions

Claudia A. Haas: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Validation (lead); Writing – original draft (lead). **Nick W. Luymes:** Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Rosemary Hohnen:** Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Writing – review and editing (equal). **Frances E. C. Stewart:** Funding acquisition (equal); Supervision (lead); Writing – review and editing (equal).

Data availability statement

Research was produced using information that was co-produced and supplied by Łutsël K'é Dene First Nation, Government of Northwest Territories, and Parks Canada. The information is confidential as it relates to Indigenous well-being and data sovereignty, so requests to use the data must be made directly to and reviewed by these parties.

Supporting information

The Supporting information associated with this article is available with the online version.

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