

Influences of industrial land use features on small-scale movements of an
expanding white-tailed deer population

by

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Abstract

Land use features associated with the forestry and energy sectors increasingly permeate the boreal landscape of northeastern Alberta. I investigated the effects of industrial land-use features on small-scale deer movement choices by applying step selection functions to three years of satellite-telemetry locations from 30 female white-tailed deer in this region. Recent invasion of white-tailed deer into northern boreal forests is considered a conservation issue because they are apparent competitors to threatened woodland caribou. At a broad scale, the northward expansion of white-tailed deer has been attributed to the availability of early seral stage forage in disturbed habitats (*e.g.* forestry cutblocks) and decreased winter severity due to climate change. However, the effects of land use features on small-scale movement choices of white-tailed deer are largely unknown. Characterizing the major factors affecting deer movement can better inform predictions of future areas of expansion, development of management thresholds to minimize deer use of modified habitats, and prioritization of deer control efforts. To evaluate deer responses to several land use features, I used step selection functions, which compare the observed deer movements to simulated random movements in order to determine whether certain features are selected or avoided. Deer responses to linear features (*i.e.* roads, pipelines, seismic lines) were highly variable across individuals and generally weak. Results of two-stage conditional logistic regression models indicated that deer moved significantly closer to forestry cutblocks than expected by chance during the snow-free period. The snow period models did not detect any significant influences on deer movement choices. The lack of strong, consistent responses may be indicative of deer adaptability to industrial landscapes, supporting observations of their expansion into increasingly developed northern ranges. However, my results only represent small-scale movement choices and were limited by the exclusion of important factors known to influence deer movement and habitat selection (*e.g.* snow depth). Therefore, future research should include more detailed characteristics of land use and habitat variables and incorporate topography, temperature, and snow depth to improve the explanatory power of my models.

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Introduction

Anthropogenic landscape modifications can impact wildlife across multiple ecological scales, from changes in individual behaviour to altered population and community dynamics (Johnson & St-Laurent 2011). Human land use features, including roads and forestry cutblocks, may influence animal movement choices at small scales through mechanisms like fear-induced predator avoidance (James & Stuart-Smith 2000), avoidance of human traffic due to hunting or vehicle collisions (Kilgo *et al.* 1998; Glista *et al.* 2009), or attraction to early seral stage forage in disturbed sites (James *et al.* 2004). As the biological scale of impact increases, changes in movement behaviour can influence an animal's physiology and nutrition, which in turn may affect the population's vital rates and distribution, ultimately prompting ecological changes at the community level (Johnson & St-Laurent 2011). Land use features associated with the forestry and energy sectors increasingly fragment the boreal forests of northeastern Alberta, with scale-dependent impacts on species behaviour and community dynamics (Latham *et al.* 2011a).

Linear features in particular (*e.g.* roads, pipelines, seismic lines) can have disproportionately large effects on ecological processes (Trombulak and Frissell 2000; Whittington *et al.* 2005; Tigner 2012). For example, seismic lines cut 2-10 m wide for oil and gas exploration are used as travel corridors by wolves (*Canis lupus*; James & Stuart-Smith 2000). These straight-line trails increase wolf travel speeds, enhance visual encounters with prey, and permeate lowland caribou habitat previously inaccessible to predators (Latham *et al.* 2011a). In response to increased risk of mortality near seismic lines, woodland caribou (*Rangifer tarandus caribou*) avoid these linear features, inducing physiological costs of avoidance behaviour and population-level consequences of decreased effective habitat availability (Fortin *et al.* 2004; James & Stuart Smith 2000).

Furthermore, apparent competition (*i.e.* indirect competition between two prey species mediated by a shared predator) is considered another major proximate cause of caribou decline facilitated by human land use (Holt 1977; DeCesare 2010). Apparent competitors of caribou, namely moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*), thrive in early seral stage disturbed habitats and increasingly subsidize

predator populations (Cairns & Tefler 1980; DeCesare *et al.* 2010). In particular, white-tailed deer, which have only recently invaded the boreal forests of northeastern Alberta, have become the most prevalent component of wolf diet within the past couple of decades (Latham *et al.* 2011b). Northward expansion of white-tailed deer has been attributed not only to the availability of forage in increasingly disturbed landscapes (*e.g.* *Populus* spp., *Alnus* spp., shrubs, and grasses), but also to decreased winter severity with climate change (Dawe *et al.* 2014). The role of white-tailed deer as novel apparent competitors to threatened woodland caribou has prompted the proposal of deer reduction as a potential caribou conservation strategy (James *et al.* 2004). However, the effectiveness of prey reductions as a conservation strategy is uncertain, with risks of even increasing predation pressure on caribou during the lag phase between prey reduction and predator numeric response (Serrouya *et al.* 2015).

As white-tailed deer continue to expand northward, early detection and response should prove more effective in mitigating effects of apparent competition on caribou (Pyšek & Richardson 2010). Determining what factors influence white-tailed deer habitat selection can help managers model where early-stage deer control efforts should be focused. Characterizing the anthropogenic influences on deer movement and selection can also inform the development of management thresholds, above which deer invasion is likely to be facilitated (Northrup & Wittemyer 2013). Although Dawe *et al.* (2014) outlined climate change and human land use as the broad factors driving white-tailed deer expansion at a large scale (first-order selection of the species' geographical range; Johnson 1980), prioritizing deer control areas and developing management thresholds requires a better understanding of the relative influences of specific land use features at a finer scale of habitat selection.

Here, I focus on the small-scale movement responses of 30 female white-tailed deer to human land use features in the Christina Lake/Winefred Lake region of northeastern Alberta. The aim of my research was to determine whether human land use features influence deer movement at a small-scale and whether these influences differ between snow and snow-free periods. I applied Step Selection Functions to three years of telemetry data (2012-2015) to investigate the influences of linear features, cutblocks, and

industrial areas on deer movement choices. I hypothesized that the tradeoff between fear-induced avoidance and forage-mediated attraction to seismic lines would be season-dependent with a stronger avoidance in the snow period when early seral-stage vegetation is not available. An attraction to seismic lines, roadsides, and cutblocks was expected in the snow-free period when deer forage among shrubs, forbs and grasses (Hewitt 2011; Roseberry & Woolf 1998).

Methods

Study Site

The 4500-km² study site encompasses the Christina Lake/Winefred Lake area of northeastern Alberta (Fig. 1). This boreal landscape is a mosaic of lowland spruce and muskeg, with upland deciduous and coniferous forests. Alberta-Pacific Forest Industries Inc. runs active timber harvesting operations throughout the region. Oil sands operations by Canadian Natural Resource Ltd. and MEG Energy Corporation are *in-situ* developments involving construction of seismic lines, processing plants, well pads, pipelines, and access roads (OSIP 2015). Additional seismic exploration within the study site indicates planned development by Cenovus Energy. The eastern boundary of the study area was the Alberta-Saskatchewan border and the remaining boundaries of the study site were defined as 10 km from the outermost telemetry points.

White-tailed deer monitoring

Between March 2012 and December 2015, GPS telemetry points from 30 female white-tailed deer were collected at 2 hour intervals (6400 to 8000 seconds). Only females were satellite-collared to reduce variability in movement patterns associated with sex-specific behavior (*e.g.* fawning, rutting). IridiumTrackM 3D satellite collars (LOTEK Wireless Inc., Newmarket, Ontario) were fitted to deer either captured in Clover traps or netted by helicopter, in accordance with Alberta Wildlife Animal Care Committee class protocol #008. The 30 deer in this study were a subset of the total deer satellite-collared by Alberta Innovates—Technology Futures (AITF; Fisher *et al.* unpublished reports). Deer were monitored for AITF's Boreal Deer Project, which aims to estimate and understand changes in deer density across Alberta's northeastern boreal forest. Telemetry points within 10 km of Alberta's eastern border were excluded, due to lack of comparable land use and habitat data for Saskatchewan.

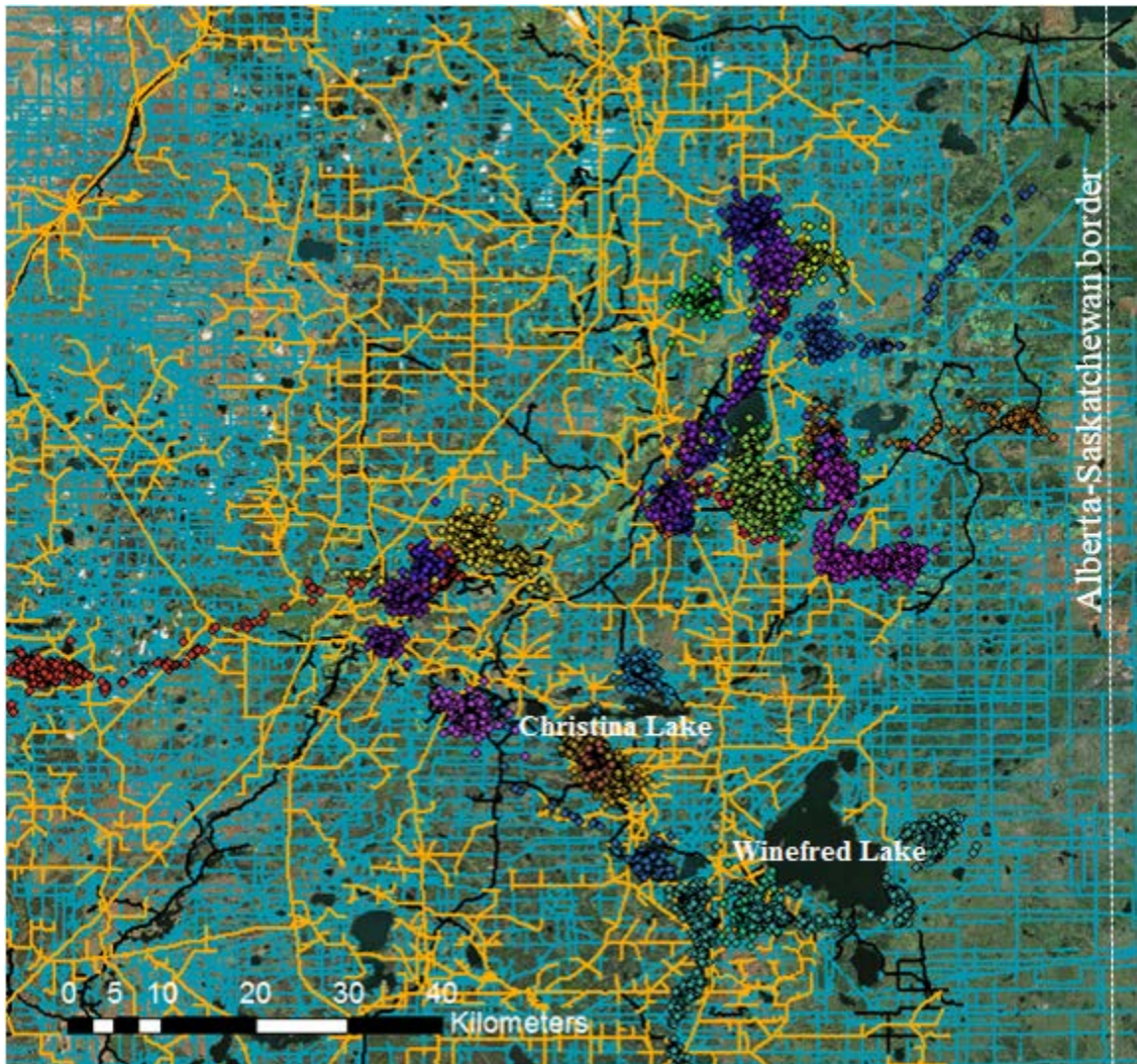


Figure 1. Map of the study site with industrial land features and white-tailed deer telemetry locations. The 4500-km² site occurs in the Christina Lake/Winefred Lake area of northeastern Alberta. Each dot represents a 2-hour fix location, with a different colour for each of 30 female satellite-collared white-tailed deer. Black lines represent roads, orange lines represent pipelines, and blue lines represent seismic lines. Pale green polygons represent forestry cutblocks and pale gray polygons represent paved industrial areas.

Simulating available steps using step selection functions

To understand the movement behaviour of collared deer, I used the telemetry relocations to characterize observed movement pathways by calculating step lengths and turning angles (Fig. 2) with the movement .pathmetrics function in Geospatial Modelling Environment (GME; Beyer 2012). Step lengths were compared across days and months of the year to determine if there were seasonal patterns in deer movements (Appendix A). Accordingly, each year was divided into “snow” and “snow-free” seasons to account for variability in step length between seasons. The snow period was defined as any day between mid-November (319th day of the year) and mid-March (73rd day of the year) across all years and represented the period from late fall through to early spring when temperatures are colder and snow restricts deer movements. Due to the lack of snow data, these cutoff dates were chosen according to the time of year that mean daily temperatures, which were recorded by the satellite-collars, began to trend below zero in autumn and rise above zero in the springtime.

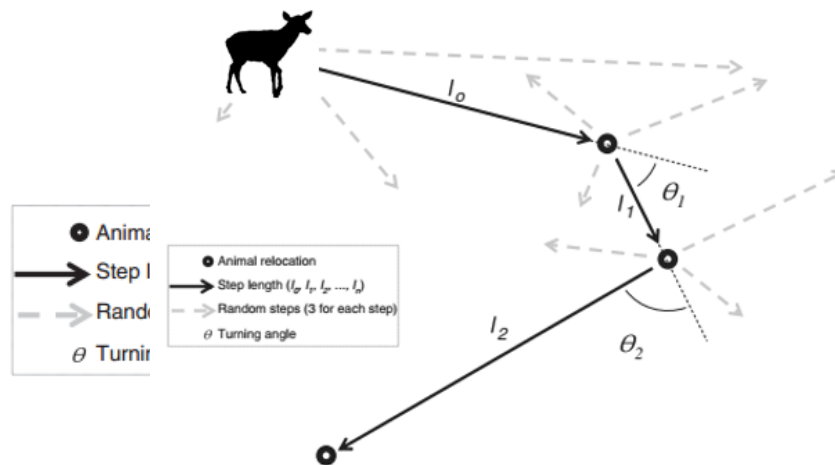


Figure 2. Step Selection Functions. The straight line between two successive satellite-collar fix locations is called a “step”. The distance between the two fix locations is the step length and the angle between one step and the next is the turning angle. Random steps are simulated from each fix location to represent locations that were available to the deer from that point. (Adapted from Thurfjell *et al.* 2014)

After characterizing the observed steps in the snow and snow-free periods, alternative steps that were available but not selected by the animal were then simulated using empirical information on the typical movement behaviour (*i.e.* step lengths and turning angles, Fig.2; Fortin *et al.* 2005). This enabled the comparison of environmental attributes at observed and simulated endpoints to determine whether the animal is likely to select locations *closer to or further from* certain landscape features than expected by chance (Thurfjell *et al.* 2014). Unique frequency distributions of step length (20 m bins) and turning angle (20° bins) were prepared for each deer by compiling the step length and turning angle values of all other deer, to avoid circularity (Fortin *et al.* 2005; Appendix B). Although narrower bins for frequency distributions more closely match real distributions (Beyer 2012), I chose 20 m bins for step lengths to accommodate the limits in spatial accuracy of the GIS layers (Appendix D). Since average step lengths were markedly higher in the snow-free period (Appendix A), I constructed separate snow and snow-free step length frequency distributions for each deer. In contrast, frequency distributions for turning angles, which showed no seasonal patterns, included turning angles compiled from both seasons.

I created one simulated step for each observed step using the `movement.ssf.samples` function of GME projected in ArcMap v. 10.2.2 (ESRI 2014). Steps were simulated by creating straight lines from the start point of each observed step, with step lengths and turning angles drawn independently from their respective frequency distribution using a rejection algorithm (Beyer 2012). I determined Pearson correlation between step length and turning angle to ensure that these two parameters could be drawn independently for step simulation. Endpoints of each simulated step represented locations that were available for deer to move to from their previous fix location.

Landscape variables

In order to test deer movement responses to industrial development, I used ArcMap v. 10.2.2 to measure the distance from endpoints of observed and simulated deer steps to the nearest road, pipeline, seismic line, cutblock, and industrial site. Non-linear features, namely forestry cutblocks and industrial sites, were mapped as polygons on the Human Footprint Inventory for 2012 conditions (ABMI 2015; Appendix D). The high density of 3-D seismic lines within the study area was not well represented in the 2012 ABMI Footprint dataset, therefore, I used a separate dataset detailing linear features (*i.e.* roads, pipelines, seismic lines) based on interpretation of 2012 satellite imagery (ABMI n.d; Appendix D).

I also included habitat data to control for confounding variables in step selection. Since a detailed habitat model was not the primary aim of my study, I used the Alberta Biodiversity Monitoring Institute Land Cover Maps (ABMI 2012) to categorize coarse habitat type at each endpoint as grassland, deciduous forest/shrubland, or coniferous forest (Appendix C).

Two-stage conditional logistic regression

I used a two-stage conditional logistic regression approach to test for relationships between deer movements and footprint features while accounting for habitat variation. For snow and snow-free periods, I fitted fixed-effects conditional logistic regression models for each individual deer, treating observed and simulated steps originating from the same start point as a matched pair. By stratifying steps by start point, case-control logistic regression minimized the autocorrelation associated with steps taken over short time intervals (Craiu *et al.* 2008). Conditional logistic regression investigates the likelihood of a step being selected based on a set of predictor covariates (*e.g.* proximity to a land use feature). The set of predictor covariates used for snow and snow-free periods were selected by assessing Akaike Information Criterion weights of five alternative models for each individual deer to assess hypotheses about the relative importance of

different types of variables (*e.g.* linear features, forestry cutblocks, habitat variables, Table 1; Appendix H; Appendix I; Burnham & Anderson 2004). Before constructing the alternative models, I evaluated collinearity of variables with Pearson's pairwise correlation analyses (all $|r| < 0.7$; Appendix E).

Using the `clogit` function of the R package `survival` (Therneau 2015; R Core Team 2014), I fitted conditional logistic regression models to each individual deer assuming an exponential selection function of the form:

$$\text{SSF} = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_n x_n)$$

with coefficients β_1 to β_n representing coefficients associated with landscape variables x_1 to x_n . Locations with higher SSF scores represented habitat features with a greater probability of being chosen by individuals (Fortin *et al.* 2005). I evaluated the fit of the best models for each deer in the snow and snow-free periods using R^2 values, a proxy for explained variation (Mittelböck & Schemper 1996).

To account for inter-individual variation, I used the `TwoStepCLogit` R package to obtain population-level β -coefficient estimates averaged across individual deer (Craiu *et al.* 2011). This two-stage approach addressed differences in individual behaviour and the resulting correlation within individuals in habitat-selection studies (Fieberg *et al.* 2010). Thus, each animal was considered an experimental unit for developing a population-level conditional logistic regression model (Squires *et al.* 2013). Variables with absolute population-level β -coefficient estimates greater than two times the standard error were considered significant influences on deer movement. I interpreted the magnitude and sign of significant β -coefficient values at the population level to estimate the degree and direction of overall influence on deer movements.

Results

I modeled how female white-tailed deer responded to landscape heterogeneity based on 23 individuals (30,996 total GPS locations) during the snow period and 27 individuals (105,108 locations) during the snow-free period (Appendix F; Appendix G). Mean step lengths (\pm SE) for snow and snow-free periods were 118 m (\pm 1.6 m) and 200 m (\pm 1.0 m), respectively. Pearson correlation between step length and turning angle for all deer was very low, with a mean correlation coefficient of 0.005 ($N=30$ deer; $|r|_{\max}=0.069$), confirming that simulated steps could draw independently from separate step length and turning angle distributions. Overall, there was a high degree of variation across individuals and the responses to predictor covariates were generally low (Table 2; Table 3).

For the snow period, the footprint-only model had the highest Akaike Information Criterion weight (AIC_w) averaged across individuals. This model included the distance to the nearest road, pipeline, seismic line, cutblock, and industrial site, but did not include the habitat variables (Table 1). In contrast, the best model for the snow-free period was the comprehensive model, which included the footprint covariates and habitat variables for grassland, deciduous/shrubland, and coniferous habitat types (Table 1).

Table 1. Mean Akaike Information Criterion weights (AIC_w) for alternative models in the snow and snow-free periods averaged across individuals

Model	Covariates included	mean AIC_w	
		Snow	Snow-free
<i>Comprehensive</i>	Road + Pipeline + Seismic + Cutblock + Industrial + Grassland + Deciduous/Shrubland + Coniferous	0.19	0.55
<i>Linear + Habitat</i>	Road + Pipeline + Seismic + Grassland + Deciduous/Shrubland + Coniferous	0.15	0.19
<i>Non-linear + Habitat</i>	Cutblock + Industrial + Grassland + Deciduous/Shrubland + Coniferous	0.18	0.14
<i>Habitat only</i>	Grassland + Deciduous/Shrubland + Coniferous	0.19	0.08
<i>Footprint only</i>	Road + Pipeline + Seismic + Cutblock + Industrial	0.29	0.03

Since AIC_w represent relative values for each individual deer (*e.g.* the AIC_w of the best model for one deer may be lower than another deer's lowest-scoring model), AIC_w averages alone were unable to retain the animal as the experimental unit (Squires *et al.* 2013). Therefore, individual AIC_w rankings of each deer were additionally considered by determining which set of variables was the most frequently highest-ranked model across individuals (Appendix H; Appendix I). AIC_w for individual deer model sets were variable in the snow period (Fig. 3a), but the footprint model was the most frequently highest-ranked model (Appendix H). For the snow-free period, the most frequently highest-

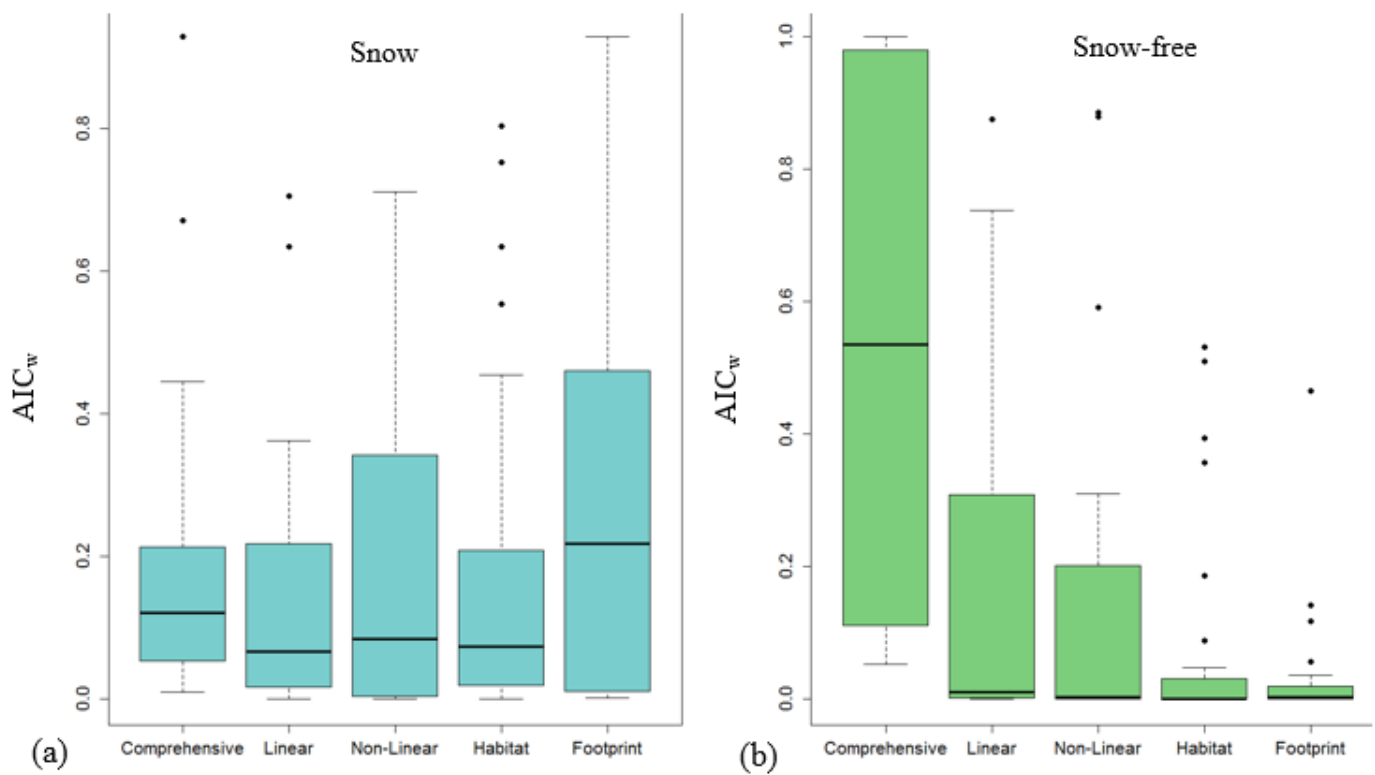


Figure 3. Akaike Information Criterion weights (AIC_w) of alternative conditional logistic regression models for individual deer during (a) snow and (b) snow-free periods. AIC_w for snow season ($N = 23$ deer) were highly variable but were generally highest for the footprint only model, consistent with the highest mean AIC_w and most frequent best model among individuals in the snow season. The comprehensive model including all footprint and habitat covariates had the highest mean, mode, and median AIC_w among the 27 deer observed in the snow-free season.

ranked model according to individual AIC_w was the comprehensive model (Fig. 3b; Appendix I)

Overall, the models had low R^2 values indicating that covariates did not explain much variation in deer movements (Appendix F; Appendix G). The footprint conditional logistic regression model had a low mean R^2 value of 0.013 ± 0.002 across individuals for the snow period (Appendix F). Since footprint covariates represented the “distance to the nearest” of each land use feature, positive β -coefficients signified a greater observed distance from the feature than simulated steps (*i.e.* further from the feature than expected by chance), while negative β -coefficients signified a shorter observed distance from the feature than simulated steps (*i.e.* closer to the feature than expected by chance). None of the β -coefficients for footprint variables indicated a statistically significant influence on deer movement during the snow period (Table 2).

Table 2. Two-step conditional logistic regression results for footprint model in the snow period. Population-level β -coefficients and standard errors (SE) averaged across individuals for footprint covariates in the snow period calculated with `TwoStepCLogit` and counts of individuals showing significantly positive (+) and negative (-) β -coefficients. NS denotes “non-significant” responses ($p > 0.05$).

Covariate	β	SE	Individual Responses		
			+	-	NS
Distance to road	-0.00001	0.00032	2	1	20
Distance to pipeline	0.00040	0.00033	7	2	14
Distance to seismic line	0.00037	0.00033	4	2	17
Distance to cutblock	0.00000	0.00030	2	1	20
Distance to industrial site	0.00017	0.00028	4	3	16

The conditional logistic regression R^2 values for the best-supported (*i.e.* comprehensive) model in the snow-free period were also low, but higher than in the snow period, with a mean R^2 of 0.029 ± 0.005 (Appendix G). In contrast to the footprint

variables, where significantly positive β -coefficients suggests avoidance of a feature by individuals, a significantly positive β -coefficient for a habitat variable indicates that individuals were more likely to occur in that habitat type than expected by chance. Likewise, while a significantly negative β -coefficient for distance to the nearest footprint variable suggests selection of that land use feature, for habitat variables it indicates that individuals were less likely to occur in that habitat type than expected by chance.

In the snow-free period, population-level β -coefficient averages indicated that deer moved significantly closer to cutblocks than expected by chance ($\beta = -0.0006$), although individual responses were variable (Table 3). Observed steps in the snow-free period were also significantly closer to deciduous forests/shrubland ($\beta = 0.1935$) and significantly further from coniferous forests ($\beta = -0.1906$) than expected by chance (Table 3).

Table 3. Two-step conditional logistic regression results for comprehensive model in the snow-free period. β -coefficients and standard errors (SE) for footprint and habitat covariates in the snow-free period and counts of individuals showing significantly positive (+) and negative (-) β -coefficients. NS denotes “non-significant” responses ($p > 0.05$). Values in bold indicate significant β -coefficients greater than 2 SE from zero.

Covariate	β	SE	Individual Responses		
			+	-	NS
Distance to road	-0.0003	0.0002	4	7	16
Distance to pipeline	0.0000	0.0002	7	6	14
Distance to seismic line	-0.0001	0.0002	5	5	17
Distance to cutblock	-0.0006	0.0002	2	10	15
Distance to industrial site	0.0000	0.0002	8	4	15
Grassland	0.0023	0.0893	7	5	15
Deciduous/Shrubland	0.1935	0.0647	11	2	14
Coniferous	-0.1906	0.0951	4	11	12

Discussion

I constructed conditional logistic step selection functions to estimate the influence of anthropogenic features and habitat types on female white-tailed deer within an industrialized landscape in northeastern Alberta. In general, the explanatory power of all models for both seasons were low, suggesting deer movements were not well explained by the landscape variables included in my assessment. Contrary to my hypotheses that deer would avoid seismic lines during the snow period as a predator avoidance strategy and select for seismic lines during the snow-free period for early seral stage forage, I did not discern a significant population-level influence of seismic lines on deer movement in my models. However, selection of cutblocks in the snow-free period was consistent with my hypothesis and the similar findings of Casabon and Pothier (2007).

The general preference for cutblocks (as well as deciduous forests and shrubland) during the snow-free period (Table 3) can be corroborated with existing knowledge that deer prefer open areas in order to detect predators and maximize distance from them (Kunkel & Pletscher 2001). Accordingly, vigilance behaviour is known to increase among deer in dense vegetation compared to those in sparsely vegetated areas (LaGory 1987). Deer are also attracted to cutblocks and other early seral stage habitats for the abundance of shrubs, forbs, and grasses (Hewitt 2011).

Despite the importance of predator evasion in the winter, the best model for the snow period was the footprint-only model, which did not include habitat variables (Figure 3a; Appendix H). Kittle *et al.* (2008) also found that winter resource selection by white-tailed deer was not strongly influenced by cover type, but rather was strongly influenced by snow conditions (*e.g.* snow depth and density). Given this importance of snow conditions on white-tailed deer movement and habitat selection (Dawe *et al.* 2014; Mech *et al.* 1987; Kittle *et al.* 2008), the fact that my SSF models did not include spatial variation in snow conditions may have accounted for the general weakness of all models in the snow period (Appendix F; Appendix G).

Furthermore, inclusion of terrain ruggedness (Boyce *et al.* 2003), climatic conditions (Dussault *et al.* 2004), and proximity to water (Johnson *et al.* 2000) as predictor covariates would likely improve my models for both seasons. Ungulate resource

selection is also influenced by forage distribution (Fryxell *et al.* 2004), predation (James & Stuart-Smith 2000), and competition (Kittle *et al.* 2008). For white-tailed deer, these factors would manifest as the observed distributions of forage, predators (*e.g.* cougars (*Puma concolor*), bears (*Ursus spp.*), coyotes (*Canis latrans*), wolves; Kunkel & Pletscher 1999), and presence of exploitative and apparent competitors, such as mule deer (*Odocoileus hemionus*) and moose (Robinson *et al.* 2002; Jenkins & Wright 1988).

Non-consumptive effects of predators may also strongly influence the spatial distribution of prey—a phenomenon termed the “landscape of fear” (Brown *et al.* 1999; Laundré *et al.* 2001). Mapping areas of direct predation risk (*i.e.* the frequency of a predator’s occurrence across the landscape; Fortin *et al.* 2005) was not a feasible option for my study site, due to a lack of predator monitoring specific to the area. However, seismic lines were considered areas of *indirect* predation risk since they represented landscape features associated with a higher risk of predation by wolves (Hebblewhite *et al.* 2005; Latham *et al.* 2011).

Kittle and colleagues’ (2008) investigation of the relative importance of direct and indirect predation risk on white-tailed deer space-use suggested that areas with high observed wolf frequencies were more influential on deer distribution than areas of high perceived risk (*e.g.* linear features travelled by wolves). Although sources of indirect predation risk are more spatially predictable by deer than actual locations of predator presence, indirect predation sources like seismic lines or low-traffic roads often present higher forage availability to offset the risk of mortality (Kittle *et al.* 2008).

The tradeoff between bottom-up (*e.g.* forage availability), and top-down (*e.g.* predation risk) factors also varies with temporal scale across times of the day, across seasons, and across years of varying winter severity (Boyce 2006). The contingency of selection on such fluctuations may speak to some of the great variability in responses among individual deer (Table 2; Table 3). Naturally, when behaviour of individuals is highly variable, population models based on average individual responses will have poor predictive capacity and population-level generalizations become difficult (Nielsen *et al.* 2002). However, Thurfjell *et al.* (2011) emphasized that “striving for the strongest selection coefficients may not always be the answer to biologically relevant questions”.

Variability within a population may present interesting questions on how behaviour differs between individuals of different ages (Thurfjell *et al.* 2014), migratory habits (Killeen *et al.* 2014), or future survival (*e.g.* depredated individuals *vs.* survivors; Losier *et al.* 2015). Ages were not determined for this sample of 30 deer, but telemetry data could indicate whether each animal was a disperser or a non-disperser by investigating displacement throughout the study period and characterizing home range parameters (Figure 1). Existing mortality data determining which deer were depredated and which were survivors are also available for comparing selection coefficients in future studies. Comparisons of β -coefficients based on survival may suggest which behavioural responses to habitat features presented higher mortality risk (*e.g.* Losier *et al.* 2015).

Although I have divided step length distributions between snow and snow-free periods, past studies have also constructed separate distributions depending on time of day (Roever *et al.* 2010; Northrup *et al.* 2012) or behavioural activity (*e.g.* foraging, migrating; Squires *et al.* 2013; Leblond *et al.* 2010). Broken-stick models can help distinguish between different behaviours such as intra-patch foraging, inter-patch movement, migration, hunting, or predator evasion based on movement metrics like step length and turning angles (Squires *et al.* 2013). After classifying the different movement types detected by the broken-stick model, regression models could be tested separately for each behavioural state to determine how the factors influencing movement decisions vary across behaviours (Thurfjell *et al.* 2014). For example, Johnson *et al.* (2002) found that caribou intra-patch foraging movements were more strongly associated with cover type and were closer to areas of higher indirect predation risk than inter-patch travelling movements.

However, I confront a limitation in the resolution of the telemetry data which restricts assessment of how the influences of anthropogenic landscape features varies during different behavioural activities. Defining behavioural activities often depends on characterizing the combinations of step length and turning angle (Thurfjell *et al.* 2014). Typically, the higher the fix rate, the greater the expected correlation between step length and turning angle, and the more easily the characteristics of different movement behaviours (*e.g.* foraging, dispersing, escaping) can be resolved (Thurfjell *et al.* 2014).

The low correlation between step lengths and turning angles in my study ($|r|_{\text{mean}} = 0.005$) suggest that the 2-hour fix rate would be inadequate in applying broken stick models to resolve behavioural movement metrics for white-tailed deer.

While the spatiotemporal scale allowed by the 2-hour fix rate may not have been fine enough for classifying individuals' behavioural activities, it presented a small enough spatial scale to address the fourth order of selection (selecting food patches within habitat components; Johnson 1980). However, the 2-hour fix rate presented limitations in the scales of movement choices I could investigate. Step selection functions are typically used to analyze third and fourth order selection—habitat components within home ranges and patches within habitat components (Johnson 1980). The short average step length (118 m in snow period, 200 m in snow-free period) of white-tailed deer within the programmed 2-hour intervals restricted my spatiotemporal scale to small-scale movement choices—selection of patches within habitat components.

However, the probability of selecting a patch depends on the qualities of both the patch and the surrounding habitat (Potts *et al.* 2014a). Models which investigate small-scale selection without incorporating the broader-scale qualities of the selected habitat tend to ignore patch size and connectedness, and as a result, erroneously predict that animals are just as likely to choose a small isolated patch as a large contiguous patch of equal habitat quality (Barnett & Moorcroft 2008; Potts *et al.* 2014a). For example, I aimed to understand the relative influence of seismic lines on deer movement choices by comparing proximity to the nearest seismic line between observed and simulated steps from the same start-point. This proximity parameter did not take into account the relative density of seismic lines in that area compared to other components of a deer's home range. Thus, my models may predict that deer are just as likely to choose a patch within an area of high seismic line density as a patch within an area of low seismic line density, as long as that patch occurs at the same distance from the nearest seismic line.

Hence, exclusion of larger scale landscape variables (*e.g.* density of land use features) may have contributed to the low explanatory power of my models. These deficiencies that arise from overlooking third-order selection may be addressed in future studies using two concurrent methods: (1) including larger scale landscape variables (*e.g.*

linear feature densities) as predictor covariates, and (2) repeating SSFs at larger spatiotemporal scales to investigate broader orders of selection.

For this first strategy—including larger-scale landscape variables—our footprint and habitat layers would benefit from the inclusion of densities and area values. For example, each seismic line feature should be classified as either 2D or 3D seismic to provide a better idea of the density of seismic lines in a given habitat component. Two-dimensional (2D) seismic lines are cut further apart for coarse delineation of bitumen resources in the ground while 3D seismic lines are spaced closer together in a cross-hatch pattern (often < 100 m spacing) to more accurately profile the subterranean rock strata for placement of horizontal wells (Van Rensen 2014; Vermeer & Beasley 2002). Traffic data for roads and regeneration classes of cutblocks and seismic lines are also important considerations for third order selection (Northrup *et al.* 2012; Fisher & Wilkinson 2005).

The second strategy—to replicate SSFs at larger scales—would involve re-characterization of observed path metrics and re-simulation of available steps based on longer time intervals between steps. Since the time interval between consecutive telemetry points determines the spatiotemporal scale of the SSFs, fix rates should be determined based on the research question and knowledge of the ecology of the species (Boyce 2006; Boyce *et al.* 2003). For example, a 2-hour fix rate may address questions of habitat selection for wolves, which have broad-scale movement (Latham *et al.* 2011), but deer typically cover less ground within 2 hours, making their average step length shorter and SSFs better suited to smaller scale selection of patches within habitat components (Boyce 2006).

If the time interval is too short considering the species' travel speeds, the patches or habitats that are avoided by deer might not be included in the simulated step either (Thurfjell *et al.* 2014). For example, if the fix rate for white-tailed deer were 5 minutes, the steps would be so short that the observed versus simulated distance to the nearest seismic line would be practically the same and any avoidance or selection of seismic lines could not be detected (Thurfjell *et al.* 2014). Although higher fix rates permit higher resolution behavioural studies (*e.g.* Potts *et al.* 2014b using 1- and 5- min fix rates), step length and turning angle could be biased if the average step length is shorter than five

times the GPS locational error (Jerde & Visscher 2005). Collar batteries also last longer with lower fix rates (Thurfjell *et al.* 2014).

Ideally, models constructed from SSFs using different fix rates could be compared using Akaike Information Criteria (AIC) to determine the spatiotemporal scale most suitable for addressing the research question (Boyce 2006). To repeat my methods at larger spatiotemporal scales of resolution, I could redefine steps in the existing data as the lines between points taken 4, 6, or 8 hours apart. Sensitivity analyses including AIC could also be used to compare multiple ratios of simulated to observed steps to test whether my single simulated sample per observed step was an adequate representation of available space (Northrup *et al.* 2013). However, since SSFs use conditional regression approaches, Thurfjell *et al.* (2014) argued that the number of simulated steps can be low with no effect on parameter estimation, which supported my choice to simulate only one step per observed start location.

Conclusions

In summary, my models suggested that white-tailed deer generally selected steps closer to cutblocks in the snow-free season than expected by chance, while other land use features showed no significant influences on deer movement choices at this small scale. Selection for cutblocks was consistent with prior knowledge of deer's preference for early seral stage forage and open areas for predator detection and evasion. Small average step lengths, limited breadth and scale of predictor covariates, and low resolution of habitat and footprint data restricted the ability of my models to address hypotheses on season-dependent seismic line avoidance with sufficient confidence. High variability in individual movement responses to human land use features reflected the behavioural plasticity that allows for the adaptation and expansion of white-tailed deer into novel landscapes. This variability makes it difficult to predict generalizable responses of deer to human land use.

Incorporating environmental factors important to deer selection, such as snow depth, terrain ruggedness, climatic conditions, and proximity to water would likely improve the explanatory power of my models. Improving the detail of my existing human footprint data (*e.g.* age of cutblocks, road traffic) may also help clarify some of the large variability in individual responses to human land use features. Since selection of patches is contingent on larger scale selection of habitat components and home ranges, future studies should also consider broader landscape characteristics such as linear feature density (*e.g.* 2D vs. 3D seismic), patch size (*e.g.* cutblock area), and patch connectance (*e.g.* percent cover of the given habitat type at a larger scale) in my models. Increasing the spatiotemporal scale of my SSFs by redefining steps at 4-, 6-, or 8-hour intervals may also help to investigate larger-scale selection of habitat components and home ranges.

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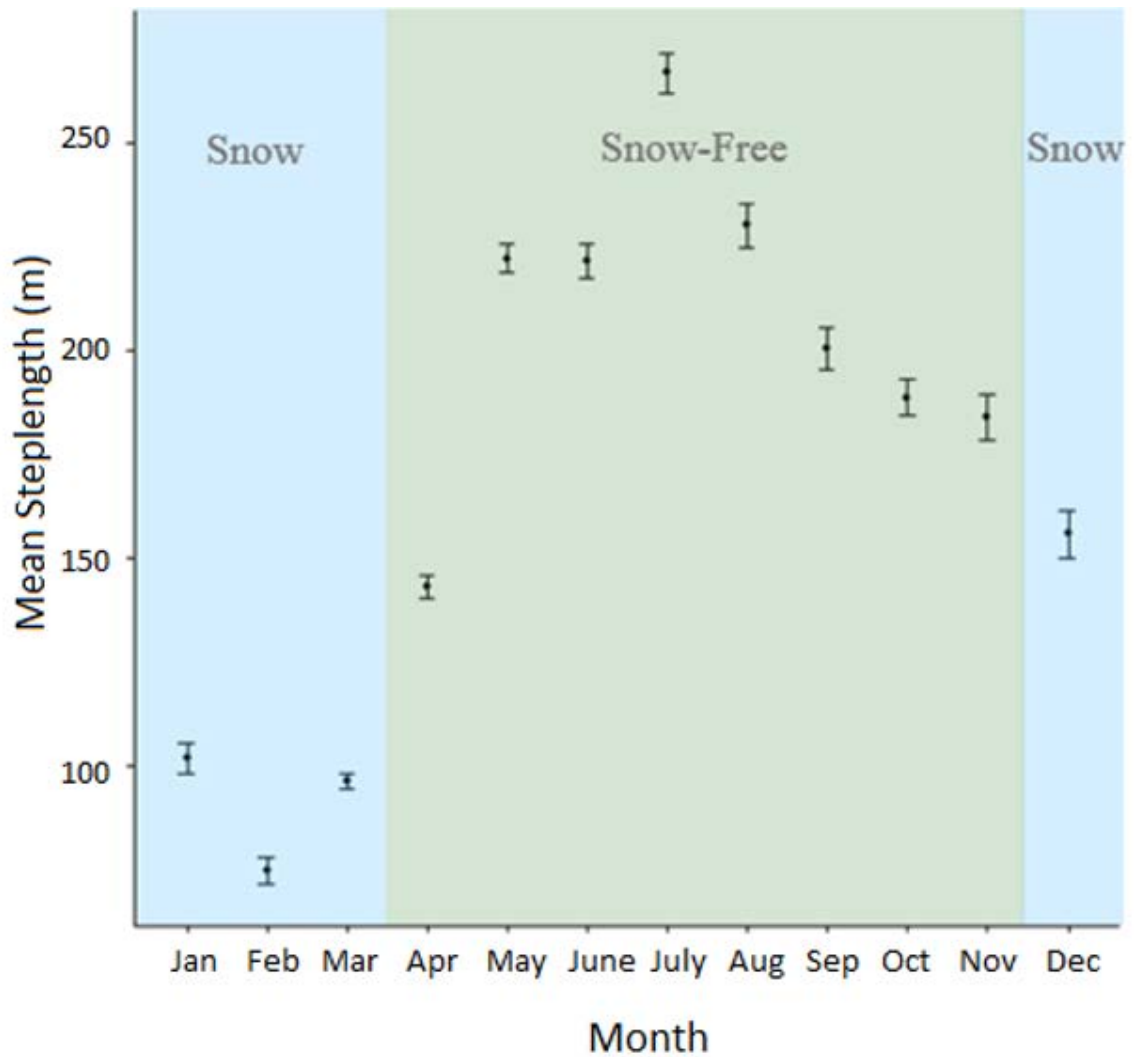
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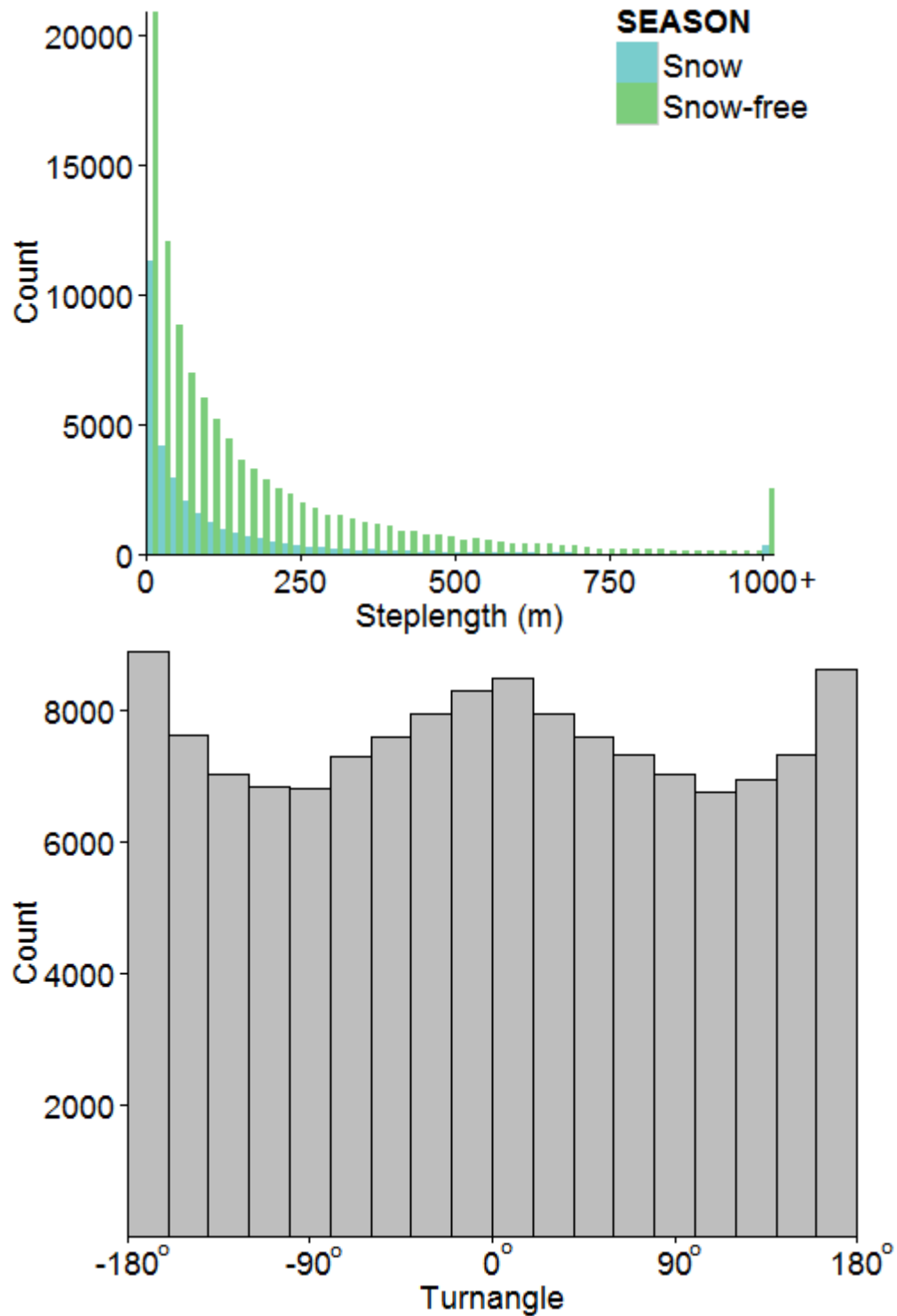
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Appendix A: Seasonal changes in step length. Mean monthly step lengths (m) pooled across telemetry data from 30 female white-tailed deer from March 2012 to January 2015.



Appendix B: Step length and turning angle frequency distributions. Histograms of (a) step length stratified by season and (b) turning angle pooled across seasons. Frequency distributions drawn upon for each individual deer were constructed from step length and turning angle data of all other deer. Step length distributions were season-specific (*e.g.* steps simulated from telemetry locations of the snow period drew from step length histograms of only snow steps) while the same year-round turning angle distribution was used to simulate steps in both seasons.



Appendix C: ABMI Land Cover Map habitat descriptions. Descriptions of each habitat type classification used in the study area (ABMI 2012).

Habitat type	Description
Grassland	<p>Predominantly native grasses and other non-woody vegetation (e.g., forbs) with a minimum of 20% ground cover. May include some shrub cover (but less than a third of the vegetated area) or a few trees (but the tree cover cannot exceed 10%). Land used for range with native unimproved grasses (a.k.a. rough pasture) is included in this class. Alpine meadows fall into this class. Marshes and other non-woody wetlands with at least 20% vegetation cover (sedges, cattails, or moss) belong to this class. NB. A forestry cutblock harvested more than year ago that contains seedlings, but where the latter cover less than 10% of the area of the cutblock, belongs to this class. If the cutblock had no successful regeneration and was covered by more than 20% shrubs, then it would belong to the 'shrubland' class.</p>
Shrubland	<p>At least 20% ground cover which is at least one-third shrub (shrub: a woody plant not considered a tree), with no or little presence of trees (less than 10% crown closure). Examples of plants belonging to this class in Alberta are alder, willow, juniper, and sagebrush. Shrubby fens and other non-treed woody wetlands, usually associated with floodplains and the shores of lakes and streams, belong to this class. NB. A dense patch of regenerating young trees is still considered forest and not shrub, no matter that the trees are still small.</p>
Deciduous Forest	<p>Treed areas with at least a 10% ground cover of trees, where broadleaf trees (trembling aspen, balsam poplar, white birch) are 75% or more of the crown closure. Young plantations or regenerating cutblocks of broadleaf trees belong to this class no matter that the trees are less than 5 m tall, providing crown closure has reached 10%. Treed swamps along river floodplains and other treed wetlands are included in this class providing they are broadleaf dominated and crown closure exceeds 10%.</p>
Coniferous Forest	<p>Treed areas with at least a 10% ground cover of trees (a.k.a. crown closure), where coniferous trees (spruce, pine, fir, larch) are 75% or more of the crown closure. Young plantations or regenerating cutblocks of conifer trees belong to this class no matter that the trees are less than 5 m tall, providing crown closure has reached 10%. Treed wetlands (e.g., black spruce bogs and fens) are included in this class providing they are conifer dominated and crown closure exceeds 10%.</p>

Appendix D: Human footprint descriptions. Descriptions of each human footprint type used in the analysis (ABMI n.d.; ABMI 2015).

Feature	Description	Source	Accuracy
Roads	All paved and gravel roads, does not include vegetated margins. Linear features 2 to >20 m wide.	Digitized from satellite imagery (SPOT)	Information not available (ABMI n.d)
Pipelines	Oil and gas pipelines with buffers added. Linear industrial features >20 m wide.	Digitized from satellite imagery (SPOT)	Information not available (ABMI n.d)
Seismic lines	Linear industrial features 2-10 m wide.	Digitized from satellite imagery (SPOT)	Information not available (ABMI n.d)
Cutblock	Areas where forestry operations have occurred (clearcut, selective harvest, salvage logging, etc.)	SRD, FRI, Individual timber harvesting companies	Digitized by the ABMI using 2011-2012 SPOT imagery at 1:15,000. Cut blocks < 5 ha were not included in layer. Data have a spatial accuracy of approximately 7.5 m.
Industrial site	Industrial sites with high human density, intense industrial and commercial development (airports, industrial parks, factories, refineries, hydro generating stations, pulp & paper mills, pump stations, malls, parking lots, zoos, etc.) and/or bare ground cleared for industry (communication towers, etc.)	Created by the ABMI using SPOT imagery. The SRD Base Layer was used as a reference in interpretation	Digitized from 2011-2012 SPOT imagery at 1:15,000 scale. Data have a spatial accuracy of approximately 7.5 m.

Appendix E: Assessing collinearity among predictor covariates using pairwise Pearson correlation. Pairwise Pearson $|r|$ coefficients for all predictor covariates used in the alternative conditional logistic regression models, pooled across seasons, years, and individuals. Footprint variables were quantified as *distance to the nearest* of each listed land use feature. Habitat variables were binary characterizing presence or absence of the step in each habitat type.

	Road	Pipeline	Seismic	Cutblock	Industrial	Grassland	Deciduous /Shrub	Coniferous
Road	1	0.174	-0.112	0.611	0.420	-0.141	0.205	-0.063
Pipeline	0.174	1	0.088	0.062	0.256	-0.096	0.012	0.061
Seismic	-0.112	0.088	1	0.053	-0.130	0.036	-0.085	0.001
Cutblock	0.611	0.062	0.053	1	0.301	-0.158	0.093	0.023
Industrial	0.420	0.256	-0.130	0.301	1	-0.065	-0.032	-0.041
Grassland	-0.141	-0.096	0.036	-0.158	-0.065	1	-0.373	-0.232
Deciduous/Shrub	0.205	0.012	-0.085	0.093	-0.032	-0.373	1	-0.419
Coniferous	-0.063	0.061	0.001	0.023	-0.041	-0.232	-0.419	1

Deer ID	Number of fixes	R ²	β-coefficients				
			Road	Pipeline	Seismic	Cutblock	Industrial
1	436	0.023	0.0009	0.0023	0.0002	-0.0017	0.0019
7	524	0.007	0.0004	-0.0013	0.0017	0.0017	0.0008
8	604	0.009	0.0010	0.0005	0.0006	-0.0018	-0.0005
9	2480	0.013	0.0001	0.0018	0.0013	0.0020	0.0018
10	620	0.019	-0.0020	0.0006	0.0013	-0.0025	-0.0019
11	494	0.029	0.0035	0.0040	-0.0003	0.0014	0.0023
12	1578	0.007	0.0001	0.0013	0.0015	-0.0004	0.0021
13	3382	0.011	-0.0007	0.0010	0.0014	0.0019	0.0012
14	4644	0.002	-0.0003	-0.0004	<0.0001	-0.0007	0.0002
15	244	0.032	0.0010	0.0043	-0.0056	0.0026	-0.0003
18	1000	0.013	-0.0030	-0.0018	-0.0008	-0.0082	0.0117
19	2598	0.005	0.0011	<0.0001	0.0003	-0.0006	-0.0012
20	1546	0.032	-0.0032	-0.0008	-0.0026	-0.0003	0.0006
21	1370	0.004	-0.0002	-0.0002	-0.0002	0.0003	-0.0003
22	512	0.009	-0.0002	-0.0009	0.0022	0.0005	0.0005
23	662	0.015	0.0015	-0.0010	-0.0027	0.0007	-0.0004
24	1900	0.008	-0.0006	0.0011	0.0013	<0.0001	-0.0002
25	1126	0.010	-0.0002	0.0020	0.0007	-0.0005	-0.0009
26	402	0.016	-0.0018	-0.0008	-0.0023	-0.0004	-0.0002
27	898	0.011	0.0015	0.0011	0.0019	-0.0013	0.0009
28	750	0.017	0.0036	-0.0063	0.0016	-0.0021	-0.0007
29	1920	0.012	0.0011	0.0023	0.0016	0.0002	-0.0017
30	1306	0.001	0.0001	-0.0001	<0.0001	-0.0003	0.0001

Deer ID	Number of fixes	R ²	Road	Pipeline	Seismic	Cutblock	Industrial	Grassland	Deciduous/ Shrub	Coniferous
1	3833	0.032	-0.0008	0.0008	0.0001	-0.0020	0.0009	-0.2279	-0.5552	-0.7546
2	2688	0.014	-0.0004	0.0005	-0.0006	-0.0002	0.0006	0.0854	0.5659	-1.0251
3	2417	0.010	-0.0005	0.0004	-0.0001	-0.0007	-0.0001	0.9513	1.0401	0.3971
4	2955	0.012	-0.0002	-0.0006	0.0003	-0.0004	0.0004	-0.3433	0.1268	-0.1360
5	2338	0.008	-0.0002	0.0000	-0.0007	0.0003	0.0004	0.2000	0.3050	-0.1535
6	2018	0.044	-0.0030	0.0028	-0.0001	-0.0001	-0.0006	0.8497	0.9342	-0.5800
7	2960	0.047	-0.0030	-0.0002	-0.0006	-0.0017	-0.0025	0.2841	0.6115	-0.6534
8	1548	0.026	0.0004	0.0001	0.0000	-0.0021	0.0000	-0.3968	0.3775	-0.2870
9	5246	0.015	-0.0008	0.0006	-0.0010	-0.0006	0.0004	0.2950	0.2128	-0.0043
10	660	0.109	0.0005	-0.0015	-0.0022	-0.0004	0.0002	-2.0384	-0.1146	-1.6598
11	5755	0.017	0.0002	0.0002	0.0007	-0.0008	0.0000	-0.0348	0.1777	-1.0859
12	5816	0.027	-0.0012	0.0009	-0.0017	-0.0022	0.0001	0.2683	0.0792	-0.2380
13	8830	0.014	-0.0001	0.0005	0.0006	-0.0012	0.0005	0.0043	-0.0959	-0.2780
14	11657	0.021	-0.0002	0.0000	-0.0014	-0.0022	0.0007	-0.0864	0.0187	-0.2972
15	4484	0.025	-0.0024	-0.0001	0.0004	0.0013	0.0007	0.6639	0.1558	0.3853
16	572	0.079	-0.0017	-0.0039	0.0061	-0.0016	0.0008	0.3816	0.1969	0.9663
17	1244	0.029	0.0013	-0.0007	-0.0007	0.0001	0.0001	-0.5658	0.5061	0.0017
18	5764	0.010	0.0001	-0.0011	-0.0001	0.0000	0.0000	-0.6355	-0.3207	-0.6742
19	5840	0.016	0.0009	-0.0018	0.0000	-0.0001	-0.0008	-0.1737	0.0601	-0.2634
20	2522	0.037	-0.0021	-0.0009	-0.0011	-0.0027	-0.0021	0.3527	0.2770	-0.2214
21	5738	0.015	-0.0002	-0.0002	0.0007	0.0001	0.0000	-0.2834	0.3979	-0.2810
23	281	0.082	-0.0034	0.0001	0.0022	0.0010	0.0002	-0.7832	-0.0150	0.9768
24	5790	0.005	-0.0002	-0.0003	0.0000	0.0007	-0.0002	0.0428	0.2874	0.0735
27	792	0.047	0.0049	-0.0033	0.0016	-0.0165	0.0120	0.0789	-0.1344	0.5502
28	1804	0.010	0.0004	0.0000	-0.0007	-0.0001	0.0003	1.4670	1.0815	1.0831
29	5790	0.028	0.0019	0.0018	0.0014	-0.0011	-0.0020	-0.3921	-0.0300	-0.4300
30	5766	0.005	0.0000	-0.0001	0.0001	0.0002	0.0002	0.1012	0.0634	-0.4739

Appendix H: Individual Akaike Information Criterion weights (AIC_w) for snow period. AIC_w for each of 23 deer with >200 recorded steps in the snow period. Values in bold denote the maximum AIC_w for each individual, tallied at the bottom to portray the summed occurrence of each model as the “best model”. *Comprehensive*: Road + Pipeline + Seismic + Cutblock + Industrial Site + Grassland + Deciduous/Shrubland + Coniferous; *Linear*: Road + Pipeline + Seismic + Grassland + Deciduous/Shrubland + Coniferous; *Non-linear*: Cutblock + Industrial Site + Grassland + Deciduous/Shrubland + Coniferous; *Habitat*: + Grassland + Deciduous/Shrubland + Coniferous; *Footprint*: Road + Pipeline + Seismic + Cutblock + Industrial Site

Deer ID	Comprehensive	Linear	Non-linear	Habitat	Footprint
1	0.126	0.081	0.065	0.104	0.624
7	0.014	0.066	0.113	0.803	0.005
8	0.035	0.055	0.220	0.554	0.137
9	0.928	<0.001	<0.001	<0.001	0.072
10	0.184	0.011	0.549	0.034	0.222
11	0.055	0.017	0.003	0.008	0.917
12	0.444	0.016	0.393	0.146	<0.001
13	0.072	<0.001	<0.001	<0.001	0.928
14	0.161	0.085	0.711	0.043	<0.001
15	0.024	0.049	0.291	0.634	0.002
18	0.120	0.008	0.396	0.141	0.336
19	0.334	0.004	0.412	0.030	0.221
20	0.276	0.277	<0.001	<0.001	0.448
21	0.076	0.121	0.584	0.209	0.010
22	0.050	0.188	0.092	0.453	0.217
23	0.080	0.361	0.014	0.073	0.472
24	0.195	0.634	0.003	0.013	0.155
25	0.230	0.132	0.016	0.050	0.572
26	0.050	0.247	0.083	0.207	0.413
27	0.131	0.705	0.048	0.102	0.015
28	0.067	0.064	0.004	0.025	0.840
29	0.671	0.313	0.001	0.005	0.010
30	0.009	0.057	0.178	0.752	0.004
<i>Tally:</i>	3	2	6	5	7

Appendix I: Individual Akaike Information Criterion weights (AIC_w) for snow-free period. AIC_w for each of 27 deer with >200 recorded steps in the snow-free period. Values in bold denote the maximum AIC_w for each individual, tallied at the bottom to portray the summed occurrence of each model as the “best model”. *Comprehensive*: Road + Pipeline + Seismic + Cutblock + Industrial Site + Grassland + Deciduous/Shrubland + Coniferous; *Linear*: Road + Pipeline + Seismic + Grassland + Deciduous/Shrubland + Coniferous; *Non-linear*: Cutblock + Industrial Site + Grassland + Deciduous/Shrubland + Coniferous ; *Habitat*: + Grassland + Deciduous/Shrubland + Coniferous; *Footprint*: Road + Pipeline + Seismic + Cutblock + Industrial Site

Deer ID	Comprehensive	Linear	Non-linear	Habitat	Footprint
1	0.998	<0.001	0.002	<0.001	<0.001
2	0.888	0.010	0.092	0.009	<0.001
3	0.052	0.225	0.214	0.509	<0.001
4	0.715	0.127	0.015	0.001	0.141
5	0.073	0.099	0.295	0.532	0.002
6	0.348	0.652	<0.001	<0.001	<0.001
7	~1	<0.001	<0.001	<0.001	<0.001
8	0.107	<0.001	0.885	0.007	<0.001
9	0.892	0.092	<0.001	<0.001	0.015
10	0.113	0.671	0.031	0.185	<0.001
11	0.779	0.086	0.123	0.011	<0.001
12	0.941	0.004	<0.001	<0.001	0.056
13	0.998	<0.001	<0.001	<0.001	0.002
14	0.982	<0.001	<0.001	<0.001	0.018
15	~1	<0.001	<0.001	<0.001	<0.001
16	0.335	0.547	0.001	<0.001	0.117
17	0.065	0.391	0.187	0.357	<0.001
18	0.125	0.875	<0.001	<0.001	<0.001
19	0.986	<0.001	<0.001	<0.001	0.014
20	0.981	0.001	<0.001	<0.001	0.018
21	0.241	0.738	0.008	0.014	<0.001
23	0.102	0.499	0.277	0.087	0.035
24	0.388	0.001	0.591	0.011	0.008
27	0.535	<0.001	<0.001	<0.001	0.465
28	0.071	0.219	0.309	0.393	0.008
29	0.981	<0.001	<0.001	<0.001	0.019
30	0.064	0.009	0.880	0.047	0.001
<i>Tally:</i>	14	7	3	3	0