





Research Article


Evaluating the Mechanisms of Landscape Change on White-Tailed Deer Populations

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ABSTRACT Understanding how landscape change influences the distribution and densities of species, and the consequences of these changes, is a central question in modern ecology. The distribution of white-tailed deer (*Odocoileus virginianus*) is expanding across North America, and in some areas, this pattern has led to an increase in predators and consequently higher predation rates on woodland caribou (*Rangifer tarandus caribou*)—an alternate prey species that is declining across western Canada. Understanding the factors influencing deer distribution has therefore become important for effective conservation of caribou in Canada. Changing climate and anthropogenic landscape alteration are hypothesized to facilitate white-tailed deer expansion. Yet, climate and habitat alteration are spatiotemporally correlated, making these factors difficult to isolate. Our study evaluates the relative effects of snow conditions and human-modified habitat (habitat alteration) across space on white-tailed deer presence and relative density. We modeled deer response to snow depth and anthropogenic habitat alteration across a large latitudinal gradient (49° to 60°) in Alberta, Canada, using motion-sensitive camera data collected in winter and spring from 2015 to 2019. Deer distribution in winter and spring were best explained by models including both snow depth and habitat alteration. Sites with shallower snow had higher deer presence regardless of latitude. Increased habitat alteration increased deer presence in the northern portion of the study area only. Winter deer density was best explained by snow depth only, whereas spring density was best explained by both habitat alteration and the previous winter's snow depth. Our results suggest that limiting future habitat alteration or restoring habitat can alter deer distribution, thereby potentially slowing or reversing expansion, but that climate plays a significant role beyond what managers can influence. © 2020 The Wildlife Society.

KEY WORDS Alberta, climate, density, distribution, habitat alteration, *Odocoileus virginianus*, snow depth, white-tailed deer.

Understanding the mechanisms leading to changes in species abundance and distribution, and the consequences of these changes, is a fundamental pursuit of modern ecological studies (Chen et al. 2011, Gilbert et al. 2019). Increasing and expanding prey populations may destabilize existing predator-prey dynamics, leading to fluctuations and reductions of native species via competition or apparent competition (Holt 1977, Serrouya et al. 2015). In North America, white-tailed deer (*Odocoileus virginianus*) populations have increased in abundance and expanded their distribution since the late 1900s (Webb 1967, Veitch 2001, Côté et al. 2004, Dawe and Boutin 2016, Hanberry and Hanberry 2020). The expansion of white-tailed deer is implicated in the decline of woodland caribou (*Rangifer tarandus caribou*) in western Canada (Latham et al. 2011, Hervieux et al. 2013). Woodland caribou are listed as

threatened under the Canadian Species at Risk Act. Caribou declines are caused by increasing predation, primarily by wolves (*Canis lupus*) but also cougars (*Puma concolor*), and bears (*Ursus* spp.; McLoughlin et al. 2003, Wittmer et al. 2005, Whittington et al. 2011). Predator populations are thought to be sustained at higher densities than historical levels as a result of increasing primary prey populations, such as white-tailed deer and moose (*Alces alces*; Seip 1992, White and Garrott 2005, Latham et al. 2013). Increased predator abundance sustained by expanding primary prey can also threaten other prey species, including mule deer (*O. hemionus*; Robinson et al. 2002, Cooley et al. 2008). What influences these changes in prey abundance and distribution is therefore a critical knowledge gap to support effective species management because the management options that address expanding white-tailed deer will differ based on the mechanisms behind their expansion.

In western North America, rapid development of petroleum and forest industries has altered the natural landscape by the creation of extensive networks of roads, seismic lines,

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and well sites (Fischer and Lindenmayer 2007, Kemper and Macdonald 2009, Allred et al. 2015). Latham et al. (2011) reported that such industrial development coincided with a 17.5-fold increase in white-tailed deer populations between 1997 and 2005. One hypothesis explaining increased abundance and distribution of white-tailed deer is an increase in early successional forests caused by human-modified habitat (i.e., habitat alteration) such as forestry cutblocks, well sites, and linear features (e.g., roads, seismic lines; Rempel et al. 1997, Latham et al. 2011, Fisher and Burton 2018). Young forests and associated shrub communities provide increased forage for deer (Alverson et al. 1988, St-Louis et al. 2000, Fisher and Wilkinson 2005). Furthermore, agricultural fields can provide food sources for ungulates (Bonnot et al. 2013, Bleier et al. 2017).

An alternate hypothesis explaining white-tailed deer expansion is a changing climate. Milder winter conditions with lower cumulative snow depth, lower snow cover, shallower snow (Beier and McCullough 1990, Vavrus 2007, Richard et al. 2014), and warmer temperature (Ozoga and Gysel 1972) have been linked to increased deer densities. Winter severity is also a strong predictor of deer distribution in boreal forests (Dawe et al. 2014, Dawe and Boutin 2016). Longer winters with cold temperatures and deep snow increase the energy required for ungulates (Parker et al. 1984, Mysterud and Østbye 2006) and simultaneously decrease food availability, making it difficult for deer to sustain sufficient energy intake. As a result, white-tailed deer survival rates decrease with increasing winter severity and snow depth (Ballard et al. 1999, DelGiudice et al. 2002). Furthermore, these climate effects can influence deer survival rates in subsequent years (Post and Stenseth 1998, Dawe 2011). Less severe winters are becoming more frequent in Alberta, Canada (Brown and Braaten 1998, Vincent et al. 2015, Kienzle 2018), which could lead to increased deer populations.

The relative contribution of climate and habitat alteration to explain deer expansion is difficult to disentangle. In most northern landscapes, winter severity and habitat alteration are inversely correlated across space, such that as latitude increases, there is typically an increase in winter severity with a decrease in habitat alteration. The interactions of climate, latitude, and habitat alteration make it difficult to isolate and measure the relative effects of key variables influencing deer distribution and densities.

Our objective was to evaluate the relative influence of climate and habitat alteration on white-tailed deer populations across the province of Alberta, including core white-tailed deer distribution to the northern range limit. We predicted that sites with shallower snow and greater habitat alteration would be more likely to have deer present and at higher densities in winter, and that density, given presence, would be higher. Conversely, we predicted that spring presence and density would be more influenced by habitat alteration than the previous winter's snow depth because deer distribution can rebound following harsh winters via seasonal movement or site recolonization (Fisher et al. 2020). Because the relative effect of snow depth and

habitat alteration likely varies between core white-tailed deer range and the range limits, and human land-use types vary between the southern and northern portions of the province, we expected factors influencing deer abundance and distribution to differ between the south and the north of the province.

STUDY AREA

We conducted the study between 2015 and 2019 in Alberta, Canada. The province of Alberta (662,583 km²) extends from the United States-Canada border at 49° latitude, north to 60° (Fig. 1). The province has 6 natural regions, from south to north: Grasslands, Rocky Mountains, Parklands, Foothills, Boreal Forest, and the Canadian Shield. The elevation varies substantially across these regions, and ranges from approximately 550 m in the grasslands up to approximately 3,747 m in the mountains, with an average of 773 m. Approximately half of Alberta is composed of boreal forest, characterized by a mosaic of upland mixedwood forest and lowland peatlands. Dominant tree species in the boreal forests include balsam fir (*Abies balsamea*), larch (*Larix* spp.), black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*). A large portion of Alberta is composed of prairie and parkland prairies, which are dominated by mixed grass, fescue, and aspen parkland (Olson 1994). The boreal, parklands, and grasslands of Alberta contains numerous large-mammal species such as moose, pronghorn (*Antilocapra americana*), elk (*Cervus canadensis*), black bears (*U. americanus*) and brown bears (*U. arctos*), grey wolves, white-tailed deer, mule deer, and woodland caribou.

Alberta has a continental climate and 4 seasons (winter from Dec to Mar, spring from Mar to Jun, summer from Jun to Sep, fall from Sep to Dec). Annual precipitation varies across the province (250 to >700 mm), with higher rainfall typical in the southwest along the mountain ranges and foothills (Schneider 2013). Winter temperatures tend to vary between -5°C and -15°C but can be as low as -40°C (Schneider 2013).

Habitat alteration covered 29% of Alberta in 2016 (Alberta Biodiversity Monitoring Institute [ABMI] 2018a). Agriculture is the dominant human land-use type across Alberta and largely occurs in the grassland and parkland. Forestry is the second most dominant land-use type and largely occurs in the boreal forest and foothills. A small part of the province is continuously occupied by humans within 2 main cities (Calgary and Edmonton), representing approximately 44% of the provincial population.

METHODS

Deer Observations

Using motion-sensitive cameras from 49.06° to 60.01°N degrees of latitude, we evaluated the relative support for snow depth and habitat alteration in predicting presence and density of white-tailed deer. We used data compiled from motion-sensitive cameras (Reconyx PC900, Holmen,

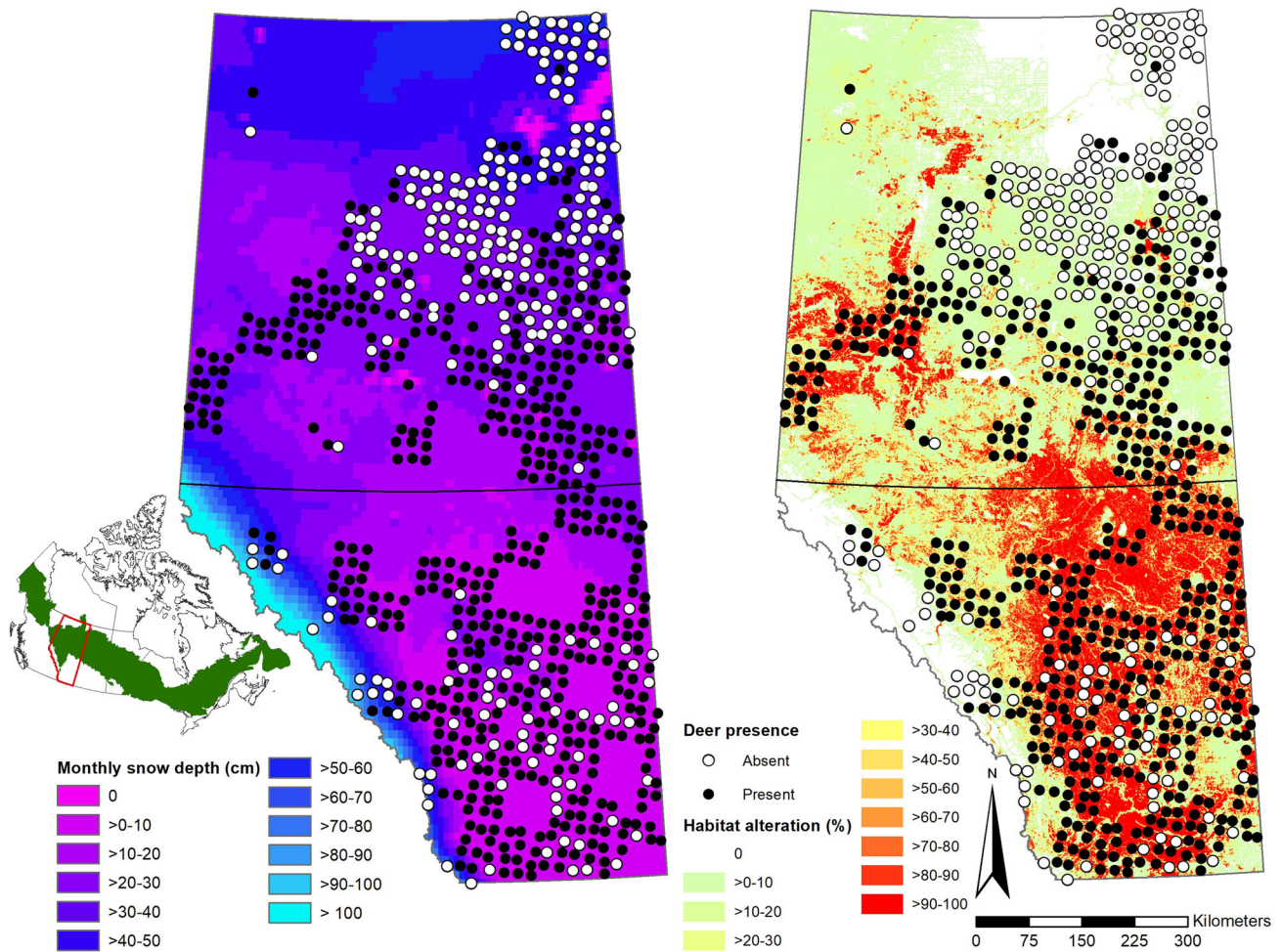


Figure 1. The distribution of snow depth (cm), habitat alteration (%), and motion-sensitive camera sites used to study white-tailed deer distribution and density across Alberta, Canada, 2015–2019. Filled and hollow data points represent where deer were present or absent, respectively, during any point in the study. The snow depth map depicts data from the Copernicus Climate Change Service's ERA5-Land dataset and corresponds to the snow depth in February 2016. Habitat alteration depicts data from the Alberta Biodiversity Monitoring Institute's 2017 Human Footprint Inventory (ABMI 2017). Inset represents the location within Canada, where green represents the extent of boreal forest.

WI, USA) deployed across Alberta from 2015 to 2019 by the ABMI (ABMI 2019). The sites ranged from 49.06° to 60.01°N latitude, and 110.00° to 117.67°W longitude (Fig. 1). Each site was systematically placed 20 km apart, and sampled sites represented approximately 46% of the potential sites (Fig. 1). Motion-sensitive cameras are non-invasive and are considered Category A level of invasiveness; there is little to no animal manipulation. Therefore, a research permit and formal Animal Care and Use Committee approval from the University of Alberta is not necessary. Each site had 4 cameras placed in a 600-m² plot at the northeast, southeast, southwest, and northwest corners. Technicians fastened cameras to a tree or pole 1 m above ground and positioned them to have an unobstructed view for ≥10 m. Crews placed a 1-m tall pole 5 m away from the camera, with the camera aimed at the 80-cm mark on the pole. The pole was colored with 10-cm stripes to aid with photo interpretation and analyses, and to verify correct positioning of the camera. The motion-triggered cameras were active at all times (i.e., 24 hrs). These data are part of a broader research program in which cameras monitor

multiple species (ABMI 2019), and therefore cameras on the northeast and southwest corners were lured with 15 ml of skunk and musk scent blend (O'Gormans Long Distance Call lure) to increase detection of rare species, particularly of carnivores.

We used an automated neural network (Huggard 2018) to analyze all photographs to identify and remove images not containing animals. The accuracy of images identified as containing vegetation only was high (accuracy=0.99; ABMI, unpublished data), though we periodically visually checked random images and did not find incorrectly identified images. We manually processed the remaining images to identify captured animals and confirmed observations independently to prevent misidentification. If we could not identify animals to species level, we did not include the image in the analyses. We used only white-tailed deer data in this study.

Motion-sensitive camera data used in this study were collected from 2 February 2015 to 17 June 2019, with a mean active period of 157 days/year. We obtained 195,224 images of white-tailed deer. Cameras were not all active

during the same time period. For this reason, we separated data into 2 time periods: winter (1 Nov–31 Mar) and spring (1 Apr–17 Jun). Winter generally consisted of temperatures below 0°C and snow covering the ground. In spring, the number of active cameras over time varied by year; 90% of cameras were active until mid-June or 1 July. We therefore limited our analyses to 17 June as a conservative cut-off in which the landscape was adequately sampled. In winter, 2,789 cameras across 759 sites were active ≥ 1 month, and in spring, 2,750 cameras were active over 763 sites. Only 34 cameras from 17 sites had data for multiple years.

White-Tailed Deer Presence and Density

We calculated the presence and an index of density given presence of white-tailed deer for each site in winter and spring of each year monitored. Because we were interested in changes in presence and density of deer as a function of changes in snow depth throughout winter, we calculated presence and density for each month separately and treated each month as an observation. For each month in winter and through spring, we recorded cameras as having deer present (1) if there was ≥ 1 instance of a white-tailed deer recorded, or having deer absent (0) if there were none for the time period considered.

We calculated an index of deer density given presence using a modified random encounter and staying time model (REST; Nakashima et al. 2018, Garland et al. 2020). The number of animals observed within a defined area over time, sampled using motion-sensitive cameras, is counted and divided by the area and time monitored using the formula:

$$D = \frac{\sum(N \times T_F)}{A_F \times T_O},$$

where density (D) at each camera is calculated as the number of individual animals observed (N) multiplied by the time in front of the camera field of view (T_F), divided by the area of the camera field of view (A_F) multiplied by the total camera operating time (T_O). The units are animal-seconds per area-seconds, which equates to the number of animals per unit area, here defined as km^2 . To estimate density from motion-sensitive camera images, it is therefore essential to quantify the time animals spent in front of the cameras, sampling area, and sampling time. We provide additional details on how camera trapping images are classified into time and area (Appendix A). We used density for our study instead of a count of independent detections per camera because movement rates and density are inversely related, which can confound interpretations of relative abundance from detection rates (Sollmann et al. 2013, Broadley et al. 2019). It is important to consider that density estimates presented do not represent the absolute density of the white-tailed deer population but an index of relative density among sites, though we hereafter use the term density. We also assumed perfect detection of animals within the defined sampling area (Appendix A).

Among sites, few cameras remained active throughout an entire winter. Therefore, we included only data from cameras active for >10 days/month and ≥ 1 winter month in the

analyses. We calculated the mean density per site for each month in winter. We pooled data from lured and unlured cameras for presence and density analyses. We did not specifically include lure effects when evaluating presence because lure was available similarly across sites and we pooled all cameras at a site when quantifying presence. We included the use of lures when modeling density at each camera by adjusting the final density estimate using the ratio of lured:unlured cameras (Appendix A). Because we were interested in variation in density at sites where deer were present only, we did not include cameras with no deer present when calculating mean density per site. We included only sites within the observed white-tailed deer distribution (i.e., the maximum latitude in which deer were observed; 59.31958° latitude) in analyses.

Model Covariates

We obtained climate data collected by the Copernicus Climate Change Service and it corresponded to the C3S ERA5-Land dataset (Copernicus Climate Change Service 2019). We extracted mean monthly snow depth from records within cells of 9 km^2 at each camera location using ArcGIS (version 10.3.1; Esri, Redlands, CA, USA) and averaged snow depth by site. We also estimated monthly snow cover at each camera location, using moderate resolution imaging spectroradiometer data (MODIS; Hall and Riggs 2018). Cell size was 0.05° latitude \times 0.05° longitude. We estimated mean snow depth and cover for each winter before the calculated spring density. Snow depth and cover were highly correlated. We used snow depth in our models because although snow cover data were available at a finer spatial resolution, we were interested in the variation in snow depth that occurs even after snow cover has reached 100%. We suspected the monthly anomaly patterns within a given season to be relatively large so that resolution would not be an issue.

We measured the percent area covered by habitat alteration within a 1-km^2 area (564-m radius) around each camera using ArcGIS. We measured habitat alteration as the total from all land cover types related to the energy, forestry, and agriculture industries, and urban development (for a comprehensive description, see ABMI 2020). We also calculated the percent area covered by linear features only, harvested forests (cutblocks) only, and agricultural areas only to investigate relative effects independently from other human land-use types. Each of these variables were highly correlated. Because we were interested in the cumulative effect of all human land-use types, we chose to use all features (total % of habitat alteration). We used a 1-km^2 area to represent a mean seasonal deer home range ($\sim 0.50\text{--}2 \text{ km}^2$; Larson et al. 1978, Tierson et al. 1985, Etter et al. 2002, Webb et al. 2007). We used habitat alteration data that most closely matched the year preceding camera deployment: cameras installed in 2015 and 2016 were associated with data from 2014 (ABMI 2017), cameras installed in 2017 and 2018 with data from 2016 (ABMI 2018*b*), and cameras from 2019 with data from 2018 (ABMI 2020).

Snow conditions and habitat alteration co-vary with latitude (in spring, snow depth and latitude: $r = 0.31$, habitat

alteration and latitude: $r = -0.56$ Appendix B, Fig. B1), which makes it challenging to decouple their relative effects. Furthermore, human land-use types vary between the southern portion of Alberta, which is dominated by the agriculture sector, and the northern boreal forests, which are dominated by the energy and forestry sectors (Fig. 1). To help decouple the factors covarying with latitude, we therefore stratified analyses into *a priori* categories of latitude, south (49° to $\leq 54^\circ$) and north ($>54^\circ$), and included latitude class in all models. Latitude classes were based on the breakpoint between a bimodal distribution in the distribution of monitored sites and also corresponded to differences in land-use types (Appendix B).

Differences in monitoring effort at each site can influence the detection of species, such that with increased effort, the likelihood of detecting a species increases (Fisher and Burton 2018). For presence analyses, we calculated monitoring effort as the number of days each camera was active at a site, divided by the number of days within the monitoring period (monthly for winter, and from 1 Apr to 17 Jun in spring). Density estimates using REST already account for the time cameras were active, and therefore already account for monitoring effort.

Data Analysis

We evaluated the support of models predicting the presence and density of white-tailed deer when including snow depth and habitat alteration variables using a model competition framework and Akaike's Information Criterion with a correction for small sample sizes (AIC_c ; Akaike 1973, Sugiura 1978). The null model included latitude class and the monitoring effort as fixed effects, and increased in complexity to include snow depth only, habitat alteration only, snow depth and habitat alteration, and snow depth and habitat alteration both interacting with latitude class. In winter, we quantified snow depth as the mean snow depth per month. Because each winter month was included as a unique observation, we included a random intercept for each site. In spring, we quantified snow depth as the mean snow depth of the previous winter. Because we quantified spring presence, density, snow depth, and human footprint for the entire spring season, and not by month, we did not include a random effect. We chose the top competing model using a threshold of 2 AIC_c from the top model (Burnham and Anderson 2002, Arnold 2010). We further presented the magnitude of the effect of each variable with 95% confidence intervals not overlapping zero (Neyman 1937) from the top competing model.

Because 4 cameras were within 600 m of each other at each monitoring site, these cameras may not represent independent samples. We therefore treated each 600-m² site as the sampling unit. We recorded sites as having deer present (1) if ≥ 1 of the 4 cameras recorded a white-tailed deer. We averaged the estimated density across each camera with deer present at each site, and averaged environmental attributes across cameras at each site.

We used generalized linear mixed models (GLMM) with a logit link to evaluate presence, with presence versus

absence as a binary outcome, and Gaussian log-linear mixed models for the density of white-tailed deer. We checked final models for variance heterogeneity (plotting residuals over fitted values), and correlated terms (Pearson test; Tabachnick and Fidell 2012). To better meet normality assumptions of response variables, we log transformed density. We pooled data across years. We did not observe any biologically unrealistic outliers and assumed that the relationships created by the log transformation were linear.

To provide an example of the relative influence of snow and habitat alteration over time, we used observed historical changes in snow depth and habitat alteration to calculate the predicted change in deer presence and density. Habitat alteration has increased by 3.76% in the province of Alberta from 1999 to 2016 (ABMI 2018a). Conversely, winter precipitation in Alberta has decreased since the late 1940s (Brown and Braaten 1998, Vincent et al. 2015). Vincent et al. (2015) estimated that from 1948 to 2012, snow depth in Alberta has decreased by a range of 10% to 90%. Over the same time period as the change in habitat alteration was reported (1999 to 2016), these rates equate to a 3–24% decrease in snow depth, with a mean of approximately 10%. Therefore, we calculated the predicted change in deer presence and density as a function of a 10% decrease in median snow depth and a 4% increase in median habitat alteration. We performed all data analyses with R statistical software (R Core Team 2018), fit linear mixed-effect models using lme4 (Bates et al. 2015), and compared models using MuMIn (Barton 2020). Finally, we reported adjusted R^2 values for linear models using lme4 and package rsq (Zhang 2017), and Nakagawa's marginal and conditional R^2 for mixed-models (Nakagawa and Schielzeth 2013) using package performance (Lüdtke et al. 2020).

RESULTS

We used data compiled from 2,842 cameras deployed at 767 sites across Alberta from 2015 to 2019. Cameras captured photographs of white-tailed deer in 49% of the sites monitored in the south and 35% in the north. The estimated density of deer at sites where present ranged from 0.03 deer/km² to 106.00 deer/km² (winter: $\bar{x} = 7.24$ deer/km² in the south and 5.26 deer/km² in the north, spring: $\bar{x} = 2.82$ deer/km² in the south and 1.77 deer/km² in the north). Monthly winter snow depth varied between <1 cm and 172 cm (median = 15 cm) in the south and between 2 cm and 89 cm (median = 31 cm) in the north. Habitat alteration varied between zero and 100% in the south and the north, with a median of 55% in the south and 3% in the north. We observed white-tailed deer at a maximum latitude of 58.36757° in winter and 59.31958° in spring.

White-Tailed Deer Presence

The highest ranked model explaining the monthly presence of white-tailed deer in winter included snow depth and habitat alteration interacting with latitude class (Table 1; conditional $R^2 = 0.91$ and marginal $R^2 = 0.15$). Deer presence decreased as snow depth increased, regardless of latitude class (Table 2). The probability of deer presence

Table 1. Model comparisons of white-tailed deer presence and density given presence in winter months and spring across Alberta, Canada, 2015–2019. We evaluated each winter month as an observation, and included a random intercept for site (1|site). We modeled spring as 1 occasion, and included the mean snow depth from the previous winter. We present the degrees of freedom, log-likelihood (LogLik), Akaike's Information Criterion adjusted for small sample sizes (AIC_c), difference in AIC_c value from top model (Δ AIC_c), and Akaike weight. Covariates include latitude class (LatC; South vs. North), snow depth (SD; cm), habitat alteration (HA; %), monitoring effort (ME; winter = active days/maximum days per month per site, spring = active cameras/maximum number of cameras per site).

Dependent variable	Season	Model	df	LogLik	AIC _c	Δ AIC _c	Weight
Presence	Winter <i>n</i> = 712	LatC × SD + LatC × HA + ME + (1 site)	8	-712.78	1,441.70	0.00	1.00
		LatC + SD + ME + (1 site)	5	-721.92	1,453.90	12.23	0.00
		LatC + SD + HA + ME + (1 site)	6	-721.32	1,454.70	13.04	0.00
		LatC + HA + ME + (1 site)	5	-742.00	1,494.00	52.39	0.00
		LatC + ME + (1 site)	4	-743.60	1,495.20	53.57	0.00
	Spring <i>n</i> = 738	LatC × SD + LatC × HA + ME	7	-392.33	798.80	0.00	1.00
		LatC + SD + HA + ME	5	-418.35	846.80	47.98	0.00
		LatC + HA + ME	4	-428.20	864.40	65.64	0.00
		LatC + SD + ME	4	-439.32	886.70	87.88	0.00
		LatC + ME	3	-458.46	922.90	124.13	0.00
Density	Winter <i>n</i> = 273	LatC + SD + (1 site)	5	-800.54	1,611.20	0.00	0.81
		LatC + (1 site)	4	-803.15	1,614.40	3.17	0.17
		LatC + SD + HA + (1 site)	6	-803.54	1,619.30	8.04	0.01
		LatC + HA + (1 site)	5	-804.84	1,619.80	8.60	0.01
		LatC × SD + LatC × HA + (1 site)	8	-810.88	1,638.10	26.86	0.00
	Spring <i>n</i> = 495	LatC × SD + LatC × HA	7	-848.95	1,712.10	0.00	0.67
		LatC + HA	4	-853.30	1,714.70	2.57	0.19
		LatC + SD + HA	5	-852.55	1,715.20	3.09	0.14
		LatC	3	-860.09	1,726.20	14.10	0.00
		LatC + SD	4	-859.57	1,727.20	15.10	0.00

decreased abruptly to <0.01 when snow depth exceeded 65 cm in the south and 23 cm in the north (Fig. 2A). Increased habitat alteration increased the probability of presence in the north, but there was no such effect in the south (Table 2). The predicted probability of presence increased by <0.01 with every increase in percent habitat alteration until habitat alteration exceeded 52%, and then increased abruptly to a maximum of 0.87 (Fig. 2B). After accounting for snow depth and habitat alteration, deer presence was lower in the north (Table 2). The monitoring effort increased the probability of presence of white-tailed deer (Table 2).

The highest ranked model explaining the monthly presence of white-tailed deer in spring included snow depth and habitat alteration interacting with latitude class (Table 1;

adjusted $R^2 = 0.24$). White-tailed deer presence increased as the previous winter's snow depth decreased (Table 2). When snow depth varied from the minimum to maximum observed snow depths (south = 2–131 cm, north = 5–52 cm), the predicted probability of deer presence ranged from 0.85 to 0.05 in the north and 0.81 to 0.31 in the south (Fig. 2C). Increased habitat alteration increased the probability of presence in the north, but there was no effect in the south (Table 2). The predicted probability of deer presence increased abruptly from 0.47 to 0.80 as habitat alteration increased from 0 to 24% (Fig. 2D). After accounting for snow depth and habitat alteration, deer presence was lower in the north (Table 2). Increased monitoring effort increased the probability of presence of white-tailed deer (Table 2).

Table 2. Top model coefficients predicting white-tailed deer presence and density given presence based on snow depth (cm), habitat alteration (%), and latitude winter months and spring across Alberta, Canada, 2015 and 2019. We included monitoring effort (active cameras/maximum operating cameras) as a fixed effect for presence analysis. We modeled spring as 1 occasion with snow depth calculated as the mean snow depth from the previous winter. We evaluated each winter month as an observation, and included a random intercept for site. Coefficient estimates (β) for which 95% confidence intervals (1.96 × SE) are not overlapping zero are indicated with an asterisk.

Dependent variables	Independent variables	Winter			Spring		
		β	Low CI	High CI	β	Low CI	High CI
Presence	Intercept	-2.951*	-5.514	-0.388	1.215*	0.228	2.202
	North	-3.137*	-5.165	-1.109	-1.178*	-2.112	-0.243
	Snow depth	-0.062*	-0.090	-0.034	-0.038*	-0.054	-0.021
	Habitat alteration	0.014	-0.035	0.008	0.002	-0.007	0.010
	Monitoring effort	3.222*	1.711	4.732	0.805*	0.007	1.604
	Snow depth × north	-0.014	-0.055	0.026	-0.010	-0.040	0.020
Density	Habitat alteration × north	0.088*	0.048	0.128	0.061*	0.040	0.082
	Intercept	1.169*	0.925	1.415	-0.245	-0.651	0.161
	North	0.106	-0.234	0.447	-0.024	-0.617	0.570
	Snow depth	-0.016*	-0.025	-0.008	0.012	-0.003	0.027
	Habitat alteration				0.005*	0.000	0.009
	Snow depth × north				-0.021	-0.044	0.002
	Habitat alteration × north				0.008*	0.001	0.016

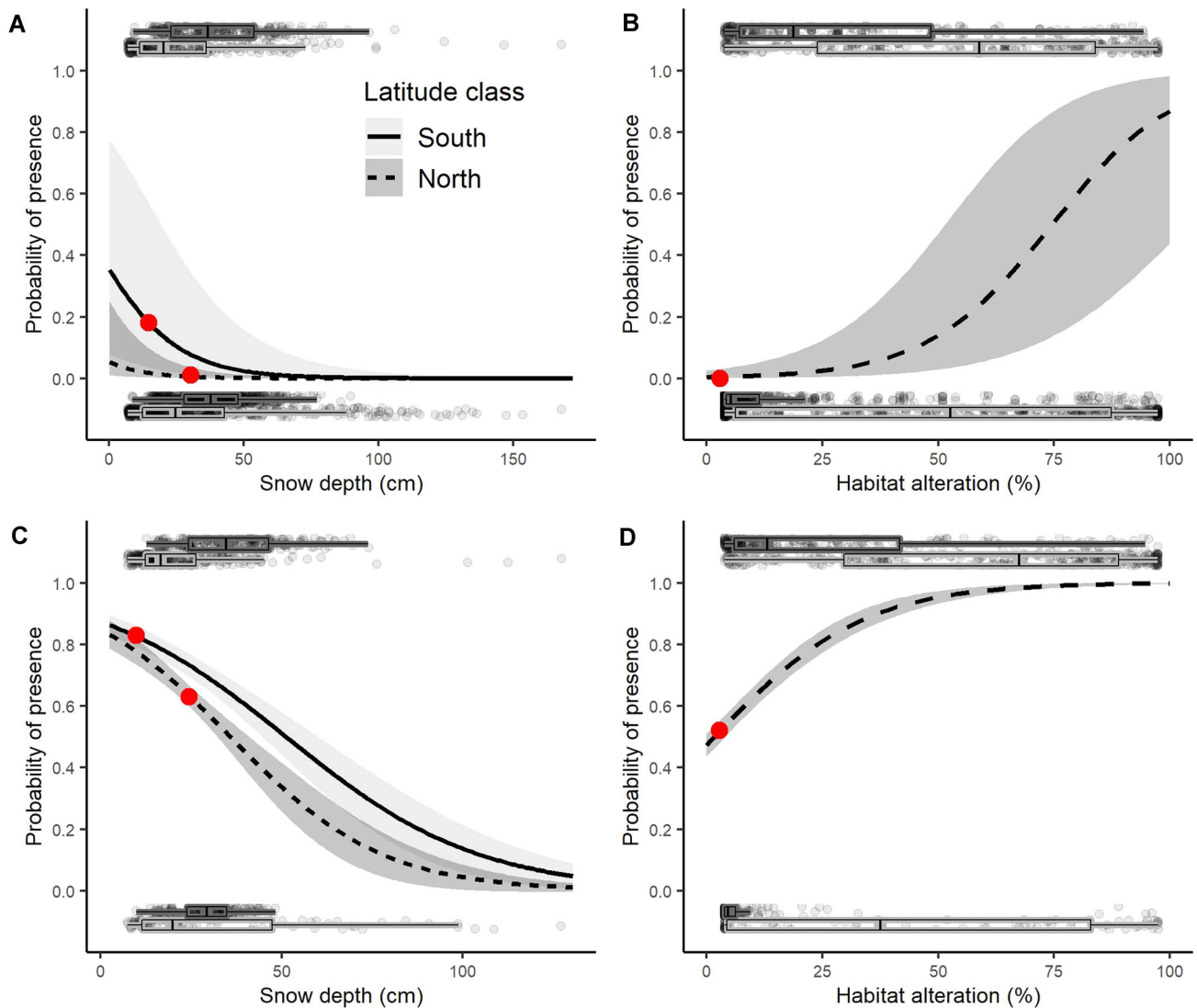


Figure 2. The effect of snow depth (cm; A) and habitat alteration (%) (B) on the presence of white-tailed deer in winter months (1 Nov–31 Mar) and in spring season (1 Apr–17 Jun; C and D) in the north (dashed line) and south (solid line) of Alberta, Canada, 2015–2019. The predicted probability of white-tailed deer presence is presented for only parameters in which the 95% confidence intervals of model estimates did not overlap zero. Monitoring effort is fixed at its mean and either habitat alteration or snow depth are fixed at their medians. Grey shading represents 95% confidence intervals (bootstrapped in the case of winter). Observed habitat alteration and snow depth across sites in the south (light grey) and north (dark grey) where deer were present (top of panel, probability of presence = 1) and absent (bottom of panel, probability of presence = 0) are shown, along with boxplots representing the median, 25th percentiles and 75th percentiles. A red dot on the predicted line represents the observed median habitat alteration or snow depth for each latitude class.

White-Tailed Deer Density

The highest ranked model explaining the monthly density of white-tailed deer given presence in winter months included snow depth and latitude class only (Table 1; conditional $R^2 = 0.49$ and marginal $R^2 = 0.04$). Deer density decreased from 3.09 to 0.71 deer/km² when snow depth varied from the minimum (2 cm) to maximum (93 cm; Fig. 3A).

The highest ranked model explaining the density of white-tailed deer given presence in spring included snow depth and habitat alteration interacting with latitude class (Table 1; adjusted $R^2 = 0.05$). Habitat alteration increased white-tailed deer density in spring, and this effect was stronger in the north (Table 2). Deer density increased from 0.94 deer/km² to 1.52 deer/km² in the south and from 0.66 to 2.50 deer/km² in the north when habitat alteration varied

from the minimum (0%) to the maximum (100%) observed (Fig. 3B). Snow depth did not affect deer density. After accounting for habitat alteration and snow depth, latitude class did not affect deer density (Table 2).

Predicted Changes in White-Tailed Deer Presence and Density

In winter, a 10% decrease in the median monthly snow depth observed across sites (median = 15 cm in the south, 30 cm in the north) increased the probability of deer presence by 0.02 in the south (from 0.18 to 0.20 in the south), and had an immeasurable change in the north (<0.01). Furthermore, the density of deer increased by 0.09 deer/km² across the province (from 2.13 to 2.22 deer/km²; median = 25 cm) with a 10% decrease in snow depth. A 4% increase in median habitat alteration observed across sites (median = 3% in the

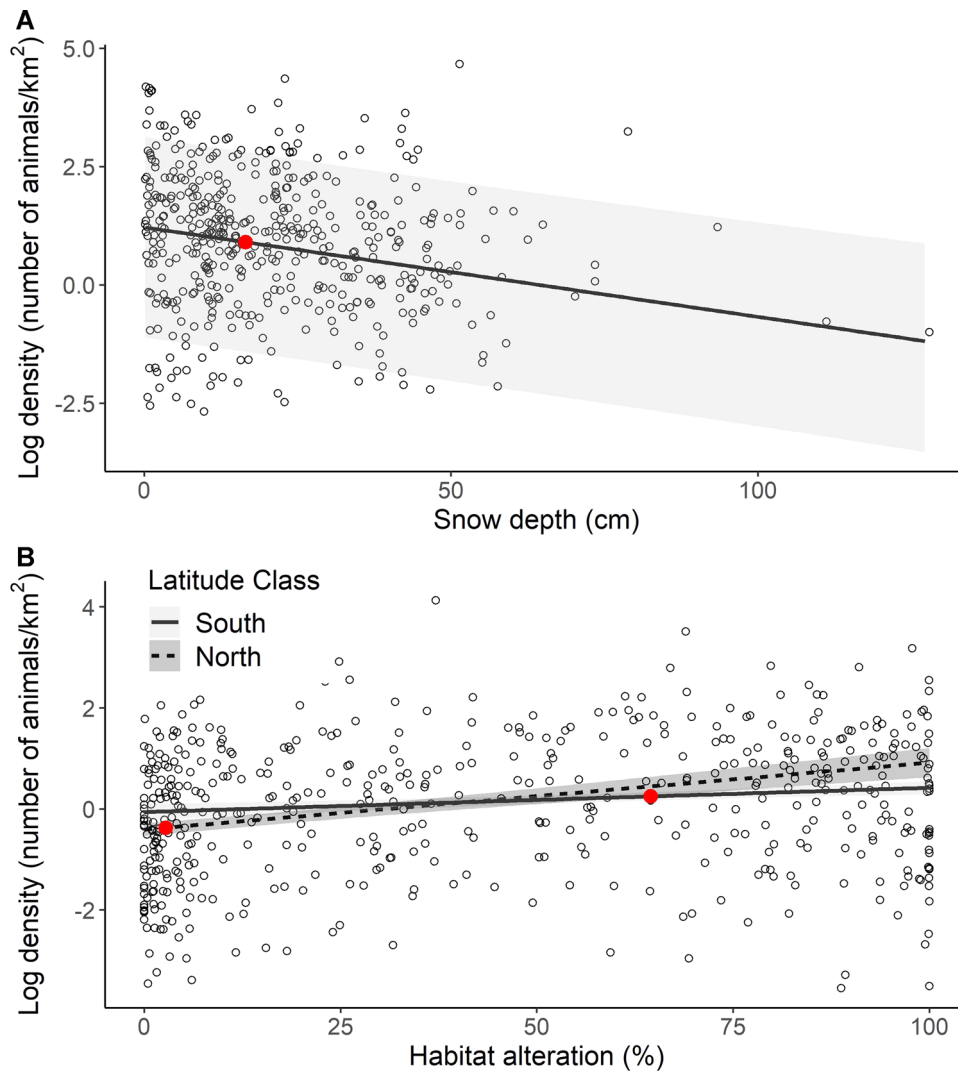


Figure 3. The effect of snow depth (cm) in winter months (1 Nov–31 Mar; A) and habitat alteration (%) in spring season (1 Apr–17 Jun; B) on the log transformed density given presence (number of animals/km²) of white-tailed deer, 2015 to 2019, in the north (dashed line) and south (solid line) of Alberta, Canada. When estimating predicted densities, either habitat alteration or snow depth are fixed at their medians. Observed data points are presented, lines represent the modeled relationship, and grey shading represents 95% confidence intervals. A red dot represents the observed median habitat alteration or snow depth for each latitude class.

north) increased the probability of monthly deer presence by 0.01 (from < 0.01 to 0.01) in the north.

In spring, a 10% decrease in the previous winter's median snow depth (median = 10 cm in the south, 24 cm in the north) increased the probability of deer presence immeasurably in the south (probability at 0.83) and by 0.03 in the north (from 0.63 to 0.66). A 4% increase in habitat alteration in the north (median = 3%) increased the probability of deer presence by 0.05 (from 0.71 to 0.76) and the density of deer by 0.04 deer/km² (from 0.69 to 0.73 deer/km²). Furthermore, the density of deer in the south increased by 0.03 deer/km² (1.28 to 1.31 deer/km²) when median habitat alteration (65%) increased by 4%.

DISCUSSION

Our study evaluated the relative effects of climate and habitat alteration on the distribution and abundance of white-tailed deer across their range in Alberta. As predicted,

we found evidence that monthly deer presence in winter was influenced by habitat alteration and snow depth (Dawe et al. 2014). Deer density also decreased with increasing snow depth but was not influenced by habitat alteration in winter. In spring however, we predicted that only habitat alteration would influence deer presence and density because deer recolonize sites following severe winters (Fisher et al. 2020). Although the density of deer at sites where they were present increased at sites with increased habitat alteration, the previous winter's snow depth influenced spring deer presence, suggesting that over-winter conditions can have effects that carry over into the following spring. Collectively, these results suggest that although habitat alteration plays a significant role in deer distribution and abundance, snow conditions also influence seasonal deer presence and distribution across seasons.

Deer presence and density in winter was sensitive to snow depth across Alberta. When snow was shallow, small

increases in snow depth resulted in a large decrease in the probability of deer being present, and increased density at those sites, regardless of latitude. These shifts in space-use are consistent with movement behaviors away from deep snow as winter progresses, and likely reflect migrations from winter to summer range (Brinkman et al. 2005). The observed range limit of deer was also farther south in winter than spring, congruent with seasonal migrations expected when deer migrate south during winter. The previous winter's snow conditions also influenced the presence of deer in the following spring, suggesting that severe winters characterized by deep snow may also result in high mortality (DelGiudice et al. 2002). Increased mortality may result from decreased ability to reach food sources (Taylor 1961), reduced food quality (McCullough 1985), or mobility limitations (Parker et al. 1984). Furthermore, large snowfall events could affect deer via increased predation (Richard et al. 2014) because snow depths have also been linked to high predation by wolves and coyotes (*Canis latrans*; Nelson and Mech 1986, Huggard 1993, Patterson and Power 2002). These events can lead to sudden die offs and cause predator switching to alternate prey, as has been observed in deer-caribou systems (Serrouya et al. 2015). If climate change continues to reduce winter severity (Shabbar and Bonsal 2003, Brown and Mote 2009, Jeong et al. 2016), the system studied here will move closer to the observed inflection point in which winter deer distribution is no longer limited by snow depth.

Habitat alteration influenced deer presence only at sites in the northern portion of the study area, and the effect of habitat alteration on deer density was stronger in the north. Above approximately 50% habitat alteration, deer presence in winter increased substantially. In spring, the greatest variation in presence occurred from 0 to 50% habitat alteration, and 66% of used sites occurred within this range. The relationship between deer presence and habitat alteration suggests a disproportionate benefit of habitat protection in northern areas to reduce deer expansion, particularly in areas that are lightly disturbed. Furthermore, these results suggest that even small increases in human-modified habitat could facilitate the expansion of white-tailed deer (Latham et al. 2011, Fisher and Burton 2018).

Severe winters have the potential to suppress deer populations, regardless of the level of habitat alteration. Our results, however, suggest that the system has likely reached a state where deer distribution is established, unless intensive habitat restoration occurs (May 1977, Scheffer et al. 2001). Habitat alteration might increase hunter access into deer habitat with the outcome of suppressing deer populations, as has been observed with moose (Rempel et al. 1997, Lebel et al. 2012, Mysterud et al. 2020). But experimental evidence suggests hunter harvest may not effectively reduce deer densities even if hunting pressure is high (Simard et al. 2013). The effectiveness of reducing high densities of white-tailed deer at the northern range limit where human population densities are lower should continue to be evaluated.

In the context of historical changes to habitat alteration and snow depth, the presence of white-tailed deer in the

northern portion of the province was more sensitive to a 4% increase in habitat alteration (ABMI 2018a) than a 10% decrease in snow depth (Brown and Braaten 1998, Vincent et al. 2015) in both spring and winter. This increase in habitat alteration also had a slightly greater effect on spring deer density than did the decrease in snow depth. A 10% decrease in snow depth, however, had a larger effect on winter presence in the south and on winter deer density. Applying our spatial models to estimate temporal trends can provide useful context for interpreting observed variation in deer presence and density but should not be interpreted as predictions of changes in deer distribution and abundance over time. As monitoring continues, understanding temporal trends in deer distribution and abundance coinciding with variation in winter severity will become increasingly important.

Although deer density was influenced by snow depth in winter, and habitat alteration in spring, the effect sizes were small. Instead, other habitat attributes that were not measured here, such as forage availability or fine-scale variation in snow depth or compaction, are likely influencing deer density within established deer distribution. Therefore, future work should evaluate the influence of changing snow conditions on summer and winter distribution and density over time to elucidate seasonal movement patterns compared to long-term distributional range shifts (Mahoney et al. 2018).

Motion-sensitive cameras are an effective method of assessing distribution and density (O'Connell et al. 2011, Burton et al. 2015, Campos-Candela et al. 2018, Nakashima et al. 2018), but modeling techniques for these data are in their infancies and the limitations and biases associated with these methods should be considered. Our presence models assume that sites where deer were not observed were truly absent, and that detection was not significantly influenced by habitat alteration or snow depth, similar to other studies in the Canadian boreal landscape (Fisher and Burton 2018). Further, behavioral attraction to the camera likely inflates calculated densities (Abolaffio et al. 2019). If behavioral responses to the camera change across our habitat attributes of interest, density estimates would be influenced by habitat.

MANAGEMENT IMPLICATIONS

When evaluating strategies to recover species like caribou, managers can consider that habitat alteration is a modifiable risk factor, whereas climate cannot be actively managed at a regional scale. Restoring altered caribou habitat may decrease white-tailed deer presence and density if habitat alteration is reduced to relatively low levels. This objective is much more likely to be effective in northern areas for 2 reasons: the effort required for restoration is lower, and habitat protection and restoration actions are expected to have a disproportionate benefit given the current level of habitat alteration. If restoration is successful, this could lead to reduced predator densities, thereby reducing predation by wolves on caribou. Nevertheless, the effectiveness of habitat restoration at restoring predator-prey dynamics must be considered carefully, particularly in the context of reduced

winter severity from climate change. Ultimately, additional caribou recovery measures, such as predator and prey population management, should be considered in tandem with habitat restoration.

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APPENDIX A. METHODOLOGICAL DETAILS OF ESTIMATING DEER DENSITY USING RANDOM ENCOUNTER AND STAYING TIME

To estimate density using random encounter and staying time (REST), it is essential to have an accurate measure of the time animals spent in front of the camera and the sampling area. We used data from all unlured motion-sensitive cameras that collected data in 2015, plus an additional 1,110–1,500 random subset of images from 2016–2018 to improve the estimation of time spent in front of the camera and sampling area (Table A1).

The duration of an animal being in front of the motion sensitive camera's field of view can be calculated as the end of the event minus the start of the event. Remote wildlife cameras take discrete snapshots rather than continuously sampling time. During capture events animals may exit and enter the camera in this time period or may simply remain still, thereby not triggering the camera, and the likelihood of this occurring likely depends on the duration between photos. Including time where animals have left the field of view would inflate estimates of time in front of the cameras and therefore density. We modeled the probability of animals leaving the field of view and returning as a function of time between images developed for each season, and used this model to correct the estimated time in front of the camera.

We visually evaluated data from successive images to identify clear evidence of animals walking out of the field of view and returning, not necessarily assuming the same

individual, or if the animals stayed within the field of view, for example by remaining in the same location or disconnected places. We combined data from white-tailed deer with other ungulates, excluding moose, which are larger in body size. To estimate the probability of leaving and returning, we modeled whether the animal left the field of view as a function of time between successive images using a logit-link binomial model and smoothing splines. Animals typically showed no signs of leaving the field of view for successive images with durations <20 seconds, whereas animals typically left and returned between successive images with durations >120 seconds. Therefore, we classified only images between 20 and 120 seconds and assumed that in successive images with durations <20 seconds the animals stayed within the field of view, but for durations >120 seconds the animals left the field of view.

To calculate time in front of the cameras, we therefore subtracted the time the animals left the field of view from the time they entered the field of view, and modified this time by the probability of leaving the field of view between successive images. We multiplied the duration spent within the field of view between photos by 1 minus the probability of the animal leaving. Lastly, we added the average time between images in all series from 2015 to 2018 (4.95 sec, $n = 272,138$ successive photos) to the duration of each series to account for how long animals are typically in the field of view before and after the first and last images, respectively, are taken. We also added these times to the start and end of photos between successive images that were separated by 20–120 seconds.

The probability of detecting an animal decreases as the distance from the camera increases, similar to distance models (Howe et al. 2017), and this is likely land cover-specific. Therefore, for each land cover type we modified the camera field of view by the effective detection distance (EDD) in which deer can be detected. By placing a 1-m-tall pole 5 m from the camera, the effective detection distance EDD (m) can be calculated as the proportion of images with the animals <5 m away versus >5 m away from the cameras, given as:

$$EDD = \frac{5}{\sqrt{(1 - p_{>5m})}}$$

where $p_{>5m}$ is the proportion of images with the animals >5 m away. All animals were recorded as being closer than the pole (<5 m), farther than the pole (>5 m), or uncertain. We modeled the proportion of animals behind the pole (>5 m), as a function of land-cover type and season, weighted by the number of animals in the image using generalized additive models using package *mgcv* (Wood 2011). We created detection-distance models for 14 broad land-cover types (Table A2) and a Bayesian Information Criterion-weighted model average prediction for each season and land-cover combination.

Overall, the EDD ranged from approximately 6.4 m to 8.7 m (Table A3). In most land-cover types, the EDD ranged from 7 m to 8 m, though shrublands typically having

Table A1. The number of cameras used in Alberta, Canada, for each year from 2015 to 2018 to calculate the probability of white-tailed deer leaving and returning the camera field of view and the effective detection distance.

Year	Number of cameras for probability of leaving	Number of cameras for effective detection distance
2015	226	159
2016	88	0
2017	193	2
2018	121	22

Table A2. *A priori* categorization of land-cover types used to model the effective detection distance, to study white-tailed deer in Alberta, Canada, from 2015 to 2019.

Category	Land-cover types
0	Coniferous + deciduous + grass + shrub + wetland grass + wetland treed + water + human footprint
1	Coniferous or deciduous + grass and shrub + wetland + human footprint
2	Treed upland or wetland + grass or water + shrub + human footprint
3	Coniferous or deciduous + grass, shrub, or human footprint + wetland
4	Treed upland or wetland + grass, water or human footprint + shrub
5	Treed upland or wetland + grass, shrub, water, or human footprint

lower distances (Table A3). The effective detection distance was consistently higher in winter than in summer.

We used these models to estimate the detection distance of white-tailed deer at each camera based on the land-cover type and the dates the camera was operating. Using these detection distances, the area surveyed by the camera (A_F in m^2) is calculated as:

$$A_F = \frac{\pi \cdot \text{EDD}^2 \cdot \angle}{360},$$

where \angle is the angle of the camera's field of view in degrees, which is 42° with the cameras used here. We also ran a test using simultaneous deployments of motion-activated cameras and cameras taking images every 3 seconds. These showed nearly complete detection of animals larger than coyotes within 5 m, but the motion detectors missed some smaller animals.

We explicitly modeled habitat alteration as a land-cover type when calculating EDD and the distance fell within the range of other land-cover types. Therefore, our results are likely robust to the assumption that detection probability was not biased by habitat alteration. Although we did not evaluate the effect of snow depth on the EDD, the distance

was consistently higher in winter than summer. This provides confidence that snow depth does not systematically reduce detection probability such that our interpretations would over-emphasize the effect of snow depth on deer.

APPENDIX B. INCORPORATING LATITUDE IN WHITE-TAILED DEER PRESENCE AND DENSITY MODELS

Across the province of Alberta, there is a decrease in habitat alteration moving northward, and an increase in winter severity (Fig. 1). This spatial correlation between the 2 main hypothesized factors influencing deer populations makes it difficult to evaluate the relative influence of these 2 variables on deer densities. Therefore, we statistically accounted for latitude when evaluating the effect of habitat alteration and snow depth on deer presence and density.

Furthermore, the effect of habitat alteration and snow depth may vary by latitude. For example, snow may only be important at greater snow depths, more typical of northern sites. Likewise, habitat alteration types are different in the south (agriculture sector) compared to the north (energy and forestry sectors). Moreover, the relative importance of snow depth and habitat alteration may be different in the southern and northern portions of deer range.

There is no *a priori* reason to assume a linear effect of latitude itself on deer density, habitat alteration, or snow depth (Fig. B1). Indeed, snow depth shows increased variation at lower latitudes than higher latitudes (Fig. B1). We therefore did not make explicit assumptions about the shape of these relationships, and instead chose to use a categorical variable. Further, there was a binomial distribution of latitudes captured within our data (Fig. B2). We used the breakpoint between the 2 normal distributions within the bimodal distribution to define our latitude categories. This category break-point between the south and north latitude class also incorporated the decrease in snow depth variation in the north (Fig. B1, Panel A).

Table A3. Effective detection distances (m) of white-tailed deer for each land-cover type and season in Alberta, Canada, from 2015 to 2019.

Land cover	Summer	Winter
Coniferous	7.997	8.181
Deciduous	7.698	7.866
Grassland	7.889	8.068
Human footprint	7.609	7.772
Shrubland	7.044	7.176
Water	6.405	6.500
Wet grassland	7.515	7.674
Wet shrubland	7.044	7.176
Treed wetland	8.481	8.690

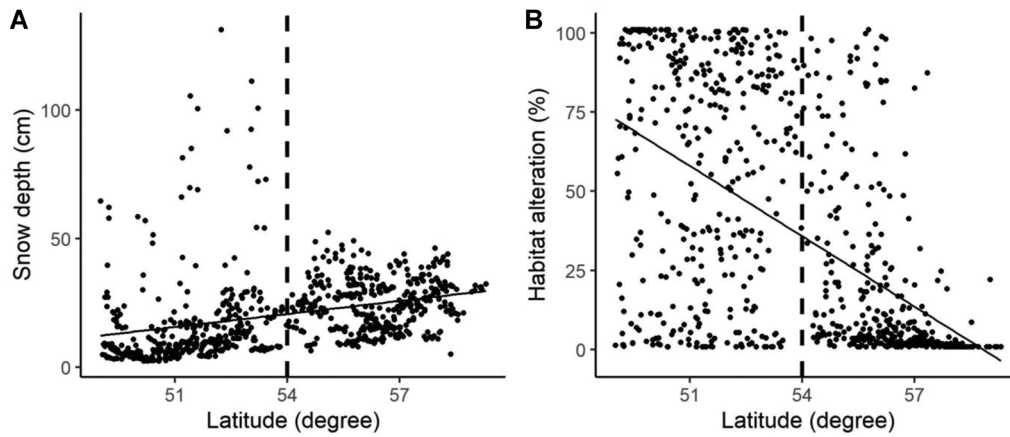


Figure B1. A) Mean winter snow depth (cm) at each motion-sensitive camera site used to study white-tailed deer presence and density given presence in Alberta, Canada, in spring from 2015 to 2019 as a function of latitude ($^{\circ}$), and B) habitat alteration (%) within a surrounding 1-km² circular area of each site as a function of latitude ($^{\circ}$). Solid lines represent data fitted to a Gaussian (linear) model. The dashed line represents separation of the 2 latitudinal classes (south, north). Only sites within the maximum latitude observed in our data are included.

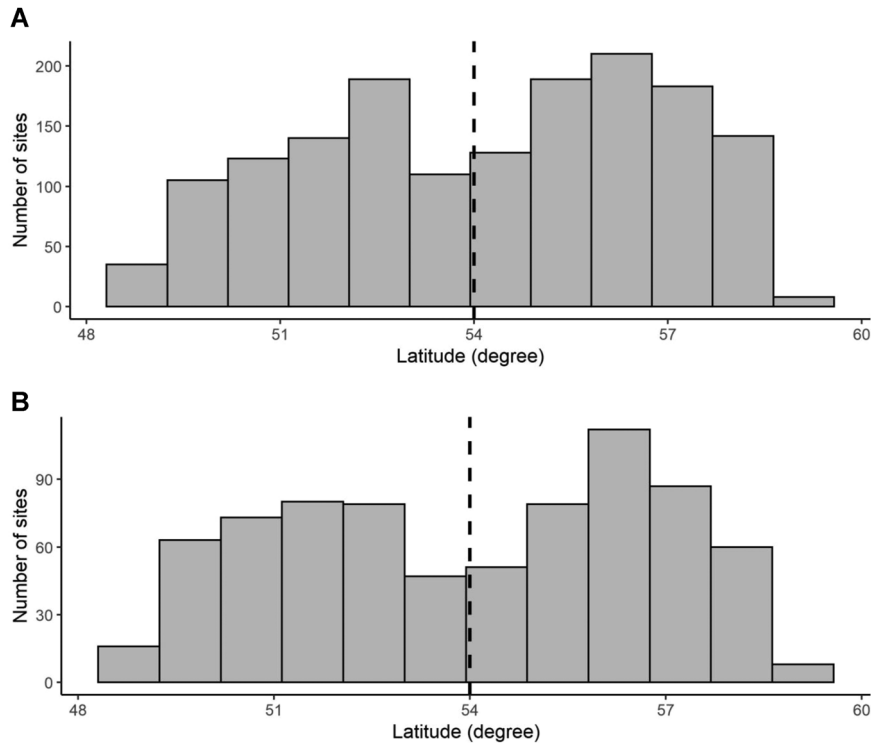


Figure B2. A) Distribution of the number of motion-sensitive camera sites used to study white-tailed deer presence and density given presence from 2015 to 2019 in Alberta, Canada, as a function of latitude ($^{\circ}$) in winter and B) in spring.