

Effects of linear features on resource selection and movement rates of wood bison (*Bison bison athabascae*)

C.A. DeMars, S.E. Nielsen, and M.A. Edwards

Abstract: Human-mediated disturbances can lead to novel environmental features that can affect native biota beyond simple habitat loss. In boreal forests of western Canada, linear features (LFs; e.g., pipelines, seismic lines, and roads) are known to alter behaviour, movements, and interactions among species. Understanding LF impacts on native species has therefore been a management priority. Here, we investigate how LFs affect the spatial behaviour of wood bison (*Bison bison athabascae* Rhoads, 1898), which are designated as “threatened” in Canada. Using data collected from the Ronald Lake population in northeastern Alberta, we assessed how LFs influenced habitat selection and movement of bison by testing support among three hypotheses explaining whether LFs (i) increased forage availability, (ii) enhanced movement efficiency, or (iii) increased predation risk. Results supported the movement efficiency hypothesis as bison were generally ambivalent toward LFs, showing weak selection or avoidance depending on land-cover type, but moved slightly faster when on them. These findings contrast with avoidance behaviours reported for sympatric woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)), which are also “threatened.” Our results should inform critical habitat decisions for wood bison, but we caution that further research is needed to understand the effects of LFs on bison demography.

Key words: wood bison, *Bison bison athabascae*, linear features, boreal forest, seismic lines, anthropogenic disturbance, critical habitat.

Résumé : Les perturbations d'origine humaine peuvent mener à de nouveaux éléments du milieu qui peuvent avoir des effets sur le biote indigène autres que la simple disparition d'habitat. Dans les forêts boréales de l'Ouest canadien, il est établi que les éléments linéaires (EL; p. ex. pipelines, lignes sismiques et routes) modifient les comportements, les déplacements et les interactions d'espèces. La compréhension des impacts d'EL sur les espèces indigènes constitue donc une priorité de gestion. Nous examinons l'incidence d'EL sur le comportement spatial des bisons des bois (*Bison bison athabascae* Rhoads, 1898), qui figurent sur la liste des espèces « menacées » au Canada. En utilisant des données obtenues de la population du lac Ronald, dans le nord-est de l'Alberta, nous avons évalué l'influence des EL sur la sélection d'habitats et les déplacements des bisons en nous penchant sur les observations qui appuieraient trois hypothèses, à savoir que les EL (i) accroissent la disponibilité de fourrage, (ii) accroissent l'efficacité des déplacements ou (iii) accroissent les risques de prédation. Les résultats appuient l'hypothèse de l'efficacité des déplacements, puisque les bisons sont généralement ambivalents en ce qui concerne les EL, présentant une faible sélection ou un faible évitement selon le type de couverture, mais se déplaçant légèrement plus vite quand ils sont dans ces zones. Ces constatations diffèrent des comportements d'évitement signalés pour les caribous des bois (*Rangifer tarandus caribou* (Gmelin, 1788)) sympatriques, qui sont également « menacés ». Nos résultats devraient être pris en considération dans la prise de décisions concernant les habitats essentiels pour le bison des bois, mais nous tenons à souligner que d'autres travaux sont nécessaires pour comprendre les effets des EL sur la démographie des bisons. [Traduit par la Rédaction]

Mots-clés : bison des bois, *Bison bison athabascae*, éléments linéaires, forêt boréale, lignes sismiques, perturbation d'origine humaine, habitat essentiel.

Introduction

Across the globe, human activities are altering natural landscapes at rates and spatial scales exceeding those associated with natural disturbance regimes (Seidl et al. 2016). In addition to habitat loss and fragmentation (Fischer and Lindenmayer 2007), human-mediated disturbances result in the creation of environmental features that may have disproportionate effects on native biota because they are evolutionarily novel (Sih et al. 2011; Hendry et al. 2017). For any one species, predicting its response to such

features is often difficult because observed outcomes likely depend upon the interaction between a species' behavioural plasticity and how these features alter resource distribution and predation risk (Sih et al. 2011; Wong and Candolin 2015). The intensity of human use associated with a particular environmental feature may further influence species' responses and community dynamics (Muhly et al. 2011). With these often-complex interactions increasingly being recognized as contributing factors to species endangerment, understanding species-specific behavioural responses in

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modified landscapes can play an integral role in developing effective conservation strategies (Caro and Sherman 2011).

In the boreal forests of western Canada, linear features (LFs) such as roads, pipelines, and natural resource exploration lines (seismic lines) are a prominent form of human disturbance (Pattison et al. 2016) and understanding their effects on wildlife has become a management priority (Venier et al. 2014; Dabros et al. 2018). Recent research has demonstrated that LFs can exert a myriad of effects, including influencing animal movement rates and direction (Dickie et al. 2017b; Riva et al. 2018), facilitating dispersal (Doncaster et al. 2001; Roberts et al. 2018), contributing to range expansion (Dawe et al. 2014; Jung 2017; Fisher and Burton 2018), and altering predator–prey dynamics (DeGregorio et al. 2014; DeMars and Boutin 2018). For prey species, LFs have had generally negative effects and, in certain instances, have contributed to species endangerment (Fahrig and Rytwinski 2009). Perhaps the most prominent example is the boreal ecotype of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) currently listed as “threatened” under Canada’s *Species at Risk Act*. In this case, LFs are thought to contribute to caribou population declines by increasing wolf (*Canis lupus* Linnaeus, 1758) hunting efficiency and facilitating caribou–wolf spatial overlap, resulting in unsustainable rates of caribou predation (Whittington et al. 2011; Dickie et al. 2017b; DeMars and Boutin 2018). Although caribou have generally responded by avoiding LFs (Dyer et al. 2001; DeMars and Boutin 2018; but also see Serrouya et al. 2017), this response has been insufficient to overcome the positive response of wolves to LFs, causing increased spatial overlap between predator and prey (i.e., the predator wins the behavioural “space race”; sensu Sih 1984). Because of these negative effects, a primary focus of caribou conservation has been in developing effective strategies for restoring or deactivating LFs, which has required understanding the various behaviourally mediated mechanisms by which LFs affect caribou (Dabros et al. 2018).

Linear features have received considerable attention in the context of caribou conservation; however, other species may respond differently to LFs, including “threatened” wood bison (*Bison bison athabasca* Rhoads, 1898). Effects of LFs on wood bison are not well understood, and the few studies to date have been equivocal, with some suggesting that LFs improve habitat suitability by increasing forage availability (Mitchell and Gates 2002; Leverkus 2015) and others suggesting that they may be detrimental because they increase bison–human conflict (Thiessen 2009; Jung 2017; Doney et al. 2018; Jung and Larter 2018) and increase hunting pressure (Environment and Climate Change Canada 2018b). Such effects may not be mutually exclusive and their relative importance on bison behaviour and demography may be context-dependent. Understanding LF effects has important ramifications for identifying critical habitat for wood bison, which is required within the federal recovery strategy for this subspecies (Environment and Climate Change Canada 2018b). Because of differences in life history strategies, the wood bison’s response to LFs may fundamentally differ from those reported for caribou. For example, bison diets are composed largely of sedges and graminoids (Larter and Gates 1991; Jung 2015; Jung et al. 2015) and they may select LFs because these disturbances have an increased abundance of grasses and sedges compared with the surrounding forest (Leverkus 2015; Finnegan et al. 2018). Selection may occur despite the potentially increased predation risk associated with LFs because adult bison have a lower probability of death on wolf encounter compared with caribou (Mech et al. 2015). From a management perspective, such a potential difference, i.e., bison selection versus caribou avoidance, could result in LFs having much lower impact on critical habitat designation for wood bison than they currently do for caribou (Environment Canada 2012). More specifically, LFs result in a functional loss of critical habitat for caribou (Dyer et al. 2001), whereas LFs could potentially increase the value of critical habitat for bison.

We evaluated responses of wood bison to LFs using spatial data collected from the Ronald Lake population, which is situated in northeastern Alberta, Canada. This population has recently become a conservation focus due to its perceived disease-free status (Shury et al. 2015), potentially unique genetic structure (Committee on the Status of Endangered Wildlife in Canada (COSEWIC) 2013; Ball et al. 2016), cultural significance to First Nations and Métis, and location relative to proposed oil sands development (Government of Alberta 2013). Because part of the population’s range occurs in landscapes impacted by industrial development, understanding how anthropogenic disturbances such as LFs influence patterns of habitat selection and space use is critical for developing effective conservation plans for this population.

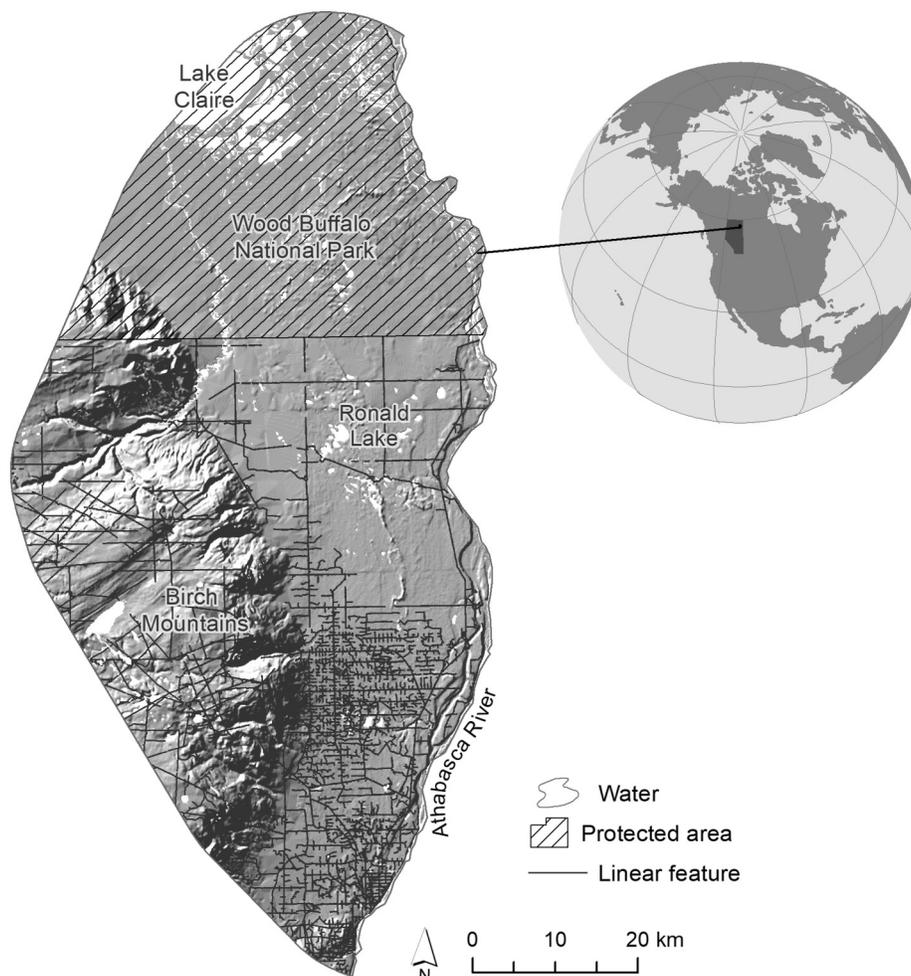
We assessed the responses of wood bison to LFs at two spatial scales and across two biologically defined seasons. At a fine scale, we assessed how LFs influenced habitat selection and movement rates. At a coarser scale, we evaluated whether LF density influenced bison space use within their range. We further evaluated the relative support for three hypotheses explaining potential outcomes. These hypotheses described whether LFs (i) increased forage availability, (ii) enhanced movement efficiency, or (iii) increased predation risk. Under the forage availability hypothesis, bison are predicted to select for LFs and move slower while on them because LFs have higher abundances of preferred forage (e.g., graminoids, forbs, and shrubs; Larter and Gates 1991; Jung 2015) compared with the surrounding forest (Leverkus 2015; Finnegan et al. 2018). The movement efficiency hypothesis similarly predicts for LF selection, but movement on them will be faster (Dickie et al. 2017b; Serrouya et al. 2017). The predation risk hypothesis predicts bison avoidance of LFs because these features are highly selected by wolves (Dickie et al. 2017b; DeMars and Boutin 2018) and (or) provide access for human hunters (Bonnot et al. 2013). To further evaluate this latter mechanism, we assessed how human activity on LFs has influenced bison response. We emphasize that only predictions of bison responses were evaluated and do not directly test the mechanisms underlying each hypothesis. We further recognize that results from our analyses reflect the average response of bison over a given season and that, within this period, an individual’s response could vary depending on its unknown state or condition (i.e., risk-sensitive foraging; Caraco et al. 1980) or short-term changes in environmental conditions (e.g., the recent passage of a predator; Latombe et al. 2014).

Materials and methods

Study area

The study area was north of the community of Fort MacKay, Alberta, Canada, and extended into the southeastern portion of Wood Buffalo National Park (Fig. 1). Boundaries were delineated by applying a 15 km buffer to a minimum convex polygon using locations from GPS-collared bison (see Bison spatial data section next) and then clipping the eastern boundary to the Athabasca River as no bison locations occurred east of the river. This area was situated within the Boreal Plains ecoregion and consisted of a mosaic of upland forests, low-lying peatlands (i.e., fens and bogs), marshes, and other riparian areas. Elevation ranged from 240 to 300 m above sea level and the climate was northern continental. In the eastern portion of the study area, upland conifer forests were dominated by jack pine (*Pinus banksiana* Lamb.), while white spruce (*Picea glauca* (Moench) Voss) was the leading species in western conifer stands. Low-lying peatlands were dominated by black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Common deciduous tree species included trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and, in more mesic areas, paper birch (*Betula papyrifera* Marshall). Other large mammals in the study area included moose (*Alces alces* (Linnaeus, 1758)), woodland caribou,

Fig. 1. The study area was situated in northeastern Alberta, Canada, and encompassed the known distribution of radio-collared wood bison (*Bison bison athabasca*) in the Ronald Lake population from April 2013 to March 2017. [Base map of provincial and continental boundaries, as well as protected areas, from ESRI Canada © 2003. A hillshade model of the region was developed using the ESRI hillshade function and digital elevation data from an open government licence (CDEM, edition 1.1, [Natural Resources Canada 2013](#)). Shapefile of mapped linear features from combined sources of Government of Alberta and Teck Resources Ltd. (see main text).].



deer (*Odocoileus* spp.), wolves, and black bears (*Ursus americanus* Pallus, 1780).

Forest fire was the dominant form of natural disturbance, with a mean return interval of ca. 40 years for jack pine and aspen forests and ca. 80 years for spruce forests (Larsen 1997). Anthropogenic disturbances from petroleum exploration and forest harvesting were also present in the study area, with the greatest concentrations occurring in the southern portions (petroleum exploration) and along the Athabasca River (forest harvesting). Among LFs, seismic lines and access trails were the most common types (95% of the total 3946 km length; mean line width = 7.0 m \pm 2.3 m). Other LF types included secondary roads (<5% of LFs) and pipelines (<2 km total length). The mean density of LFs (all types combined) was 0.87 ± 1.61 km \cdot km $^{-2}$, ranging between 0 and 13.47 km \cdot km $^{-2}$.

Bison spatial data

We used location data collected from 33 adult female bison fitted with Lotek GPS radio-collars (model IridiumTrackM; Lotek Wireless Inc., Newmarket, Ontario), a number representing ca. 15% of the most recent minimum population count for the Ronald Lake population (Government of Alberta 2013). These collars were deployed as part of a larger project investigating the ecology of these bison, and females were primarily targeted because the pop-

ulation dynamics of ungulates are highly influenced by adult female survival (Gaillard et al. 2000). Collars were deployed in March 2013 ($n = 10$), March 2014 ($n = 11$), and April 2016 ($n = 12$), with individuals captured by aerial net-gunning from a helicopter. All captures and handling were in accordance with approved class protocols and procedures of the Alberta Wildlife Animal Care Committee (permit nos. 51244, 53893, 54723, and 55748). All collars were programmed to acquire one GPS location (or fix) every 90 min. The mean monitoring interval per collar was 554 days (standard deviation (SD), 271; minimum, 141; maximum, 1082) and we used data extending to 20 March 2017.

Prior to analyses, we screened the data for potential errors. To do so, we first removed the initial two weeks of GPS locations after capture to reduce effects of capture-related behavioural alterations (Jung et al. 2019). Second, we removed all locations with low positional accuracy (i.e., two-dimensional GPS locations (or fixes) with positional dilution of precision values > 5 ; Lewis et al. 2007). Third, we used the method of Bjørneraas et al. (2010) to exclude outlying locations beyond the range of possible bison movement within the 90 min fix-acquisition interval. In this method's two-step process, we flagged GPS locations as potential outliers if the location was >10 km from an individual's general position — averaged in a moving window analysis ($n = 10$ locations) — and (or)

the location was associated with a movement “spike,” defined as a movement where an individual leaves its general location at a high rate of speed (here, $>1.5 \text{ km}\cdot\text{h}^{-1}$) and then immediately returns to the same general location at a similar high rate of speed. All flagged locations were visually inspected within the animal’s movement trajectory prior to their removal. Finally, we specified a regular sampling interval across all bison by removing GPS locations that fell outside of the normal sampling interval (every 90 min), a procedure necessitated by a few collars having periods of aberrant fix acquisition (e.g., recording fixes every minute for a 30 min period). Following these procedures, the mean rate of fix success per collar (i.e., the percentage of fixes remaining divided by the number of attempted fixes at the specified sampling interval (every 90 min)) was 93% (SD, 8.5%; range, 54%–98%).

Evaluating bison response to linear features: general framework

We evaluated bison response to LFs by estimating step selection functions (SSFs), an analytical framework that compares environmental variables (or resources) associated with each observed movement step (i.e., an animal’s movement between successive GPS locations) with resources associated with a matched set of random steps (Fortin et al. 2005; Avgar et al. 2016). With our focus on LFs, we compared resource values at the end of each step, an approach that is likely more effective at estimating the selection of a linear resource than averaging resource values along each step (Thurfjell et al. 2014). To adequately characterize resource availability, we generated 20 random steps for each observed step, sampling random steps from a parameterized distribution of the observed movement process (Forester et al. 2009; Northrup et al. 2013; Supplementary material A¹).

We estimated SSFs at two spatiotemporal scales in each of two biologically defined seasons. At the fine scale, we estimated SSFs at the temporal resolution of the GPS-collar data (i.e., 90 min fix interval) and specifically assessed bison selection of LFs themselves (i.e., the proportion of observed versus random locations falling within the LF footprint). At the coarse scale, we assessed bison response to LF density. Because LF density was measured within a 500 m radius around each observed and random location (see Statistical analyses section later), we subsampled the GPS-collar data at an interval of once every 24 h for each bison to allow sufficient movement into areas with differing LF densities.

Previous research suggested that animal use of LFs may be affected by snow (Latham et al. 2011; Dickie et al. 2017b). We therefore estimated SSFs at both scales during the snow and snow-free seasons. To define the snow season, we used “daily-snow-on-ground” data from the Fort McMurray meteorological station (Environment and Climate Change Canada 2018a) to identify the period of continuous snow cover. When the start date of continuous snow cover was unavailable in a given year, we used 1 November (snow seasons: 1 November 2013 – 25 April 2014; 7 November 2014 – 7 April 2015; 1 November 2015 – 15 April 2016; 1 November 2016 – 20 March 2017). The snow-free season extended from after calving to the first day of continuous snow cover. We excluded the calving season from our analyses because bison aggregate for calving (ca. late May to late June) in a small area within the northwestern part of their range that is generally devoid of LFs. We defined the start date of the snow-free season as when the last GPS-collared female left the calving area (snow-free seasons: 29 June – 31 October 2013; 26 June – 6 November 2014; 24 June – 31 October 2015; 14 June – 31 October 2016). Within this period, females may be accompanied by young calves, which could influence their response to LFs (e.g., DeMars and Boutin 2018). Although we could not test for such effects because we did not have

information on the parturition status of each female, discerning whether the presence of a calf affects a female’s behaviour toward LFs would be difficult due to the herding strategy of bison and the group defense behaviour exhibited by groups with calves (Carbyn and Trotter 1987).

Environmental covariates

We estimated SSFs using GIS data characterizing land cover, natural disturbances, and LFs. For land cover, we used Enhanced Wetlands Classification (EWC) data from Ducks Unlimited Canada (30 m pixel resolution from 2010 satellite imagery; overall accuracy 80%; Supplementary material B¹). These data constitute 29 land-cover classes, which for our analyses were reduced to 24 as we combined classes with small extents (e.g., mudflats: $<0.02\%$) with other biologically similar classes. For natural disturbances, we obtained data representing historic wildfire perimeters up to 2016 (Government of Alberta 2017). For our analyses, we only considered fires occurring within the last 10 years because, as grazers, bison response to fire should be strongest in early successional stages after fire (i.e., when grass and forb abundance is relatively high; Strong and Gates 2009; Leverkus 2015). For LFs, we used recent disturbance data (≥ 2006) related to petroleum exploration provided by industry (Royal Dutch Shell PLC, Teck Resources Limited, and SilverWillow Energy Corporation, unpublished data). These LFs were mapped using high-resolution aerial imagery with the accuracy exceeding the location accuracy of the GPS collars (see later in this paper; Teck Resources Limited, unpublished data). Older LF data (≤ 2005) representing a lower density of distributed legacy disturbances were provided by the Government of Alberta. All data sets included LFs (e.g., roads, pipelines, and seismic lines) and, in some cases, industrial sites (e.g., exploratory well sites, camps, and log decks) that occurred at the end of LFs and comprised a small proportion of the total LF footprint. Note that the EWC land-cover data also included an “anthropogenic” class, but this class did not include LFs. Because of the small spatial extent of roads and pipelines (i.e., $<5\%$ of LFs), we did not test for effects of line type, rather we combined all LF data sources to create a parsimonious disturbance layer while retaining attributes describing relative disturbance age (≤ 2005 versus ≥ 2006). We buffered all disturbances by 20 m, a width incorporating the mean GPS measurement error estimated for a similar model of Lotek GPS collars (14 m; McKenzie et al. 2009) and potential edge effects on vegetation composition and structure extending into the surrounding forest (Finnegan et al. 2018). Locations falling within this buffered distance were therefore considered within the footprint.

We also assessed whether the level of human activity on LFs affected bison responses. This analysis was conducted using snow-season data when activity levels were known on post-2005 LFs located within an industrial lease, which covered $\sim 30\%$ of the study area and was situated in its southwestern corner (Teck Resources Limited, unpublished data). For a given year, a LF was classified as active if human activity occurred on it; otherwise, it was classified as inactive (i.e., a binary variable with the assigned value dependent on year). Data describing human activity were provided by industry (Teck Resources Limited, unpublished data) and therefore reflects human activity related to industrial exploration and development.

Statistical analyses

At both scales of analysis, we estimated SSFs for each individual bison using conditional logistic regression formulated in a generalized estimating equation framework, which allows for the calculation of robust standard errors to account for potential

¹Supplementary materials A, B, and C are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2019-0013>.

autocorrelation among steps (Craiu et al. 2008; Oliveira-Santos et al. 2016). We used a multistage selection process to build final models for inference, discriminating among models at each stage using the quasi-likelihood under independence criterion (QIC; Craiu et al. 2008). All models included dummy variables representing the EWC land-cover types. For fine-scale SSFs, we first discriminated between models with and without LF age effects. We then assessed model fit when an interaction between step length (i.e., the distance moved between successive locations) and LF (starting location on or off the LF) was added. This model formulation can potentially improve precision of parameter estimates (Forester et al. 2009; Avgar et al. 2016) and directly evaluates whether LFs influence bison movement rate. For the snow season, we further assessed bison response to human activity levels, classifying post-2005 LFs by activity status within a given year (binary classification: active or inactive). The final stages of model selection considered the addition of interactions among LFs, land-cover type, and fire. For LF \times land cover interactions, we focused on treed land covers (e.g., upland deciduous), hypothesizing that because bison diet is dominated by sedges, grasses, and shrubs (Larter and Gates 1991; Jung 2015), bison may show greater response to the early seral habitat created by LFs within forests. All interaction variables were coded directly as dummy variables (e.g., LF in upland deciduous); thus, each of these variables became an additional land-cover type. For all analyses, we set upland conifer as the reference category.

At the coarse scale, we assessed bison response to LF density, which was estimated in a 500 m radius around each observed and random location. While other studies have used an information-theoretic framework to identify the most predictive radius (e.g., DeCesare et al. 2012), we maintained the 500 m radius for two reasons. First, this radius approximates the metric by which LF density is most commonly measured (i.e., km \cdot km $^{-2}$). Second, LFs are typically spaced >200 m apart (Boutin and Arienti 2008); therefore, smaller radii do not capture meaningful variation in LF density at the landscape scale. Moreover, multiscale information-theoretic analyses usually find smaller radii to be more predictive (e.g., 70 m; DeCesare et al. 2012), but such scales likely represent an organism's response to LFs in terms of proximity to a single LF rather than LF density per se. Within coarse-scale SSFs, we also assessed whether a functional response in LF selection was present by interacting a LF dummy variable (1, on LF; 0, off LF) with LF density (Moreau et al. 2012).

For both scales, we developed population-level inferences by averaging parameter estimates across individual bison, weighting each estimate by the inverse of its variance to give more weight to individuals with more precise estimates (Murtaugh 2007; Nielsen et al. 2009). We used bootstrapping to estimate 95% confidence intervals (CIs). We evaluated the performance of all final models using k -fold cross-validation for conditional logistic regression (Fortin et al. 2009). Briefly, this approach iteratively partitions the strata (matched observed and random steps) into five folds, using four folds to estimate SSFs and then generating predictions from model outputs for the withheld strata. Predictions are ranked within each stratum and rankings are tallied into bins across strata. We assessed the correlation between bin rank and the associated frequency of predictions by calculating Spearman rank coefficients for both observed (r_{S_Obs}) and random (r_{S_Ran}) steps. For the latter, we randomly selected one random step within each test stratum and excluded the observed step from stratum ranking, a process that yields an r_S based on random expectation. We repeated this process 30 times for each SSF with increasing model performance equating to higher \bar{r}_{S_Obs} relative to \bar{r}_{S_Ran} .

All analyses were performed in R version 3.4.0 (R Core Team 2017). To estimate conditional logistic regression models, we used the "coxph" function in the "survival" package (Therneau 2015). Models were validated using the "kfold" function in the "hab" package (Basille 2015).

Results

Analyses for the snow-free season used data from 33 individual female bison, resulting in a total of 97 169 observed steps following data screening procedures (89% of available time steps; mean (\pm SD) steps used per bison, 2945 \pm 1419; range, 720–5819). Among these steps, the mean number falling on a LF was 44 \pm 39 per bison (range, 8–150). In comparison, the mean number of random steps falling on a LF was 808 \pm 520 per bison (range, 134–2245). For snow-season analyses, only 31 individuals were available due to one collar failure and one mortality, resulting in a total of 114 137 observed steps (96% of available time steps; mean steps used per bison, 3682 \pm 1706; range, 1940–7488). During this season, the mean number of observed steps falling on a LF was 23 \pm 17 per bison (range, 3–66), whereas the mean number of random steps occurring on a LF was 655 \pm 348 per bison (range, 231–1233).

Fine-scale analyses

Bison showed limited response to LF age effects. Models without LF age were more parsimonious than those with age effects (\leq 2005 versus \geq 2006) for 26 out of 33 bison during the snow-free season and for 26 out of 31 bison during the snow season. We therefore do not consider LF age in subsequent models.

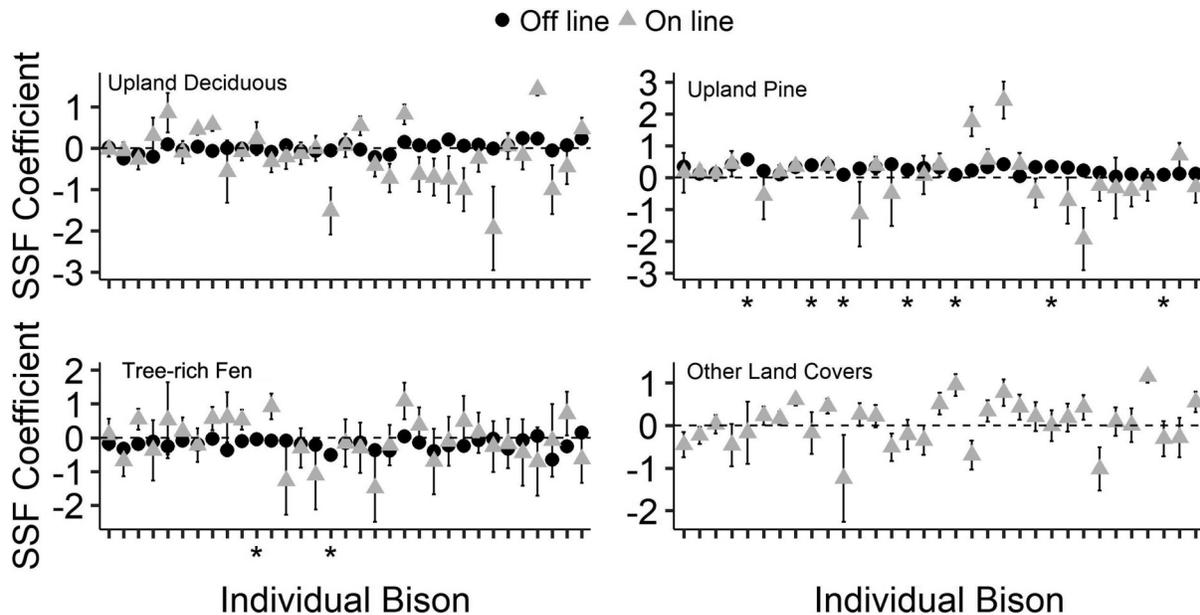
LFs also had limited influence on bison movement rate. For 19 out of 33 bison during the snow-free season, the addition of the interaction between step length and starting position (on LF vs. off LF) improved model fit (i.e., decreased QIC by >2; Arnold 2010), and for these individuals, LFs increased movement rate ($\beta = 0.0012$, 95% CI = [0.0010, 0.0014]), but the effect was small (<1% increase in speed). During the snow season, the step length \times starting position interaction improved model fit for 16 out of 31 bison; again, for these individuals, LFs appeared to slightly enhance movement rate ($\beta = 0.0020$, 95% CI = [0.0017, 0.0025]; effect size, <1% increase in speed). In subsequent analyses, we retained this movement interaction for all individuals where model fit was improved.

Analyses of bison response to human activity levels on LFs during the snow season were restricted to only four bison as all other bison did not have exposure (i.e., no data points in the observed or available samples) to areas where activity levels on LFs were known. Three of the four bison showed increased selection for inactive LFs relative to those with human activity (Supplementary material C¹). The fourth bison had only one observed step falling on a LF, which was an active one, but had available steps fall on both LF types ($n = 15$ active and 13 inactive). For this animal, these limited data resulted in selection of active LFs over inactive LFs, but the small sample size of observed and available steps suggests limited exposure of this individual to areas where human activity levels were known. Although the response of the three bison with more robust sample sizes (i.e., >15 observed steps and >150 available steps falling on active and inactive LFs) suggests relative avoidance of active LFs, inferences on bison response to human activity levels on LFs should be viewed cautiously because of the small number of bison used in this analysis.

Assessing bison response to interactions among LFs, land-cover type, and fire was restricted due to most individuals having minimal to no variation in the availability of burned and unburned LFs. The only three-way interaction considered was LF \times upland deciduous forest \times fire during the snow-free season. Because this interaction improved model fit in only 13 individuals (<40% of the sample), we excluded fire from final models used for population-level inferences.

Interactions between LF and land-cover type were similarly restricted by limited samples of observed and random steps for many individual bison. For the snow-free season, our final model considered explicit interactions between LFs and three forested land covers: upland deciduous, upland pine, and tree-rich fen (Fig. 2). We further assessed bison response to LFs collectively

Fig. 2. Fine-scale step selection function (SSF) coefficients (with standard error bars) representing the response of female wood bison (*Bison bison athabascae*) in Alberta, Canada, during the snow-free season to linear features situated in an upland deciduous forest (top left), upland pine forest (top right), tree-rich fens (bottom left), and linear features collectively situated in other land-cover types (bottom right). For upland pine and tree-rich fen, individual bison represented by an asterisk had linear feature coefficients that were inestimable (no observed or random locations on linear features). Coefficients represent selection (>0) or avoidance (<0) relative to the reference category of upland conifer.



situated in other land covers. Across individual bison, predictive performance of this model was generally good ($\bar{r}_{S,Obs} = 0.42$; $\bar{r}_{S,Ran} = -0.02$; mean difference = 0.44 ± 0.16 , range = [0.07, 0.77]). In general, bison marginally selected for LFs situated in upland deciduous forest (population-level β on LF = 0.21, 95% CI = [-0.07, 0.47]; population-level β off LF = -0.01, 95% CI = [-0.06, 0.04]), though this response was not consistent across all bison (number of individuals with positive β s = 11). Bison also showed selection for LFs collectively situated in other land covers (population-level $\beta = 0.29$, 95% CI = [0.07, 0.49]; number of individuals with positive coefficients = 19), and this interaction was the second-ranked land-cover type (Table 1). LFs appeared to be avoided when situated in the upland pine forest (on LF population-level $\beta = -2.42$, 95% CI = [-4.94, -0.65], number of individuals with positive coefficients = 15; off LF population-level $\beta = 0.25$, 95% CI = [0.20, 0.29]) and in tree-rich fens (on LF population-level $\beta = -2.50$, 95% CI = [-6.16, 0.27], number of individuals with positive coefficients = 13; off line population-level $\beta = -0.18$, 95% CI = [-0.23, -0.13]).

For the snow season, we only considered an explicit interaction between LFs and upland deciduous forest, as limited per-bison sample sizes prevented evaluating other LF \times land cover interactions (Fig. 3). This model also had good predictive performance across individual bison ($\bar{r}_{S,Obs} = 0.69$; $\bar{r}_{S,Ran} = -0.02$; mean difference = 0.70 ± 0.08 , range = [0.56, 0.85]). In contrast to the snow-free season, LFs in the upland deciduous forest appeared to be strongly avoided when snow was on the ground (population-level β on LF = -1.17, 95% CI = [-3.01, -0.18], number of individuals with positive coefficients = 4; population-level β off LF = -0.14, 95% CI = [-0.23, -0.04]). For LFs collectively situated in other land covers, bison selected LFs at rates similar to those in upland conifers (the reference category).

Coarse-scale analyses

Bison response to LF density depended on the season (Fig. 4). In the snow season, bison showed selection for areas with increasing LF density, though the effect size was small (population-level $\beta = 0.05$, 95% CI = [0.02, 0.08]). In the snow-free season, bison were

generally ambivalent to LF density (population-level $\beta = -0.01$, 95% CI = [-0.04, 0.01]). In both seasons, a functional response in LF selection was not evident, as only one out of 33 bison during the snow-free season had the LF \times LF density interaction term included in its top model, and this term was excluded from all top models during the snow season. In general, coarse-scale models estimated during the snow season had better predictive performance ($\bar{r}_{S,Obs} = 0.54$; $\bar{r}_{S,Ran} = 0.00$; mean difference = 0.54 ± 0.13 , range = [0.19, 0.80]) than those estimated during the snow-free season ($\bar{r}_{S,Obs} = 0.21$; $\bar{r}_{S,Ran} = -0.03$; mean difference = 0.24 ± 0.11 , range = [-0.03, 0.42]).

Discussion

With the global network of human-created linear features continuing to increase (Laurance and Arrea 2017), understanding species responses to these features has become a conservation focus in multi-use landscapes. Across taxa, human-created LFs are known to influence animal space use and movement behaviour, yet the relative strength and direction (positive or negative) of responses can vary even among species of the same guild, often being context-specific and dependent on species-specific traits and behavioural plasticity (Fahrig and Rytwinski 2009; Fisher and Burton 2018). We demonstrated such variation as the responses of wood bison to LFs differed from those reported elsewhere for boreal caribou, two threatened ungulate species occurring sympatrically within boreal forests of western Canada. In contrast to boreal caribou, which generally avoid LFs (Dyer et al. 2001; Mumma et al. 2017; DeMars and Boutin 2018), wood bison were somewhat ambivalent to LFs, showing weak and variable selection or avoidance of LFs depending on land-cover type and weak seasonal selection for areas with increased LF density. These differences suggest that LFs may have a lower impact on habitat quality for bison than for caribou.

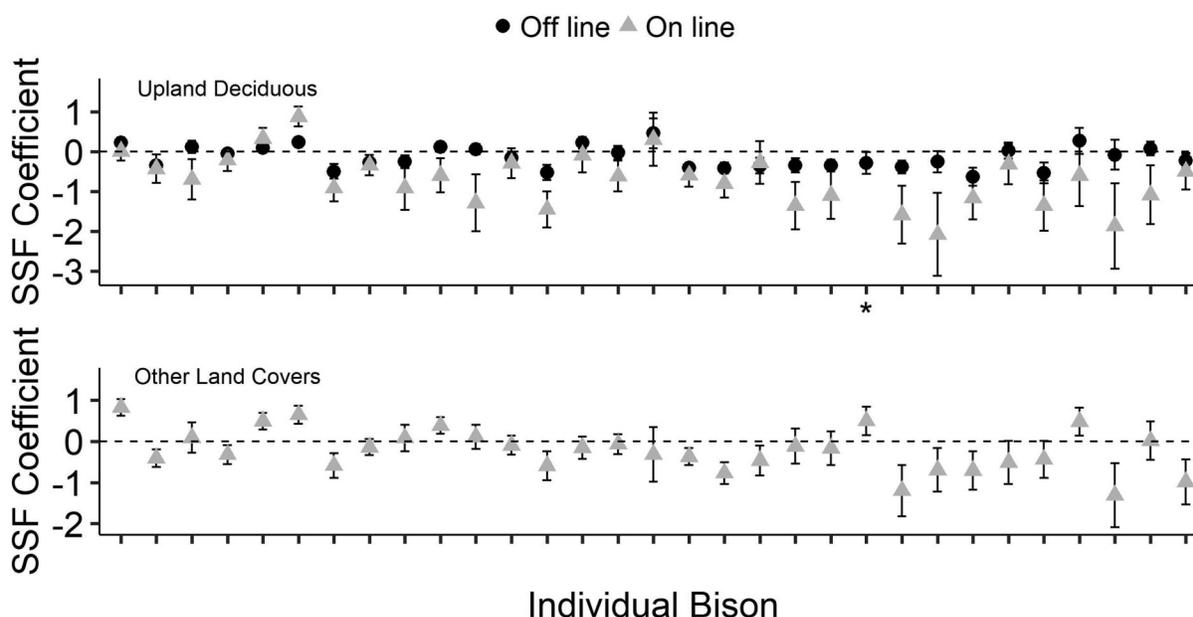
Among the three hypotheses considered for explaining bison responses, the movement efficiency hypothesis appeared to have the most support. In both seasons, bison appeared to move

Table 1. Parameter estimate (β) and 95% confidence interval (CI) for land-cover types used in fine-scale step selection functions to evaluate the response of female wood bison (*Bison bison athabasca*) to linear features (LF) during the snow-free and snow seasons in Alberta, Canada.

Snow-free season			Snow season		
Land-cover type	β	95% CI	Land-cover type	β	95% CI
Meadow marsh	0.35	0.27, 0.43	Meadow marsh	0.64	0.55, 0.72
LF in other land covers	0.29	0.07, 0.49	Graminoid-rich fen	0.37	0.23, 0.52
Emergent marsh	0.25	0.16, 0.34	Shrub swamp	0.34	0.24, 0.45
Upland pine	0.25	0.20, 0.29	Emergent marsh	0.34	0.23, 0.44
LF in upland deciduous	0.21	-0.07, 0.47	Hardwood swamp	0.27	0.13, 0.40
Shrub swamp	0.13	0.03, 0.22	Open water	0.23	0.09, 0.34
Hardwood swamp	0.04	-0.08, 0.14	Upland pine	0.19	0.04, 0.33
Conifer swamp	0.00	-0.06, 0.05	Shrub-poor fen	0.17	0.07, 0.26
Upland deciduous	-0.01	-0.06, 0.04	Graminoid-poor fen	0.12	0.02, 0.22
Graminoid-poor fen	-0.09	-0.19, 0.02	Tree-rich fen	0.08	-0.01, 0.18
Tree-poor fen	-0.12	-0.19, -0.06	Shrub-rich fen	0.05	-0.07, 0.17
Open water	-0.13	-0.21, -0.05	Tree-poor fen	-0.02	-0.12, 0.07
Shrub-poor fen	-0.15	-0.29, -0.04	LF in other land covers	-0.04	-0.24, 0.17
Shrub-rich fen	-0.16	-0.31, -0.02	Upland deciduous	-0.14	-0.23, -0.04
Tree-rich fen	-0.18	-0.23, -0.13	Shrubby bog	-0.29	-1.01, 0.12
Graminoid-rich fen	-0.58	-1.86, 0.04	Conifer swamp	-0.47	-0.63, -0.34
Upland mixedwood	-0.75	-2.37, 0.08	Mixedwood swamp	-0.82	-2.51, 0.04
Shrubby bog	-1.08	-2.78, -0.31	Cut block	-0.90	-9.16, -0.38
Tamarack swamp	-1.46	-3.20, -0.27	LF in upland deciduous	-1.17	-3.01, -0.18
Treed bog	-1.66	-4.43, -0.18	Upland mixedwood	-3.32	-7.35, -0.25
LF in upland pine	-2.42	-4.94, -0.65	Treed bog	-3.88	-6.97, -1.22
LF in tree-rich fen	-2.50	-6.16, 0.27	Tamarack swamp	-4.27	-7.52, -1.17
Mixedwood swamp	-3.69	-6.66, -0.88	Anthropogenic	-7.05	-11.00, -2.33
Cut block	-7.22	-11.52, -3.16	Aquatic bed	-7.19	-10.19, -4.00
Anthropogenic	-9.54	-12.10, -6.73			
Aquatic bed	-9.78	-11.77, -6.49			

Note: Parameter estimates for each season are presented from highest to lowest. All variables are categorical with the reference category being upland conifer forest.

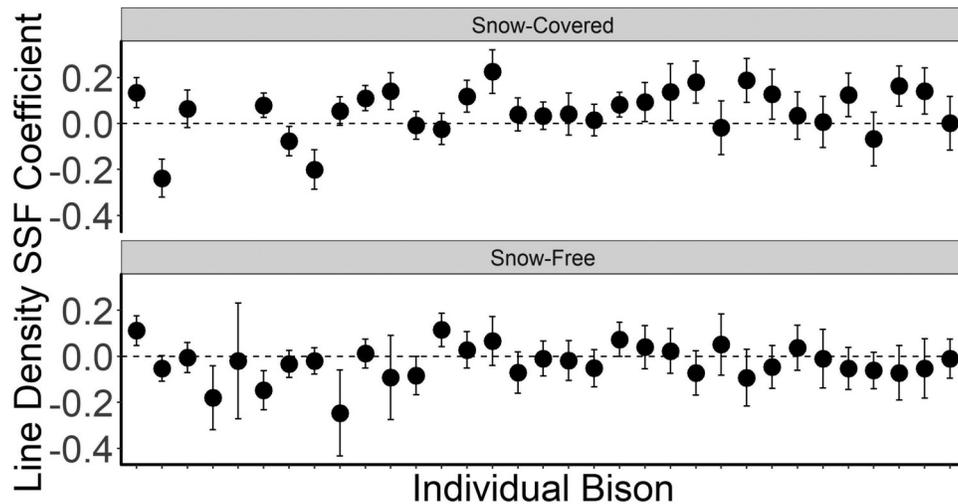
Fig. 3. Fine-scale step selection function (SSF) coefficients (with standard error bars) representing the response of female wood bison (*Bison bison athabasca*) in Alberta, Canada, during the snow season to linear features situated in upland deciduous forest (top) and linear features collectively situated in other land-cover types (bottom). For one bison (*), the coefficient for linear features in upland deciduous forest was inestimable (no observed or random locations on linear features). Coefficients represent selection (>0) or avoidance (<0) relative to the reference category of upland conifer.



slightly faster on LFs, though this response was not consistent across all individuals, particularly during the snow season. This increase in movement rate does suggest that bison may be using LFs to travel among feeding patches and (or) resting areas

(Bruggeman et al. 2007; Fortin et al. 2009). Increased movement efficiency on LFs has been documented primarily for canids (Zimmermann et al. 2014; Dickie et al. 2017b) and has rarely been reported for ungulates (c.f. Serrouya et al. 2017), with the majority

Fig. 4. Coarse-scale step selection function (SSF) coefficients (with standard error bars) representing the seasonal response of female wood bison (*Bison bison athabascae*) in Alberta, Canada, to linear feature (line) density (km-km⁻²) measured in a moving window analysis with a radius of 500 m.



of ungulate studies reporting either LF avoidance or increased movement rates when crossing LFs (e.g., Nagy 2011; Leblond et al. 2013; Prokopenko et al. 2017; Wyckoff et al. 2018). Bison, however, are known to establish trail networks for travelling (Dancose et al. 2011), and LFs such as seismic lines and secondary roads likely provide efficient travel routes for bison moving through forested systems.

Although the estimated effect of LFs on bison movement rate was small (<1%), especially when compared with LF effects on wolf movement rates (e.g., >1.25–2 times faster on LFs; Dickie et al. 2017b), the coarse sampling rate of the GPS collars (every 90 min) likely underestimates the actual effect size (Rowcliffe et al. 2012). In our modelling framework, we considered a movement step to be affected by a LF when the starting location was on a LF (Avgar et al. 2016). Because the step duration was 90 min, few steps had their start and end locations falling on a LF (summer = 14, winter = 310), and thus the actual time and distance spent travelling on LFs during this period were unknown (Serrouya et al. 2017). In the future, obtaining better estimates (i.e., less biased) of LF effects on bison movement rates will require deploying GPS collars programmed with higher sampling frequencies (e.g., every 5 min; Dickie et al. 2017b).

With bison showing only weak fine-scale selection for LFs and tending to move slightly faster when on them, the forage availability hypothesis was generally unsupported. Although other studies have shown increased abundances of forbs, graminoids, and shrubs on LFs compared with the adjacent forest (Finnegan et al. 2018), the absolute abundance of preferred forage species (e.g., sedges and willows; Larter and Gates 1991; Jung 2015) on LFs may be small compared with other more profitable foraging areas (e.g., large meadows of wet sedge or willow savannas), resulting in bison using LFs more for travelling than as sustained foraging areas. This contrast, however, may not be true when considering major road corridors. In northeastern British Columbia, Canada, Leverkus (2011) reported high use of the Alaskan Highway corridor by wood bison of the Nordquist population. This corridor is much wider than the majority of LFs in our study area (e.g., average seismic line width < 8 m; Pattison et al. 2016) and the wide right-of-way associated with primary highways such as the Alaska Highway are known to have high abundances of early seral vegetation and (or) exotic forage species with high nutritional value, making these areas attractive to ungulates (Rea 2003; T. Jung, personal communication).

The third hypothesis considered — that the increased predation risk associated with LFs will result in bison avoidance — was also unsupported. By showing weak selection or ambivalence to LFs, bison behaviour differed from those reported for other ungulates occurring within western Canadian boreal forests, and these differences likely result from how LFs interact with species-specific predation risk. For ungulates, LFs are thought to increase predation risk because they are highly used by wolves (Dickie et al. 2017b; DeMars and Boutin 2018), the primary predator of ungulates in this system. Among boreal ungulates, wood bison are likely the hardest for wolves to kill, particularly prime-aged adults (Carbyn and Trottier 1987; Jung 2011; Mech et al. 2015); consequently, in multiprey systems, bison are not generally preferred prey for wolves (Smith et al. 2000). Indeed, in our system, the primary prey of wolves are moose (Fuller and Keith 1980). Because of this relatively low vulnerability to predation, bison selection for LFs likely represents minimal increase in predation risk and any such increase may be outweighed by the enhanced movement efficiency that LFs may provide. For other boreal ungulates, relatively higher vulnerability to wolf predation has likely factored into their reported avoidance of LFs. For example, boreal caribou are relatively easy to kill for wolves once encountered (Haber 1977), resulting in caribou adopting spatial behaviours to avoid predator encounters (James et al. 2004), which likely includes avoiding LFs (Dyer et al. 2001; Mumma et al. 2017; DeMars and Boutin 2018). Moose have also shown avoidance of LFs, although not as strongly as caribou (Fisher and Burton 2018; Mumma et al. 2018), suggesting that moose vulnerability to predation is intermediate to that of bison and caribou.

Although LFs may not represent increased predation risk for bison (but see later for further discussion), these features may still increase mortality risk by providing human access to bison habitat and increasing hunting pressure. Prior to 2016, the Ronald Lake population was believed to be in decline from overharvesting due to unregulated hunting; consequently, in March 2016, the population was granted “subject animal” status under Alberta’s Wildlife Act, and non-indigenous hunting was subsequently closed (Environment and Climate Change Canada 2018b). Ungulate avoidance of LFs due to hunting pressure has been well-documented (Laurance et al. 2006; Paton et al. 2017), and we attempted to evaluate whether human activity — as a surrogate of past and (or) current hunting pressures — modified bison response to LFs. The small number of individuals exposed to active

LFs prevented a robust evaluation of this relationship, and thus, our results should be viewed as exploratory. Nevertheless, our results do suggest that Ronald Lake bison are sensitive to human activity (Supplementary material C¹). Their apparent avoidance behaviour contrasts with the Nordquist population's tolerance of a relatively high traffic volumes along the Alaska Highway, a difference likely reflecting lower hunting pressure on the Nordquist population (Leverkus 2011; Environment and Climate Change Canada 2018b). Because ungulates have been shown to modify their behaviour in response to spatiotemporal variation in hunting pressure (Thurfjell et al. 2017), the recent reduction in hunting pressure on Ronald Lake bison could lead to a future attenuation of their apparent avoidance behaviour.

Conservation implications

Native biota can be negatively affected by LFs from direct and indirect mechanisms, and the relative magnitude of these mechanisms will likely influence conservation strategies. Direct mechanisms such as LF avoidance can result in a functional loss of habitat (Dyer et al. 2001), which our findings suggest is not the case for wood bison although human activity on LFs may modify their response. With industrial activity potentially expanding within the range of the Ronald Lake population (Environment and Climate Change Canada 2018b), further investigation is warranted to understand how human activity interacts with LFs to influence the spatial behaviour and demography of wood bison. We also recognize that animal responses to LFs can vary depending on LF type (e.g., roads versus seismic lines; Dickie et al. 2017b), structural characteristics (e.g., width and (or) sinuosity; Tigner et al. 2014), and the state of vegetation recovery (Dickie et al. 2017a). We could not evaluate for such effects due to limitations in data availability and the small spatial extent of non-seismic LFs; however, determining the relative impact of these potential effects could warrant further research, particularly if the extent of non-seismic LFs increases.

Although habitat loss is commonly considered one of the more detrimental outcomes from human disturbances (Fahrig 2003), indirect effects from LFs such as increasing predation can have larger demographic effects than habitat loss per se (Wittmer et al. 2005). Ultimately, for a threatened species such as wood bison, effective conservation strategies will be best informed by understanding how LFs affect demography. Earlier in this paper, we suggested that bison selection for LFs may indicate minimally increased mortality risk, but we did not have survival data to explicitly assess the potential for demographic impacts. Such an assessment is necessary to ensure that LFs do not function as an ecological trap (Lamb et al. 2017; Serrouya et al. 2017) for bison. From a conservation perspective, understanding such habitat-performance relationships will be necessary to define critical habitat for wood bison, which is a stated objective within the recently released federal recovery strategy (Environment and Climate Change Canada 2018b). By providing an initial evaluation of bison spatial responses to LFs, which are an ubiquitous form of disturbance in boreal forests, we suggest that results from our study are an important first, but not final, step toward achieving such understanding.

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References

- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *J. Wildl. Manage.* **74**(6): 1175–1178. doi:10.2193/2009-367.
- Avgar, T., Potts, J.R., Lewis, M.A., and Boyce, M.S. 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods Ecol. Evol.* **7**(5): 619–630. doi:10.1111/2041-210X.12528.
- Ball, M.C., Fulton, T.L., and Wilson, G.A. 2016. Genetic analyses of wild bison in Alberta, Canada: implications for recovery and disease management. *J. Mammal.* **97**(6): 1525–1534. doi:10.1093/jmammal/gyw110.
- Basille, M. 2015. hab: Habitat and movement functions. R package version 1.20.4. Available from <http://ase-research.org/basille/hab>.
- Bjørneraas, K., Van Moorter, B., Rolandsen, C.M., and Herfindal, I. 2010. Screening global positioning system location data for errors using animal movement characteristics. *J. Wildl. Manage.* **74**(6): 1361–1366. doi:10.2193/2009-405.
- Bonnot, N., Morellet, N., Verheyden, H., Cargnelutti, B., Lourtet, B., Klein, F., and Hewison, A.J.M. 2013. Habitat use under predation risk: hunting, roads and human dwellings influence the spatial behaviour of roe deer. *Eur. J. Wildl. Res.* **59**(2): 185–193. doi:10.1007/s10344-012-0665-8.
- Boutin, S., and Arienti, C. 2008. BCC equation reanalysis — final report. Athabasca Landscape Team, Edmonton, Alta.
- Bruggeman, J.E., Garrott, R.A., White, P.J., Watson, F.G., and Wallen, R. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecol. Appl.* **17**(5): 1411–1423. doi:10.1890/06-0196.1. PMID: 17708218.
- Caraco, T., Martindale, S., and Whittam, T.S. 1980. An empirical demonstration of risk-sensitive foraging preferences. *Anim. Behav.* **28**(3): 820–830. doi:10.1016/S0003-3472(80)80142-4.
- Carbyn, L.N., and Trottier, T. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Can. J. Zool.* **65**(8): 2072–2078. doi:10.1139/z87-317.
- Caro, T., and Sherman, P.W. 2011. Endangered species and a threatened discipline: behavioural ecology. *Trends Ecol. Evol.* **26**(3): 111–118. doi:10.1016/j.tree.2010.12.008. PMID:21257224.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). 2013. COSEWIC assessment and status report on the Plains Bison *Bison bison* and the Wood Bison *Bison bison athabasca* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Ont.
- Craiu, R.V., Duchesne, T., and Fortin, D. 2008. Inference methods for the conditional logistic regression model with longitudinal data. *Biom. J.* **50**(1): 97–109. doi:10.1002/bimj.200610379. PMID:17849385.
- Dabros, A., Pyper, M., and Castilla, G. 2018. Seismic lines in the boreal and arctic ecosystems of North America: environmental impacts, challenges, and opportunities. *Environ. Rev.* **26**(2): 214–229. doi:10.1139/er-2017-0080.
- Dancose, K., Fortin, D., and Guo, X. 2011. Mechanisms of functional connectivity: the case of free-ranging bison in a forest landscape. *Ecol. Appl.* **21**(5): 1871–1885. doi:10.1890/10-0779.1. PMID:21830725.
- Dawe, K.L., Bayne, E.M., and Boutin, S. 2014. Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. *Can. J. Zool.* **92**(4): 353–363. doi:10.1139/cjz-2013-0262.
- DeCesare, N.J., Hebblewhite, M., Schmiegelow, F., Hervieux, D., McDermid, G.J., Neufeld, L., et al. 2012. Transcending scale dependence in identifying habitat with resource selection functions. *Ecol. Appl.* **22**(4): 1068–1083. doi:10.1890/11-1610.1. PMID:22827119.
- DeGregorio, B.A., Weatherhead, P.J., and Sperry, J.H. 2014. Power lines, roads, and avian nest survival: effects on predator identity and predation intensity. *Ecol. Evol.* **4**(9): 1589–1600. doi:10.1002/ece3.1049. PMID:24967077.
- DeMars, C.A., and Boutin, S. 2018. Nowhere to hide: effects of linear features on predator-prey dynamics in a large mammal system. *J. Anim. Ecol.* **87**(1): 274–284. doi:10.1111/1365-2656.12760. PMID:28940254.
- Dickie, M., Serrouya, R., DeMars, C., Cranston, J., and Boutin, S. 2017a. Evaluating functional recovery of habitat for threatened woodland caribou. *Ecosphere*, **8**(9): e01936. doi:10.1002/ecs2.1936.
- Dickie, M., Serrouya, R., McNay, R.S., and Boutin, S. 2017b. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* **54**(1): 253–263. doi:10.1111/1365-2664.12732.
- Doncaster, C.P., Rondinini, C., and Johnson, P.C.D. 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *J. Anim. Ecol.* **70**(1): 33–46. doi:10.1046/j.1365-2656.2001.00471.x.
- Doney, E.D., Bath, A.J., and Vaske, J.J. 2018. Understanding conflict and consensus regarding wood bison management in Alaska, USA. *Wildl. Res.* **45**: 229–236. doi:10.1071/WR17056.
- Dyer, S.J., O'Neill, J.P., Wasel, S.M., and Boutin, S. 2001. Avoidance of industrial development by woodland caribou. *J. Wildl. Manage.* **65**(3): 531–542. doi:10.2307/3803106.

- Environment Canada. 2012. Recovery strategy for the woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Environment Canada, Ottawa, Ont.
- Environment and Climate Change Canada. 2018a. Almanac averages and extremes. Available from http://climate.weather.gc.ca/climate_data/almanac_selection_e.html.
- Environment and Climate Change Canada. 2018b. Recovery strategy for the wood bison (*Bison bison athabasca*) in Canada. Environment and Climate Change Canada, Ottawa, Ont. Available from http://publications.gc.ca/collections/collection_2018/eccc/En3-4-294-2018-eng.pdf.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**(1): 487–515. doi:10.1146/annurev.ecolsys.34.011802.132419.
- Fahrig, L., and Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecol. Soc.* **14**(1): 21.
- Finnegan, L., MacNearney, D., and Pigeon, K.E. 2018. Divergent patterns of understory forage growth after seismic line exploration: implications for caribou habitat restoration. *For. Ecol. Manage.* **409**: 634–652. doi:10.1016/j.foreco.2017.12.010.
- Fischer, J., and Lindenmayer, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* **16**(3): 265–280. doi:10.1111/j.1466-8238.2007.00287.x.
- Fisher, J.T., and Burton, A.C. 2018. Wildlife winners and losers in an oil sands landscape. *Front. Ecol. Environ.* **16**(6): 323–328. doi:10.1002/fee.1807.
- Forester, J.D., Im, H.K., and Rathouz, P.J. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology*, **90**(12): 3554–3565. doi:10.1890/08-0874.1. PMID:20120822.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., and Mao, J.S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, **86**(5): 1320–1330.
- Fortin, D., Fortin, M.-E., Beyer, H.L., Duchesne, T., Courant, S., and Dancose, K. 2009. Group-size-mediated habitat selection and group fusion-fission dynamics of bison under predation risk. *Ecology*, **90**(9): 2480–2490. doi:10.1890/08-0345.1. PMID:19769126.
- Fuller, T.K., and Keith, L.B. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. *J. Wildl. Manage.* **44**(3): 583–602. doi:10.2307/3808006.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., and Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu. Rev. Ecol. Syst.* **31**: 367–393. doi:10.1146/annurev.ecolsys.31.1.367.
- Government of Alberta. 2013. Ronald Lake Bison (*Bison bison*) winter 2012–2013 activities progress report (final). Government of Alberta, Edmonton, Alta.
- Government of Alberta. 2017. Historical wildfire perimeter data: 1931–2017. Available from <http://wildfire.alberta.ca/resources/historical-data/spatial-wildfire-data.aspx>.
- Haber, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. University of British Columbia, Vancouver, B.C.
- Hendry, A.P., Gotanda, K.M., and Svensson, E.I. 2017. Human influences on evolution, and the ecological and societal consequences. *Philos. Trans. R. Soc. B Biol. Sci.* **372**(1712): 20160028. doi:10.1098/rstb.2016.0028.
- James, A.R., Boutin, S., Hebert, D.M., and Rippin, A.B. 2004. Spatial separation of caribou from moose and its relation to predation by wolves. *J. Wildl. Manage.* **68**(4): 799–809. doi:10.2193/0022-541X(2004)068[0799:SSOCFM]2.0.CO;2.
- Jung, T.S. 2011. Gray wolf (*Canis lupus*) predation and scavenging of reintroduced American bison (*Bison bison*) in southwestern Yukon. *Northwest. Nat.* **92**(2): 126–130. doi:10.1898/10-07.1.
- Jung, T.S. 2015. Winter diets of reintroduced bison (*Bison bison*) in northwestern Canada. *Mamm. Res.* **60**(4): 385–391. doi:10.1007/s13364-015-0240-2.
- Jung, T.S. 2017. Extralimital movements of reintroduced bison (*Bison bison*): implications for potential range expansion and human–wildlife conflict. *Eur. J. Wildl. Res.* **63**(2): 35. doi:10.1007/s10344-017-1094-5.
- Jung, T.S., and Larter, N.C. 2018. Observations of long-distance post-release dispersal by reintroduced bison (*Bison bison*). *Can. Field-Nat.* **131**(3): 221. doi:10.22621/cfn.v131i3.1825.
- Jung, T.S., Stotyn, S.A., and Czetwertynski, S.M. 2015. Dietary overlap and potential competition in a dynamic ungulate community in Northwestern Canada. *J. Wildl. Manage.* **79**(8): 1277–1285. doi:10.1002/jwmg.946.
- Jung, T.S., Konkolics, S.M., Kukka, P.M., Majchrzak, Y.N., Menzies, A.K., Oakley, M.P., Peers, M.J.L., and Studd, E.K. 2019. Short-term effect of helicopter-based capture on movements of a social ungulate. *J. Wildl. Manage.* **83**(4): 830–837. doi:10.1002/jwmg.21640.
- Lamb, C.T., Mowat, G., McLellan, B.N., Nielsen, S.E., and Boutin, S. 2017. Forbidden fruit: human settlement and abundant fruit create an ecological trap for an apex omnivore. *J. Anim. Ecol.* **86**(1): 55–65. doi:10.1111/1365-2656.12589. PMID:27677529.
- Larsen, C.P.S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. *J. Biogeogr.* **24**(5): 663–673. doi:10.1111/j.1365-2699.1997.tb00076.x.
- Larter, N.C., and Gates, C.C. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. *Can. J. Zool.* **69**(10): 2677–2685. doi:10.1139/z91-376.
- Latham, A.D.M., Latham, M.C., Boyce, M.S., and Boutin, S. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecol. Appl.* **21**(8): 2854–2865. doi:10.1890/11-0666.1.
- Latombe, G., Fortin, D., and Parrott, L. 2014. Spatio-temporal dynamics in the response of woodland caribou and moose to the passage of grey wolf. *J. Anim. Ecol.* **83**(1): 185–198. doi:10.1111/1365-2656.12108. PMID:23859231.
- Laurance, W.F., and Arrea, I.B. 2017. Roads to riches or ruin? *Science*, **358**(6362): 442–444. doi:10.1126/science.aao0312. PMID:29074751.
- Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P., and Ondzeano, C. 2006. Impacts of roads and hunting on Central African rainforest mammals. *Conserv. Biol.* **20**(4): 1251–1261. doi:10.1111/j.1523-1739.2006.00420.x. PMID:16922241.
- Leblond, M., Dussault, C., and Ouellet, J.-P. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity: avoidance of roads and disturbance intensity. *J. Zool. (Lond.)*, **289**(1): 32–40. doi:10.1111/j.1469-7998.2012.00959.x.
- Leverkus, S. 2011. Wood bison in north east British Columbia. BC Ministry of Forests, Lands and Natural Resource Operations, Fort St. John, B.C.
- Leverkus, S.E.R. 2015. Conservation of biodiversity in northern Canada through ecological processes and cultural landscapes. Ph.D. thesis, Oklahoma State University, Stillwater, Okla.
- Lewis, J.S., Rachlow, J.L., Garton, E.O., and Vierling, L.A. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. *J. Appl. Ecol.* **44**(3): 663–671. doi:10.1111/j.1365-2664.2007.01286.x.
- McKenzie, H.W., Jerde, C.L., Visscher, D.R., Merrill, E.H., and Lewis, M.A. 2009. Inferring linear feature use in the presence of GPS measurement error. *Environ. Ecol. Stat.* **16**(4): 531–546. doi:10.1007/s10651-008-0095-7.
- Mech, L.D., Smith, D.W., and MacNulty, D.R. 2015. Wolves on the hunt: the behavior of wolves hunting wild prey. The University of Chicago Press, Chicago, Ill.
- Mitchell, J.A., and Gates, C.C. 2002. Status of the wood bison (*Bison bison athabasca*) in Alberta. Alberta Sustainable Resource Development, Fish and Wildlife Division and Alberta Conservation Association, Edmonton, Alta.
- Moreau, G., Fortin, D., Couturier, S., and Duchesne, T. 2012. Multi-level functional responses for wildlife conservation: the case of threatened caribou in managed boreal forests. *J. Appl. Ecol.* **49**(3): 611–620. doi:10.1111/j.1365-2664.2012.02134.x.
- Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. 2011. Human activity helps prey win the predator–prey space race. *PLoS ONE*, **6**(3): e17050. doi:10.1371/journal.pone.0017050. PMID:21399682.
- Mumma, M.A., Gillingham, M.P., Johnson, C.J., and Parker, K.L. 2017. Understanding predation risk and individual variation in risk avoidance for threatened boreal caribou. *Ecol. Evol.* **7**(23): 10266–10277. doi:10.1002/ece3.3563. PMID:29238553.
- Mumma, M.A., Gillingham, M.P., Parker, K.L., Johnson, C.J., and Watters, M. 2018. Predation risk for boreal woodland caribou in human-modified landscapes: evidence of wolf spatial responses independent of apparent competition. *Biol. Conserv.* **228**: 215–223. doi:10.1016/j.biocon.2018.09.015.
- Murtaugh, P.A. 2007. Simplicity and complexity in ecological data analysis. *Ecology*, **88**(1): 56–62. doi:10.1890/0012-9658(2007)88[56:SACIED]2.0.CO;2. PMID:17489454.
- Nagy, J.A. 2011. Use of space by caribou in northern Canada. University of Alberta, Edmonton, Alta.
- Natural Resources Canada. 2013. Canadian digital elevation model. Edition 1.1. Government of Canada, Natural Resources Canada, Canada Centre for Mapping and Earth Observation, Sherbrooke, QC, Canada. Available from <https://www.nrcan.gc.ca/science-and-data/science-and-research/earth-sciences/geography/topographic-information/download-directory-documentation/17215>.
- Nielsen, S.E., Cranston, J., and Stenhouse, G.B. 2009. Identification of priority areas for grizzly bear conservation and recovery in Alberta, Canada. *J. Conserv. Plan.* **5**: 38–60.
- Northrup, J.M., Hooten, M.B., Anderson, C.R., Jr., and Wittemyer, G. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. *Ecology*, **94**(7): 1456–1463. doi:10.1890/12-1688.1. PMID:23951705.
- Oliveira-Santos, L.G.R., Forester, J.D., Piovezan, U., Tomas, W.M., and Fernandez, F.A.S. 2016. Incorporating animal spatial memory in step selection functions. *J. Anim. Ecol.* **85**(2): 516–524. doi:10.1111/1365-2656.12485. PMID:26714244.
- Paton, D.G., Ciuti, S., Quinn, M., and Boyce, M.S. 2017. Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. *Ecosphere*, **8**(6): e01841. doi:10.1002/ecs2.1841.
- Pattison, C.A., Quinn, M.S., Dale, P., and Catterall, C.P. 2016. The landscape impact of linear seismic clearings for oil and gas development in boreal forest. *Northwest Sci.* **90**(3): 340–354. doi:10.3955/046.090.0312.
- Prokopenko, C.M., Boyce, M.S., and Avgar, T. 2017. Characterizing wildlife behavioural responses to roads using integrated step selection analysis. *J. Appl. Ecol.* **54**(2): 470–479. doi:10.1111/1365-2664.12768.
- R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rea, R.V. 2003. Modifying roadside vegetation management practices to reduce

- vehicular collisions with moose *Alces alces*. *Wildl. Biol.* **9**(1): 81–91. doi:10.2981/wlb.2003.030.
- Riva, F., Acorn, J.H., and Nielsen, S.E. 2018. Narrow anthropogenic corridors direct the movement of a generalist boreal butterfly. *Biol. Lett.* **14**(2): 20170770. doi:10.1098/rsbl.2017.0770. PMID:29491029.
- Roberts, D., Ciuti, S., Barber, Q.E., Willier, C., and Nielsen, S.E. 2018. Accelerated seed dispersal along linear disturbances in the Canadian oil sands region. *Sci. Rep.* **8**: 4828. doi:10.1038/s41598-018-22678-y. PMID:29555925.
- Rowcliffe, J.M., Carbone, C., Kays, R., Kranstauber, B., and Jansen, P.A. 2012. Bias in estimating animal travel distance: the effect of sampling frequency. *Methods Ecol. Evol.* **3**(4): 653–662. doi:10.1111/j.2041-210X.2012.00197.x.
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., and Hicke, J.A. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* **53**(1): 120–129. doi:10.1111/1365-2664.12511. PMID:26966320.
- Serrouya, R., Kellner, A., Pavan, G., Lewis, D.W., DeMars, C.A., and McLellan, B.N. 2017. Time vs. distance: alternate metrics of animal resource selection provide opposing inference. *Ecosphere*, **8**(3): e01730. doi:10.1002/ecs2.1730.
- Shury, T.K., Nishi, J.S., Elkin, B.T., and Wobeser, G.A. 2015. Tuberculosis and brucellosis in wood bison (*Bison bison athabascae*) in northern Canada: a renewed need to develop options for future management. *J. Wildl. Dis.* **51**(3): 543–554. doi:10.7589/2014-06-167. PMID:25973624.
- Sih, A. 1984. The behavioral response race between predator and prey. *Am. Nat.* **123**(1): 143–150. doi:10.1086/284193.
- Sih, A., Ferrari, M.C.O., and Harris, D.J. 2011. Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* **4**(2): 367–387. doi:10.1111/j.1752-4571.2010.00166.x. PMID:25567979.
- Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Phillips, M.K., and Mack, J.A. 2000. Wolf–bison interactions in Yellowstone National Park. *J. Mammal.* **81**(4): 1128–1135. doi:10.1644/1545-1542(2000)081<1128:WBIIYN>2.0.CO;2.
- Strong, W.L., and Gates, C.C. 2009. Wood bison population recovery and forage availability in northwestern Canada. *J. Environ. Manage.* **90**(1): 434–440. doi:10.1016/j.jenvman.2007.11.002. PMID:18191321.
- Therneau, T.M. 2015. A package for survival analysis in S. Version 2.38. Available from <http://CRAN.R-project.org/package=survival>.
- Thiessen, C. 2009. Peace region boreal caribou monitoring: annual report 2008–09. British Columbia Ministry of Environment, Fort St. John, B.C.
- Thurfjell, H., Ciuti, S., and Boyce, M.S. 2014. Applications of step-selection functions in ecology and conservation. *Mov. Ecol.* **2**(1): 4.
- Thurfjell, H., Ciuti, S., and Boyce, M.S. 2017. Learning from the mistakes of others: how female elk (*Cervus elaphus*) adjust behaviour with age to avoid hunters. *PLoS ONE*, **12**(6): e0178082. doi:10.1371/journal.pone.0178082. PMID:28614406.
- Tigner, J., Bayne, E.M., and Boutin, S. 2014. Black bear use of seismic lines in Northern Canada. *J. Wildl. Manage.* **78**(2): 282–292. doi:10.1002/jwmg.664.
- Venier, L.A., Thompson, I.D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J.A., et al. 2014. Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environ. Rev.* **22**(4): 457–490. doi:10.1139/er-2013-0075.
- Whittington, J., Hebblewhite, M., DeCesare, N.J., Neufeld, L., Bradley, M., Wilmshurst, J., and Musiani, M. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *J. Appl. Ecol.* **48**(6): 1535–1542. doi:10.1111/j.1365-2664.2011.02043.x.
- Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, **144**(2): 257–267. doi:10.1007/s00442-005-0055-y. PMID:15891849.
- Wong, B.B.M., and Candolin, U. 2015. Behavioral responses to changing environments. *Behav. Ecol.* **26**(3): 665–673. doi:10.1093/beheco/aru183.
- Wyckoff, T.B., Sawyer, H., Albeke, S.E., Garman, S.L., and Kauffman, M.J. 2018. Evaluating the influence of energy and residential development on the migratory behavior of mule deer. *Ecosphere*, **9**(2): e02113. doi:10.1002/ecs2.2113.
- Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., and Liberg, O. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav. Ecol.* **25**(6): 1353–1364. doi:10.1093/beheco/aru134. PMID:25419085.