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NOWHERE TO HIDE: EFFECTS OF LINEAR FEATURES ON PREDATOR-PREY DYNAMICS IN A LARGE MAMMAL SYSTEM

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ABSTRACT

1. Rapid landscape alteration associated with human activity is currently challenging the evolved dynamical stability of many predator-prey systems by forcing species to behaviorally respond to novel environmental stimuli.

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2. In many forested systems, linear features (LFs) such as roads, pipelines and resource exploration lines (i.e. seismic lines) are a ubiquitous form of landscape alteration that have been implicated in altering predator-prey dynamics. One hypothesized effect is that LFs facilitate predator movement into and within prey refugia, thereby increasing predator-prey spatial overlap.
 3. We evaluated this hypothesis in a large mammal system, focusing on the interactions between boreal woodland caribou (*Rangifer tarandus caribou*) and their two main predators, wolves (*Canis lupus*) and black bears (*Ursus americanus*), during the calving season of caribou. In this system, LFs extend into and occur within peatlands (i.e. bogs and nutrient-poor fens), a habitat type highly used by caribou due to its refugia effects.
 4. Using resource selection analyses, we found that LFs increased predator selection of peatlands. Female caribou appeared to respond by avoiding LFs and areas with high LF density. However, in our study area most caribou cannot completely avoid exposure to LFs and variation in female response had demographic effects. In particular, increasing proportional use of LFs by females negatively impacted survival of their neonate calves.
 5. Collectively, these results demonstrate how LFs can reduce the efficacy of prey refugia. Mitigating such effects will require limiting or restoring LFs within prey refugia, though the effectiveness of mitigation efforts will depend upon spatial scale, which in turn will be influenced by the life history traits of predator and prey.

Keywords: predator-prey dynamics, linear features, anthropogenic disturbance, refuge, predator, prey, spatial overlap, caribou, wolves, black bear

INTRODUCTION

Spatial heterogeneity in landscape structure plays a fundamental role in shaping predator-prey dynamics, often being a key determinant of predator-prey coexistence (Huffaker 1958; Kauffman *et al.* 2007; Gorini *et al.* 2012). Heterogeneous landscapes contribute to long-term predator-prey stability by directly affecting the two primary components of the predation process, namely the probability of encounter and the probability of death given encounter (Lima & Dill 1990). For the former, spatial heterogeneity may create physical refugia where encounter rates between predator and prey are relatively low (Lewis & Eby 2002; Hebblewhite, Merrill & McDonald 2005). For the latter, spatial heterogeneity can create spatial variation in prey vulnerability, which may result in the probability of predator success not necessarily correlating with prey abundance (Quinn & Cresswell 2004; Gervasi *et al.* 2013). From an evolutionary perspective, variation in predation risk imposed by landscape structure will result in adaptive behavioral responses by predator and prey that will influence their joint patterns of space use (Sih 2005).

Across the globe, rapid alteration of natural landscapes by human activity is now challenging the evolved dynamical stability of many predator-prey systems (Kareiva 1987; Ryall & Fahrig 2006; DeCesare *et al.* 2009). By forcing organisms to respond to new and perhaps evolutionarily novel stimuli, rapid landscape alteration resets the behavioral “space race” (*sensu* Sih 1984) between predator and prey and the outcomes on predator-prey dynamics are not always predictable. For example, anthropogenic structures may create additional prey refugia, thereby redistributing prey space use, if prey tolerate human activity while predators do not (Berger 2007; Muhly *et al.* 2011). Alternatively, anthropogenic disturbance may diminish refugia effects if such disturbed areas are favourable to alternate prey species and their generalist predators (Peters *et al.* 2013). Altered landscape structure may also enhance predation rates by increasing predator abundance

(Andrén 1992) and/or by facilitating predator hunting efficiency (McKenzie *et al.* 2012).

Ultimately, these various outcomes may result in less stable predator-prey dynamics, increasing the extinction risk for one or both (Kareiva 1987; Wittmer, Sinclair & McLellan 2005; Layman *et al.* 2007).

In many forested systems, linear features (LFs) associated with industrial activity are a ubiquitous form of landscape disturbance (Laurance, Goosem & Laurance 2009; Pattison *et al.* 2016). Such features include roads, railways, power lines, pipelines and seismic lines. LFs have been implicated in altering predator-prey dynamics with the direction of outcomes being context-specific (Fahrig & Rytwinski 2009; DeGregorio, Weatherhead & Sperry 2014; Downing, Rytwinski & Fahrig 2015). Perhaps the most well-known example is their hypothesized influence on interactions between woodland caribou and wolves (James & Stuart-Smith 2000; Latham *et al.* 2011b; Whittington *et al.* 2011; Ehlers, Johnson & Seip 2014). In this context, LFs are thought to contribute to population declines of caribou by enhancing wolf hunting efficiency (McKenzie *et al.* 2012; Dickie *et al.* 2016) and/or by facilitating wolf movement into and within caribou habitat, thereby increasing caribou-wolf spatial overlap (spatial overlap hypothesis; James & Stuart-Smith 2000). Direct tests of either mechanism, however, are rare, particularly those using empirical data from both predator and prey (Whittington *et al.* 2011; Courbin *et al.* 2013) and further assessing whether the observed behavioural responses translate to demographic effects (James & Stuart-Smith 2000; Latham *et al.* 2011b).

In this study, we evaluated how LFs impact the spatial dynamics between the boreal ecotype of woodland caribou and its two main predators, wolves and black bears. We specifically tested the spatial overlap hypothesis by assessing whether LFs increased predator selection of peatlands (i.e. bogs and nutrient-poor fens), a habitat type highly used by boreal caribou presumably due to

its refugia effects (McLoughlin, Dunford & Boutin 2005). We also assessed whether caribou avoided LFs due to their apparent predation risk. We focused our analyses on the calving season of caribou when predation rates are particularly high (McLoughlin *et al.* 2003; Courtois *et al.* 2007). Because animals may respond to LFs at different scales (Boyce 2006), for each species we assessed actual use of LFs and how LF density affected selection of areas. Across all analyses, we explicitly tracked how individuals varied in their response to LFs.

We further assessed whether the behavioural responses of female caribou to LFs translated into demographic effects. To do so, we related the survival of neonate calves (≤ 4 weeks old) to female use of LFs and exposure to varying levels of LF density. If increasing caribou-predator spatial overlap facilitated by LFs is indeed a key mechanism contributing to elevated rates of caribou predation, then increasing female exposure to LF effects should equate to a lowered probability of calf survival. Variation in calf survival as a function of female behaviour may also give insight as to how caribou are adaptively responding to the relatively novel stimuli of LFs within their range.

MATERIALS AND METHODS

Study Area

The study area encompassed all six ranges of boreal caribou in northeast British Columbia (latitude: ~ 56.620 to 60.000 ; longitude: ~ -124.160 to -120.000). Landscape composition among these ranges was similar, consisting of a mosaic of deciduous and mixed-wood uplands, poorly drained low-lying peatlands, and riparian areas. Terrain is predominantly flat to undulating and the climate is northern continental, characterized by long, cold winters and short

summers. Forest fire is a frequent form of natural disturbance with a mean fire interval of ~100 years. The study area is further notable because it encompasses the Horn River Basin, a geologic formation containing one of the largest deposits of natural gas shale in Canada. Consequently, oil and gas extraction activities are the dominant form of anthropogenic disturbance within caribou range. The density of LFs associated with these activities averaged 4.04 km/km² (SD: 3.23; Appendix A) across all caribou ranges.

Caribou and Predator Spatial Data

We used GPS data collected from caribou, wolves and black bears fitted with Iridium satellite GPS collars (Advanced Telemetry Systems, model #2110E; Lotek Wireless, model Iridium Track M 2D). During collar deployment, we targeted mature individuals occurring within or immediately adjacent to caribou range. All capture and handling procedures followed approved animal care protocols (BC RIC 1998; BC Wildlife Act Permits FJ12-76949 and FJ12-80090; University of Alberta Animal Use protocols # 748/02/13 and AUP00001309).

For caribou, we obtained data from 56 reproductive-aged females distributed among all six caribou ranges. Individual females were captured by aerial net-gunning during the winter months of 2011 ($n = 25$), 2012 ($n = 2$) and 2013 ($n = 29$). Collars were programmed to acquire one GPS location (or fix) every two or four hours during calving (April 15 – July 15) and one to three times per day otherwise. Twenty females had functioning radio-collars through the 2014 calving season (i.e. beyond July 15, 2014).

For predators, we used data from 23 wolves and 19 black bears. All individuals were captured by aerial darting. Wolf collars were deployed during the winter months of 2012 ($n = 3$), 2013 ($n = 10$), 2014 ($n = 4$) and 2015 ($n = 6$) and were distributed among 13 packs with at least one pack being collared in each caribou range. Collars deployed in 2012 and 2013 had fix rates of every

15 minutes May 1 – June 30 and once per day otherwise. Collars deployed in 2014 and 2015 had four one-week intervals with fix rates of every five minutes and otherwise were either every two, three, or four hours. For all collars, one of the one-week intervals occurred in June to capture fine-scale movements during the calving season of caribou. Bear collars were deployed in May 2012 ($n = 4$) and May 2013 ($n = 15$) and all had fix rates of every 30 minutes May 1 – June 30 and once per day otherwise. Captured bears occurred in three of the six caribou ranges. All predator data sets spanned one calving season only.

Prior to analyses, we screened the raw data for potential errors (Appendix B). Following these procedures, fix success rate per collar for caribou averaged 93% (range: 68 – 100) during calving and 84% (range: 28 – 99) outside of calving and per collar monitoring time averaged 541 days (range: 112 – 745). For wolves, fix success rates averaged 90% (range: 60 – 100) during the high frequency monitoring intervals (i.e. every 5 or 15 minutes) and averaged 89% (range: 56 – 98) otherwise. Monitoring times per wolf collar averaged 268 days (range: 108 – 546) although one collar had a four month gap in monitoring post-calving. For bears, fix success rates averaged 81% (range: 61 – 90) during calving and 52% (range: 42 – 72) otherwise. Collar failures limited monitoring times for bears (mean time: 39 days; range: 4 - 120) and three bears were excluded from further analyses as collar failures limited monitoring time to ≤ 1 day.

Because only six bears had data sets extending beyond 30 June, we limited bear analyses to the calving season. To evaluate the potential influence of low fix success rates on inferences of resource selection (Frair *et al.* 2010), we conducted sensitivity analyses on population-level results for all three species by first excluding individuals with rates $< 80\%$ then further excluding those with rates $< 90\%$ (Appendix C).

Predicting Caribou Parturition Status and Neonate Survival

For caribou, we restricted analyses to GPS locations where a female was accompanied by a neonate calf (hereafter, calving locations). We identified calving locations using the two movement-based methods (MBMs) of DeMars *et al.* (2013; Appendix B). Briefly, MBMs predict the calving status of females (parturient vs. barren) and the survival status of neonate calves and further yield estimates of parturition date and calf loss date, where appropriate. For 2011 – 2013 data, MBM predictions of calf survival were further corroborated by data from aerial surveys conducted weekly during calving. These procedures yielded a final data set of 44 female caribou predicted to have calved at least once during the four-year study period. Nineteen females calved in two years, resulting in 63 caribou-calving seasons.

Resource Selection Analyses: General Framework

To evaluate the spatial overlap hypothesis, we conducted resource selection analyses at two spatial scales for all three species. All analyses focused on evaluating selection patterns during the calving season of caribou. At the fine scale, we assessed selection of peatlands, LFs in peatlands and LFs in other land cover types for each species. At the larger scale, we assessed how LF density affected each species selection of areas both within and outside of peatlands. For fine-scale analyses, we estimated step selection functions (SSFs), which compared resources associated with each observed movement ‘step’ (i.e. an animal’s movement linking successive GPS locations) to resources associated with a matched set of random steps sampled from a parameterized distribution of the observed movement process (Fortin *et al.* 2005; Avgar *et al.* 2016; Appendix D). For each observed step, we generated 20 random steps to adequately characterize resource availability (Northrup *et al.* 2013; Appendix D). We compared resource values at the end of each step – rather than the average resource values along each step – as this

approach is likely better for estimating selection of LFs (Thurfjell, Cuiti & Boyce 2014). To explicitly assess how LFs influence predator resource selection during movement, we constrained SSF analyses for bears and wolves to steps where the animal was actively moving and excluded those associated with resting or feeding (see *Statistical Analyses* below). For caribou, we used all steps as our interest was in quantifying total exposure to LFs. All SSF analyses were confined to locations within the calving season when GPS collars were programmed for higher fix rates (caribou: every 2 hrs, wolves: every 5 to 15 minutes; bears: every 30 minutes).

For large-scale analyses, we used two approaches, both focusing on a species' response to LF density measured over two areal extents (200-m and 1000-m radii). For caribou and wolves, we estimated third-order resource selection functions (Johnson 1980), which compared resources associated with an animal's GPS locations to resources associated with available locations randomly sampled within the animal's annual home range. We characterized home ranges using the 90% isopleth of utilization distributions (UDs; Börger *et al.* 2006). For each UD, we specified the "reference bandwidth" as the smoothing parameter, which provided a good visual approximation of space use for each caribou and wolf (mean home range size for caribou: 802 km² [range: 84 – 2904]; for wolves: 1222 km² [range: 493 – 2101]). For both species, we conducted sensitivity analyses to determine the time required for estimates of UD size to stabilize, excluding individuals falling below this minimum (Appendix E). We also conducted sensitivity analyses to determine the minimum number of random points to adequately characterize availability within the UD of each species (Appendix E; Northrup *et al.* 2013). For bears, limited monitoring times prevented estimation of annual home ranges; therefore, we used SSFs with data rarefied to two locations per day, which allows sufficient time for bears to move

among areas with potentially varying LF density. As with fine scale analyses, we generated 20 random steps for each observed step.

Environmental Covariates

We modelled resource selection with variables representing land cover and LFs. For land cover, we used Enhanced Wetlands Classification data from Ducks Unlimited Canada (Appendix F), collapsing these data into seven biologically meaningful categories (Table 1). We specifically created a peatlands category by combining bogs and nutrient-poor fens to represent land cover highly selected by caribou during calving (DeMars 2015). For LFs, we accessed provincial repositories to obtain year-specific data depicting roads, seismic lines and pipelines (Appendix F) and we matched these data by year to the GPS radio-collar data. For each line type, we buffered the features by their average width plus the estimated GPS positional error of the radio-collars (± 7.7 m, C. DeMars, unpublished data), resulting in buffered widths of 40-m for roads, 50-m for pipelines and 30-m for seismic lines. We considered any GPS radio-collar location or random location to be on a LF if it fell within this buffered footprint. Note that our objective was not to model animal response to specific LF types *per se* (e.g. Dickie *et al.* 2016), but rather to assess how LFs in general influenced spatial overlap among caribou, wolves and bears. For assessing effects of LF density, we merged data from all line types into one parsimonious layer and calculated LF densities in a moving window analysis using radii of 200-m and 1000-m. We evaluated radii up to 10000-m but these larger measures began to approximate densities measured over the entire caribou range and obscured potential finer scale variation in LF density (Boyce 2006).

Evaluating Linear Feature Effects on Neonate Survival

We used a similar multi-scale approach to assess LF effects on the survival of neonate calves. At a fine scale, we evaluated how a female's proportional use of LFs influenced calf survival. At the larger scale, we evaluated how female exposure to varying line density – measured in the same 200-m and 1000-m radii – affected calf survival. We further evaluated bivariate models representing LF effects at both scales.

Statistical Analyses

We estimated SSFs for each individual caribou, wolf and bear using conditional logistic regression (CLR). To constrain wolf and bear SSFs to actively moving steps, we used breakpoint regression to identify such steps as ≥ 150 -m (Appendix D). Across all three species, we estimated SSFs only for those individuals having ≥ 30 moving steps to allow for effective parameter estimation. For each individual, we estimated two forms of SSFs. The first incorporated covariates for land cover and LFs only (hereafter, SSF_{Res} indicating resource only models). The second form incorporated aspects of the animal's movement process into a mechanistic movement model that simultaneously estimated selection and movement parameters to potentially improve precision of parameter estimates (Avgar *et al.* 2016). With LFs likely affecting movement rates (Dickie *et al.* 2016), we incorporated the interaction of step length with LF variables into these models (hereafter, SSF_{Res*SL} ; Table 2).

Variable specification within models differed among species (Table 2). Because caribou used predominantly peatlands during calving, land cover and LFs were specified as binary variables (i.e., peatlands / other; on / off lines). With wolves and bears being more habitat generalists, we incorporated all seven land cover categories into their models by coding six dummy variables and setting upland deciduous as the reference category. We specifically assessed the interaction

of LFs with peatlands by further creating three dummy variables representing LF within a peatland, LF within other land cover types, and peatland off a LF.

For each SSF, we used generalized estimating equations (GEEs) to calculate robust standard errors, a framework that accounts for potential autocorrelation among steps (Craiu, Duchesne & Fortin 2008; Appendix D). To discriminate between SSF models within individual animals, we used the quasi-likelihood under independence criterion (QIC; Craiu, Duchesne & Fortin 2008).

For population-level inferences on each species, we averaged parameter estimates across individuals, weighting each estimate by the inverse of its variance to give more weight to individuals with more precise estimates. We used bootstrapping to calculate 95% confidence intervals (CIs).

To evaluate model performance, we used k -fold cross validation for CLR following Fortin *et al.* (2009). Briefly, this approach estimated SSFs using 75% of randomly selected strata with model outputs then used to generate predictions for observed and random steps within the withheld strata. Observed and random predictions were collectively ranked within each stratum with rankings tallied into bins across strata (nine bins for fine-scale wolf and bear SSFs; 21 bins for large-scale bear SSFs; four bins for caribou SSFs). We calculated a Spearman-rank coefficient (r_S) to assess the correlation between bin rank and its associated frequency of observed predictions (r_{S_Obs}). We repeated this process to calculate r_S based on random expectation (r_{S_Ran}), using a randomly selected random prediction within each testing strata but excluding the observed prediction from stratum ranking. We repeated the entire procedure 30 times to calculate \bar{r}_{S_Obs} and \bar{r}_{S_Ran} for each SSF with increasing model performance equating to higher \bar{r}_{S_Obs} relative to \bar{r}_{S_Ran} . Because caribou SSFs yielded only four possible predictions, we also

provide the frequency of observed steps falling within the top ranked category (TR_{FreqObs}) compared to the frequency of random steps (TR_{FreqRan}) to further assess model performance.

We estimated RSFs for caribou and wolves using generalized linear mixed-effect models, specifying individual caribou and individual wolf nested within pack as random grouping factors. We explicitly assessed the effect of LF density on peatland selection by assigning these variables – and for wolves, their interaction – as random slopes. This formulation yields variance estimates that appropriately reflect the animal as the sampling unit (Schielzeth & Forstmeier 2009). Within each species-specific RSF, variables for land cover were specified as per SSFs and LF density variables were standardized to facilitate model convergence. We used Akaike's Information Criterion (AIC) to discriminate between models with density measured within 200-m and 1000-m radii. We evaluated RSF performance using k -fold cross validation (Boyce *et al.* 2002), randomly partitioning the data into five folds, estimating RSFs with four folds then calculating r_5 to assess how well model outputs predicted the withheld spatial locations. As with SSFs, we repeated this process 30 times. Note that for LF density we considered both quadratic relationships and categorical transformations but these did not improve model performance and their results are not shown here.

For all resource selection analyses, we evaluated the robustness of inferences to functional responses, where selection may change as a function of resource availability (Myysterud & Ims 1998). To do so, we assessed the strength of correlation between individual-level selection coefficients and individual-specific resource availability (Appendix C). We considered a linear or quadratic relationship with an $R^2 > 0.10$ to be indicative of a functional response.

To assess LF effects on calf survival, we estimated mixed-effects Cox proportional hazard models, specifying individual caribou as a random grouping factor to account for females calving

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in multiple years. Cox models are time-to-event analyses and in our formulation the event is calf loss. Positive model coefficients are therefore interpreted as an increasing risk of calf mortality with an increase in the associated covariate. We considered three explanatory variables describing exposure to LFs: proportional LF use, calculated as the proportion of a female's GPS locations falling on a LF, and the mean density of LFs around each female's GPS locations measured within 200-m and 1000-m radii. Because LF density data were highly skewed, we considered log transformations of these variables. We fit univariate and bivariate models (proportional LF use and mean LF density at 200 or 1000-m) and for the latter, we used variance inflation factors (VIFs) to assess for collinearity. We discriminated among models using AIC. For the top model, we evaluated relative fit using a LRT and tested the assumption of proportional hazards by assessing for linearity and a zero slope of the scaled Schoenfeld residuals.

All analyses were performed in R, version 3.3.0 (see Appendix G for the specific packages and functions used and associated references). Animal location data used in all analyses are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b8d23> (DeMars & Boutin 2017). Data sources for explanatory variables are listed in Appendix F.

Table 1: Classification of land cover types (with abbreviations) used to model resource selection by boreal caribou, wolves and black bears in northeastern British Columbia, Canada. Land cover types were developed from Enhanced Wetlands Classification data (DU 2010).

Land Cover	EWC Class	Description
Peatland (peat)	Treed bog, Open bog, Shrubby bog, Graminoid poor fen, Shrubby poor fen, Treed poor fen	Black spruce and <i>Sphagnum</i> moss dominated bogs. Nutrient poor fens characterized by black spruce, tamarack and bog birch (<i>Betula glandulosa</i>). Areal coverage: ~42%
Nutrient-rich fen (rf)	Graminoid rich fen, Shrubby rich fen, Treed rich fen	Low nutrient peatland soils influenced by groundwater flows and characterized by bog birch, willow (<i>Salix spp.</i>) and alder (<i>Alnus spp.</i>). Areal coverage: ~4%
Conifer swamp (cs)	Conifer swamp	Tree cover >60% dominated by black or white spruce. Occur on peatland or mineral soils. Areal coverage: ~9%
Hardwood swamp (hs)	Shrub swamp, Hardwood swamp, Mixed-wood swamp	Mineral soils with pools of water often present. Dominant deciduous tree species: paper birch and balsam poplar (<i>Populus balsamifera</i>). Areal coverage: ~14%
Upland conifer (uc)	Upland conifer	Mineral soils with tree cover >25%. Dominant tree species: black and white spruce, pine. Areal coverage: ~5%
Upland deciduous (ud)	Upland deciduous, Mixed-wood upland	Mineral soils with tree cover >25%. Dominant deciduous tree species: aspen and paper birch. Areal coverage: ~20%
Other (oth)	Upland other, Cloud shadow, Anthropogenic, Burn, Aquatic	Uplands: mineral soils with tree cover <25%. Anthropogenic: urban areas, roads and cut blocks. Burns: vegetation is limited or covered by burn. Aquatic: includes a continuum from low turbidity lakes to emergent marshes where aquatic vegetation is >20%. Total areal coverage: ~6% (Cloud shadow <0.5%)

Table 2: Model specifications for evaluating resource selection by boreal caribou, wolves and black bears at fine and large scales in northeastern British Columbia, Canada.

<i>Species</i>	<i>Scale</i>	<i>Model</i> ¹	<i>Explanatory Variables</i> ²
caribou	fine	SSF _{Res}	peat + LF
		SSF _{Res*SL}	peat + LF* sl
	large	RSF	peat + LF density
wolf	fine	SSF _{Res}	peat (off LF) + rf + cs + hs + uc + oth + peat (on LF) + LF (other)
		SSF _{Res*SL}	peat (off LF) + rf + cs + hs + uc + oth + peat (on LF)*sl + LF (other)*sl
	large	RSF	peat*LF density + rf + cs + hs + uc + oth
bear	fine	SSF _{Res}	peat (off LF) + rf + cs + hs + uc + oth + peat (on LF) + LF (other)
		SSF _{Res*SL}	peat (off LF) + rf + cs + hs + uc + oth + peat (on LF)*sl + LF (other)*sl
	large	SSF _{Res}	peat*LF density + rf + cs + hs + uc + oth
		SSF _{Res*SL}	peat*LF density + rf + cs + hs + uc + oth + LF density*sl

¹ SSF_{Res} = step selection function using resource covariates only; SSF_{Res*SL} = step selection function incorporating resource covariates interacting with step length; RSF = resource selection function

² See Table 1 for abbreviations of land cover variables. ‘sl’ refers to step length.

RESULTS

Fine-Scale Response to Linear Features

Female caribou with neonate calves generally avoided LFs when moving within their calving areas. Twenty-two of the 63 calving-seasons had no GPS locations on LFs although these animals were also in areas with lower LF availability ($p < 0.001$ from a post-hoc t -test).

Assessing selection across the remaining 41 calving-seasons (mean steps / calving-season = 195 [SD = 108]), of which five had SSF_{Res*SL} as the top model, avoidance of LFs was still evident (weighted $\bar{\beta} = -0.34$ [95% CI: -0.49, -0.20]). Eight calving-seasons, however, had positive coefficients for LFs (Fig. 1). Across individuals, SSFs had good predictive performance ($\bar{r}_{S_Obs} = 0.91$ [range: 0.30, 1.00], $\bar{r}_{S_Ran} = 0.91$ [0.30, 1.00]; $\overline{TR}_{FreqObs} = 0.65$ [0.21, 0.93], $\overline{TR}_{FreqRan} =$

0.60 [0.21, 0.89]; mean difference between $\overline{TR}_{\text{FreqObs}}$ and $\overline{TR}_{\text{FreqRan}}$ among caribou = 0.25 [0.5, 0.42]).

For wolves, LFs strongly affected selection of peatlands. We used 21 wolves (mean steps / individual = 792 [SD = 401]) to estimate population-level effects, removing two wolves that had similar movement paths – and therefore parameter estimates – to other wolves within their packs. Nineteen wolves had $SSF_{\text{Res*SL}}$ as their top model. In general, wolves highly selected LFs in peatlands (weighted $\bar{\beta} = 0.85$ [95% CI: 0.68, 1.05]; Fig. 2) yet avoided peatlands off LFs (weighted $\bar{\beta} = -0.21$ [95% CI: -0.38, -0.04]). For 12 wolves, LF in a peatland was the first or second ranked land cover type while peatland off LF was ranked lowest. Wolves also selected LFs in other land covers (weighted $\bar{\beta} = 0.93$ [95% CI: 0.79, 1.11]). Overall, model prediction was good across individual wolves ($\bar{r}_{S_{\text{Obs}}} = 0.95$ [range: 0.78, 0.99], $\bar{r}_{S_{\text{Ran}}} = 0.75$ [0.55, 0.89], mean difference among wolves = 0.20 [0.04, 0.41]).

LFs also influenced selection of peatlands by bears (mean steps / individual = 350 [SD = 201]). Whereas peatlands off LFs were selected at rates similar to the reference category (weighted $\bar{\beta} = 0.13$ [95% CI: -0.02, 0.28]), selection was higher for LFs in peatlands (weighted $\bar{\beta} = 0.51$ [95% CI: 0.39, 0.68]; Fig. 2). LFs in other land covers were also highly selected (weighted $\bar{\beta} = 0.86$ [95% CI: 0.66, 1.06]). Two of 16 bears had $SSF_{\text{Res*SL}}$ as their top model and predictive performance was good across all individual models ($\bar{r}_{S_{\text{Obs}}} = 0.91$ [range: 0.74, 0.97], $\bar{r}_{S_{\text{Ran}}} = 0.82$ [0.64, 0.95, mean difference among bears = 0.08 [0.01, 0.19]).

Large-Scale Response to Linear Features

The three species had differing responses to LF density. For caribou, response was strongest at the 1000-m scale ($\Delta\text{AIC} = 3417$ units lower; $\bar{r}_s = 0.82$ [range: 0.72, 0.88]) with females generally

selecting calving locations with lower LF density ($\beta = -2.00$ [95% CI: -2.83, -1.17]). Females, however, could not completely avoid exposure to LFs at the 1000-m scale when calving (mean LF density per caribou-year = 3.36 km/km²; range: 0.33 – 12.69). Avoidance was also not consistent across all 63 females as 18 individuals had positive coefficients with 95% CIs that did not overlap zero.

Wolves were less affected by LF density. As with caribou, wolf response was strongest at the 1000-m scale ($\Delta AIC = 800$ units lower; $\bar{r}_S = 0.98$ [range: 0.96, 1.00]) but wolves only showed weak avoidance of increasing LF density within peatlands ($\beta = -0.16$ [95% CI: -0.33, 0.02]) and weak selection for increasing LF density within other land covers ($\beta = 0.20$ [95% CI: -0.12, 0.51]). Specific to LF density within peatlands, only seven of 23 wolves had positive coefficients with 95% CIs that did not include zero.

LF density had variable effects on bear selection of land cover. Across the 11 individuals evaluated (mean steps / individual = 46 [range: 32-65]), six responded most strongly to LF density measured within a 200-m radius and five bears had SSF_{Res*SL} as their top model.

Estimating population-level parameters within both measured radii, bears generally avoided increasing LF density within peatlands (200-m: $\beta = -0.32$ [95% CI: -0.53, -0.10]; 1000-m: $\beta = -0.20$ [95% CI: -0.43, 0.04]) but were generally ambivalent to LF density in other land covers (200-m: $\beta = 0.11$ [95% CI: -0.04, 0.22]; 1000-m: $\beta = 0.07$ [95% CI: -0.13, 0.25]). Only one bear selected for increasing LF density (1000-m radius) within peatlands, having a positive coefficient with a 95% CI that did not overlap zero. Small sample sizes per bear prevented robust evaluation of model performance and consequently performance was low and variable across individuals (200-m: $\bar{r}_{S_Obs} = 0.39$, $\bar{r}_{S_Ran} = -0.21$; 1000-m: $\bar{r}_{S_Obs} = 0.21$, $\bar{r}_{S_Ran} = -0.09$).

Across all resource selection analyses, inferences were generally robust to variation in fix rate and resource availability (Appendix C). For the former, excluding animals with low fix rates did not change the direction of population-level parameters or substantially affect the overlap of 95% CIs with zero. For the latter, functional responses in selection were not evident for caribou (all $R^2 < 0.10$) while only weak negative relationships were noted for wolves at both scales ($R^2 = 0.12 - 0.26$) and for bears at a fine scale ($R^2 = 0.11 - 0.16$). These negative relationships indicate that the strength of selection decreases with increasing LF availability. Given the ubiquity of LFs within caribou range (Appendix A), these relationships suggest that our results are conservative when inferring that LFs increase selection of peatlands by wolves and bears.

Linear Feature Effects on Neonate Survival

Of the 63 calves followed, 33 survived to four weeks old. Neonate survival was best predicted by a bivariate model describing a female's proportional use of LFs and the \log_2 of mean LF density within a 1000-m radius. This model was 2-3 AIC units lower than other competing models and variable VIFs were 2.12, a value acceptable for valid inference (Zuur, Ieno & Elphick 2010). Model output suggested that the risk of neonate mortality increases as female use of LFs increases ($\beta = 5.55$ [95% CI: 0.24, 10.85]) and decreases with every two-fold increase in LF density ($\beta = -0.43$ [95% CI: -0.80, -0.06]). The proportional-hazards assumption was generally supported ($p \geq 0.21$ for non-zero linear trend in the scaled Schoenfeld residuals of each variable) and model fit was marginal ($p = 0.08$ from LRT), suggesting that, in general, LF effects are weak determinants of neonate survival.

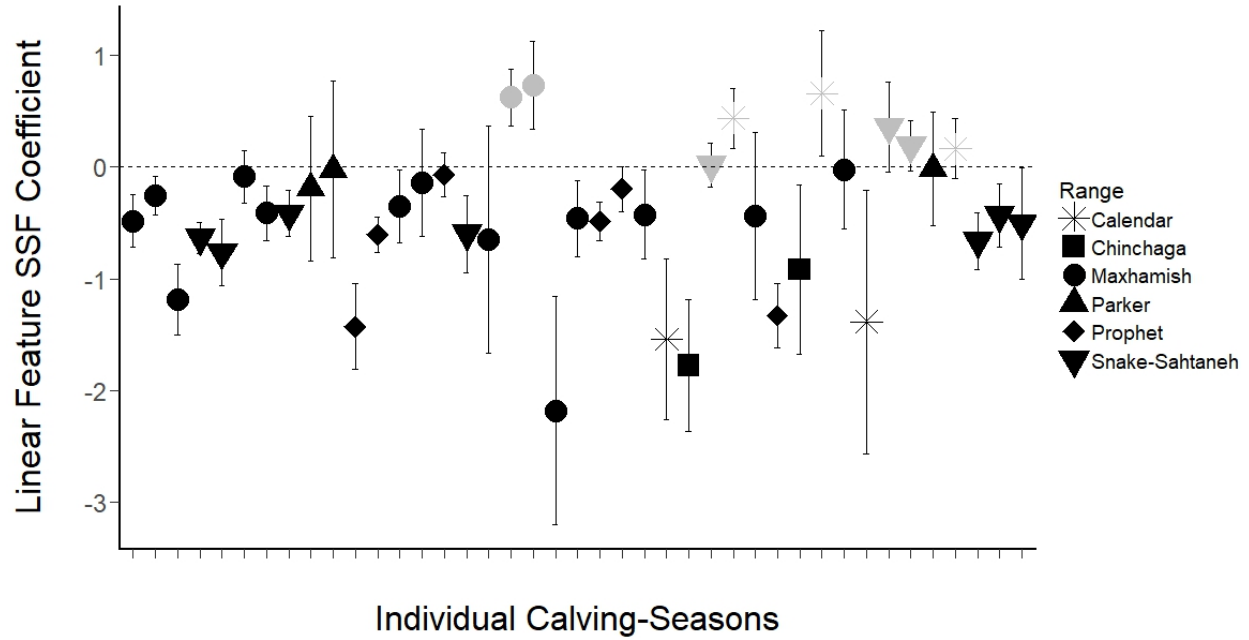


Figure 1: Individual coefficients (grey symbols = positive coefficients; black symbols = negative coefficients) with standard errors from step selection functions (SSFs) representing selection of linear features by female boreal caribou during the calving season across six caribou ranges in northeast British Columbia, Canada. SSFs were fit to females having at least one GPS location on a linear feature in a given calving season ($n = 41$ calving-seasons). Twenty-two calving-seasons had no GPS locations falling on a linear feature, suggesting complete avoidance.

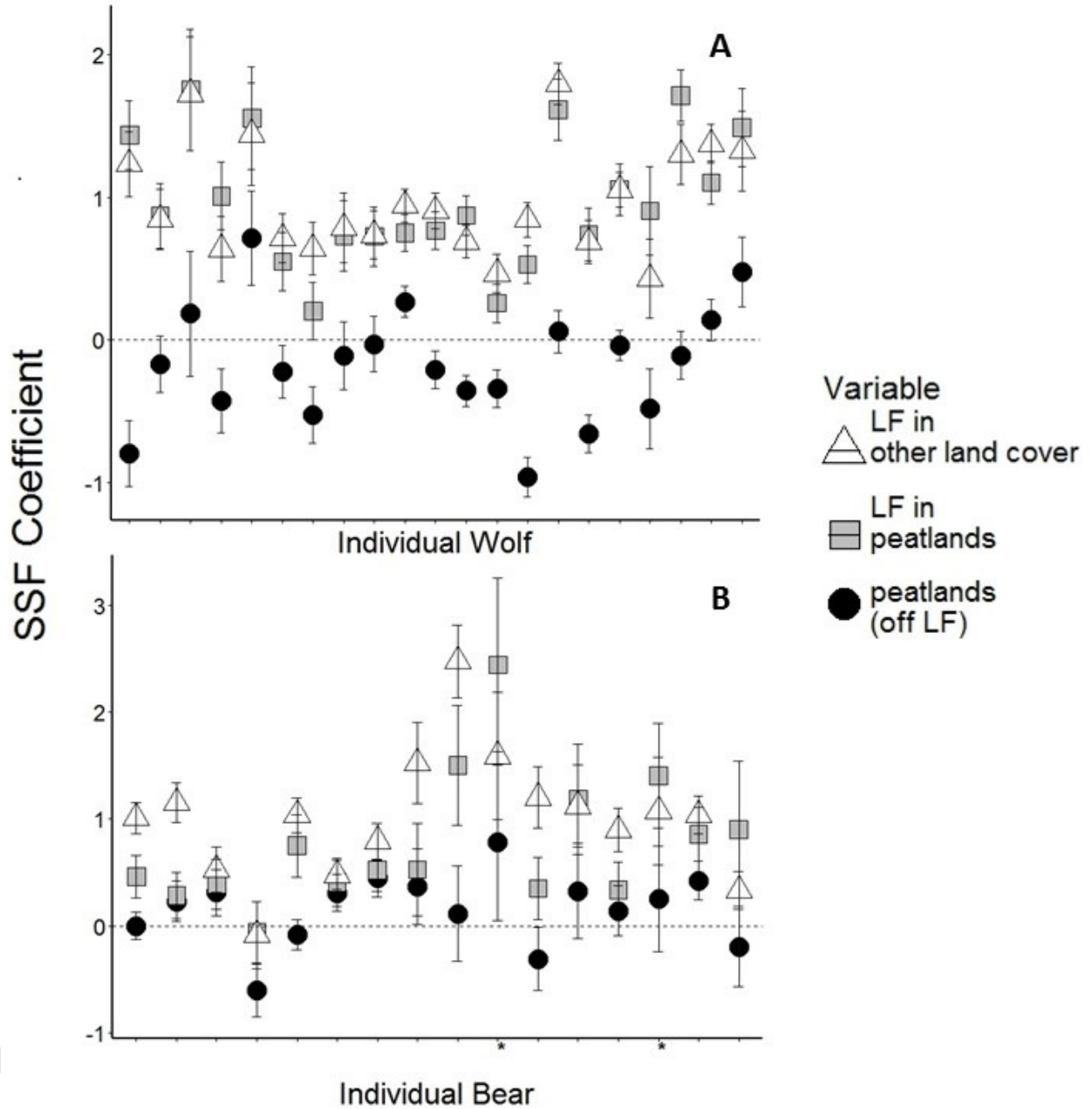


Figure 2: Individual coefficients and standard errors from step selection functions (SSFs) representing selection of linear features (LFs) in peatlands (black circles), LFs in other land cover types (white triangles) and peatlands off LFs (gray squares) by wolves (A) and black bears (B) during the calving season of boreal caribou in northeast British Columbia, Canada. Asterisks indicate bears monitored for ≤ 1 week.

DISCUSSION

In many predator-prey systems, the long-term persistence of prey populations fundamentally depends on the availability and effectiveness of spatial refugia (Huffaker 1958). Perturbations that limit such refugia or reduce their effectiveness can therefore negatively impact prey populations. In our study system, sustained declines of boreal caribou populations have been proximately attributed to increasing predation but ultimately linked to landscape alteration interacting with effects of climate change (Sorensen *et al.* 2008; Latham *et al.* 2011c; Environment Canada 2012; Dawe, Bayne & Boutin 2014). Our results here demonstrate that LFs likely contribute to these declines by facilitating predator incursions into the spatial refugia of caribou, at least during the calving season. The reduction in refugia efficacy from LFs was evidenced by lowered rates of calf survival, a key determinant of caribou population dynamics (DeCesare *et al.* 2012).

Outcomes of rapid landscape alteration on predator-prey dynamics are shaped by the behavioral responses of all involved species (Sih, Ferrari & Harris 2011; Gorini *et al.* 2012). From the prey's perspective, coping with rapid landscape alteration depends on having the behavioral plasticity to respond to novel variation in predation risk. In this study, female caribou appeared to demonstrate such plasticity as most individuals avoided LFs and/or moved to areas with lower LF density during calving, a time when females are most sensitive to predation risk (Bergerud, Ferguson & Butler 1990). Note, however, that our results do not give inference as to the mechanism(s) driving the observed behavioural responses. For example, female avoidance of LFs may be in response to olfactory cues from recent predator use or, alternatively, the behaviour may be unrelated to predation and more a foraging response if food resources on LFs are lower. The population-level avoidance of LFs could also be an artefact of the adaptation

process if, as our results suggest, LFs negatively impact caribou survival (i.e., the majority of individuals still alive are those genetically predisposed to avoid open areas such as LFs or have lowered movement rates thereby encountering LFs less). Indeed, phenotypic changes in behaviour at the population-level may become evident in short time frames following rapid landscape alteration (Hendry, Farrugia & Kinnison 2008). Regardless of mechanism, most females were unable to avoid using LFs and no female calved in areas where mean LF density was zero. While this finding may suggest that female avoidance of LFs is not strong, it likely reflects the extensive impact of LFs within our study area where areas with zero LFs – as measured on a per km² basis – constitute < 3% of caribou range (Appendix A).

In contrast to caribou, predators showed high rates of fine-scale selection for LFs and this behaviour increased their selection of caribou refugia (i.e. peatlands). Other studies have similarly suggested that LFs facilitate predator incursions into prey refugia (e.g. mesopredator incursions into the wetland refugia of waterfowl, Frey & Conover 2006; human incursions into the refugia of American marten [*Martes americana*], Wiebe *et al.* 2013). In our system, both wolves and bears selected LFs in all types of land cover – a finding consistent with other studies (Latham *et al.* 2011b; Tigner, Bayne & Boutin 2014; Dickie *et al.* 2016) – but here we show that LFs specifically increased predator selection of peatlands. Without LFs, peatlands are marginal habitat for both predators, particularly in the spring, as this land cover is generally avoided by other ungulate prey (James *et al.* 2004) and, with respect to bears, has low abundances of forage plants (Mosnier, Ouellet & Courtois 2008; Latham, Latham & Boyce 2011a). The presence of LFs, however, changed the selective value of peatlands. For both predators, LFs within peatlands may be selected because they enhance movement efficiency when traversing between more optimal foraging patches (McKenzie *et al.* 2012; Dickie *et al.* 2016) or when patrolling

territories. Predators may also select LFs in peatlands if such features are also selected by other more abundant and profitable prey (e.g. in our system, moose; Peters *et al.* 2013). For bears, wide LFs such as roads and pipelines may have higher abundances of green plants in the spring, even those within peatlands (Bastille-Rousseau *et al.* 2011).

Despite these apparent advantages, we found that increasing LF density did not increase predator selection of peatlands; rather, both predators showed weak avoidance. Such a result could occur if areas of high LF density are associated with higher levels of ongoing human activity, which predators have been shown to avoid (Berger 2007). Weak avoidance could also be indicative of a functional response in selection, particularly for wolves. Wolf selection coefficients were generally positive at low LF densities (e.g. $< 4 \text{ km/km}^2$) but turned negative at higher LF densities (Appendix C). For a cursorial predator, this result is perhaps expected as only one or a few LFs may be all that is necessary to sufficiently search or patrol a given area.

If LFs facilitate predator incursion into prey refugia, then predators should gain an advantage in the space race and, consequently, negative impacts on prey demography should become evident (Sih 1984, 2005). This outcome has been documented in forest songbirds where nest proximity to LFs highly influenced nest predation rates (DeGregorio, Weatherhead & Sperry 2014). Here, we found evidence of this effect in a large mammal predator-prey system as LFs appeared to impact survival of caribou calves, though we caution that our results are indirect and correlative.

We further note that demographic effects were relatively weak, likely indicating that other factors may exert stronger influences on calf survival (e.g. maternal condition, Cameron *et al.* 1993; disease; spatial variation in predator densities, Barber-Meyer, Mech & White 2008).

Nevertheless, increasing use of LFs by females negatively affected survival of their calves.

Because predation is the primary proximate cause of calf mortality in most caribou populations

(Adams, Singer & Dale 1995; Pinard *et al.* 2012), a possible mechanism behind this relationship is that caribou are leaving olfactory cues on a landscape feature (i.e. a LF) highly selected by predators, potentially increasing the probability of caribou-predator encounter compared to olfactory cues found off lines. Predators may also be able to see caribou on LFs though this requires both predator and prey to be on the same LF at the same time, a probability that is likely small.

LF density also weakly influenced calf survival, though the positive correlation was perhaps unexpected. This result could have occurred for a few reasons. First, many LFs in a given area may create a dilution effect as only one – or perhaps a few – are traversed by predators within a given area at any one time. Second, as noted above, areas with high LF density may function as relative refugia if such areas are associated with high levels of human activity. Third, females in areas of high LF density may limit movements and consequently have lower rates of LF use.

Post-hoc analyses, however, did not support this explanation (Pearson's correlation coefficient between movement and LF density = 0.58) although further research may be necessary to determine if females could reduce LF crossing frequency – and hence lower LF use – without reducing movement rates *per se* in areas of high LF density.

Conservation Implications

Mitigating effects of LFs has become a conservation priority because of their negative impacts on biodiversity (Laurance *et al.* 2009). Here, we demonstrated how LFs may reduce the efficacy of prey refugia, which suggests that mitigation efforts should be focused on limiting or restoring LFs that contribute to predator-prey spatial overlap. We caution, however, that spatial overlap is not the only mechanism by which LFs can affect predator-prey dynamics. For example, in our study system, LFs outside of peatlands may enhance wolf hunting efficiency of alternative prey,

resulting in increased wolf numbers, which may then “spill over” into caribou habitat (Holt 1984). Our results do not give insight into the relative importance of this mechanism versus spatial overlap in terms of impact on caribou populations. Effective prioritization of mitigation efforts will therefore require further research to disentangle the importance of such effects, particularly given the substantial costs associated with LF restoration for wide ranging species inhabiting highly impacted forested systems (Schneider *et al.* 2010).

We further caution that our results do not give insights into the spatial requirements of prey refugia. Such requirements will likely be context specific, depending on the life history traits of both predator and prey. For caribou, previous research has suggested that disturbance effects are best measured at the scale of a herd’s range and that these effects are largely negative (Sorensen *et al.* 2008; Environment Canada 2012). Given this scale, the functional response of predators in selecting LFs, and the sensory capabilities of predators to detect prey (e.g. for wolves, up to 2.5 km; Mech & Peterson 2003), our results suggest that overall LF density will likely need to be low within caribou range (e.g. $< 1 \text{ km/km}^2$; McCutchen 2007) and that many peatland complexes will need to be essentially intact. Again, given the wide spatial extent of most caribou ranges, achieving such densities through LF restoration will not be a trivial task.

Finally, we acknowledge that different types of LFs may exert unequal impacts on predator-prey dynamics. For example, wolves have shown relative avoidance of LFs that were narrow ($\leq 7 \text{ m}$ wide) and sinuous, perhaps due to decreased line-of-sight or increased movement costs (Wilson *et al.* 2013; Dickie *et al.* 2016), and bears have shown decreased use of LFs $\leq 2 \text{ m}$ wide (Tigner *et al.* 2014). Determining the relative impacts of specific LF types on predator-prey dynamics will therefore be necessary to better understand and quantify LF effects over large spatial scales.

AUTHORS' CONTRIBUTIONS

CAD and SB conceived the study. CAD collected and analyzed the data and wrote the manuscript. SB contributed critically to all manuscript drafts.

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DATA ACCESSIBILITY

Animal location data used in all analyses are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b8d23> (DeMars & Boutin 2017). Data sources for explanatory variables are listed in Appendix F.

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