

Where beavers (*Castor canadensis*) build: testing the influence of habitat quality, predation risk, and anthropogenic disturbance on colony occurrence

M.A. Mumma, M.P. Gillingham, C.J. Johnson, and K.L. Parker

Abstract: Species distributions are shaped by numerous factors that vary in importance across spatiotemporal scale. Understanding drivers of the distribution of North American beavers (*Castor canadensis* Kuhl, 1820) is paramount given their profound influence on ecological communities. Our objectives were to evaluate the influence of habitat quality, risk of gray wolf (*Canis lupus* Linnaeus, 1758) predation, and anthropogenic disturbance on the occurrence of beaver colonies in northeast British Columbia (BC), Canada. We used mixed-effects multinomial logistic regression to model the occurrence of active and inactive colonies and *t* tests to compare landscape covariates associated with active versus inactive colonies. We determined that occurrence of beavers was driven by habitat quality. Occurrence increased in areas with higher vegetation-class richness and greater proportions of open water, nutrient-rich fen, and deciduous swamp. We also observed that active colonies were surrounded by greater amounts of deciduous swamps relative to inactive colonies. We found no evidence that predation risk or industrial activities decreased the occurrence of beavers in northeast BC, although numerical changes in abundance might occur without changes in distribution. This research illuminated drivers of beaver distribution while providing a means to predict the occurrence of a keystone species in the boreal ecosystem.

Key words: boreal, *Castor canadensis*, multinomial logistic regression, North American beaver, species distribution modelling.

Résumé : La répartition des espèces est modulée par de nombreux facteurs qui varient en importance selon l'échelle spatio-temporelle. Une bonne compréhension des facteurs qui influencent la répartition des castors (*Castor canadensis* Kuhl, 1820) est primordiale étant donné sa profonde influence sur les communautés écologiques. Nos objectifs consistaient à évaluer l'influence de la qualité de l'habitat, du risque de prédation par le loup gris (*Canis lupus* Linnaeus, 1758) et des perturbations d'origine humaine sur la présence de colonies de castors dans le nord-est de la Colombie-Britannique (Canada). Nous avons utilisé la régression logistique multinomiale à effets mixtes pour modéliser la présence de colonies actives et inactives et des tests *t* pour comparer des covariables du paysage associées aux colonies actives et inactives. Nous avons déterminé que la présence de castors est modulée par la qualité de l'habitat. Leur présence est plus grande dans les zones de plus grande richesse de classes de végétation et de plus grandes proportions d'eaux libres, de tourbières basses riches en nutriments et de marécages à feuillus. Nous avons aussi observé que les colonies actives sont entourées de plus grandes quantités de marécages à feuillus que les colonies inactives. Aucune de nos observations n'indique que le risque de prédation ou les activités industrielles réduisent la présence de castors dans le nord-est de la Colombie-Britannique, bien que l'abondance des castors puisse changer sans modification de leur répartition. Ces travaux jettent un nouvel éclairage sur les facteurs qui influencent la répartition des castors tout en offrant un moyen de prédire la présence d'une espèce clé dans l'écosystème boréal. [Traduit par la Rédaction]

Mots-clés : boréal, *Castor canadensis*, régression logistique multinomiale, castor, modélisation de la répartition d'espèces.

Introduction

A variety of abiotic and biotic factors shape the distribution of species across spatiotemporal scale. Theory suggests that the most limiting of these factors will dictate species occurrence at coarser scales (Rettie and Messier 2000). For example, abiotic factors, such as temperature, restrict the geographic range of many species by exceeding species-specific environmental tolerances (Brennan et al. 2016). At finer scales, biotic factors, such as food availability or the presence of a competitor or predator, might determine species occurrence (Wisiz et al. 2013).

By 1900, North American beavers (*Castor canadensis* Kuhl, 1820) were extirpated from many parts of their historical distribution through excessive harvest (Baker and Hill 2003), but are now

abundant and restored to much of their former range following the implementation of protections in the 1920s and reintroduction efforts throughout the second half of the 20th century (Rosell et al. 2005). Understanding beaver occurrence is paramount, given their large influence on ecosystem structure and function (Naiman et al. 1988). Through the creation of dams, beavers alter plant (e.g., Wright et al. 2002), insect, fish (e.g., Malison et al. 2014), and wildlife communities, but also modify hydrological patterns (Rosell et al. 2005) and nutrient cycling (Naiman et al. 1986).

Beavers use sticks and mud to build lodges for refuge, and dams to deepen and increase the amount of open water. By increasing water depth, beavers can sink food caches adjacent to lodges, which can be accessed under the ice during winter in northern climates (Slough 1978). Increasing the amount of open water by

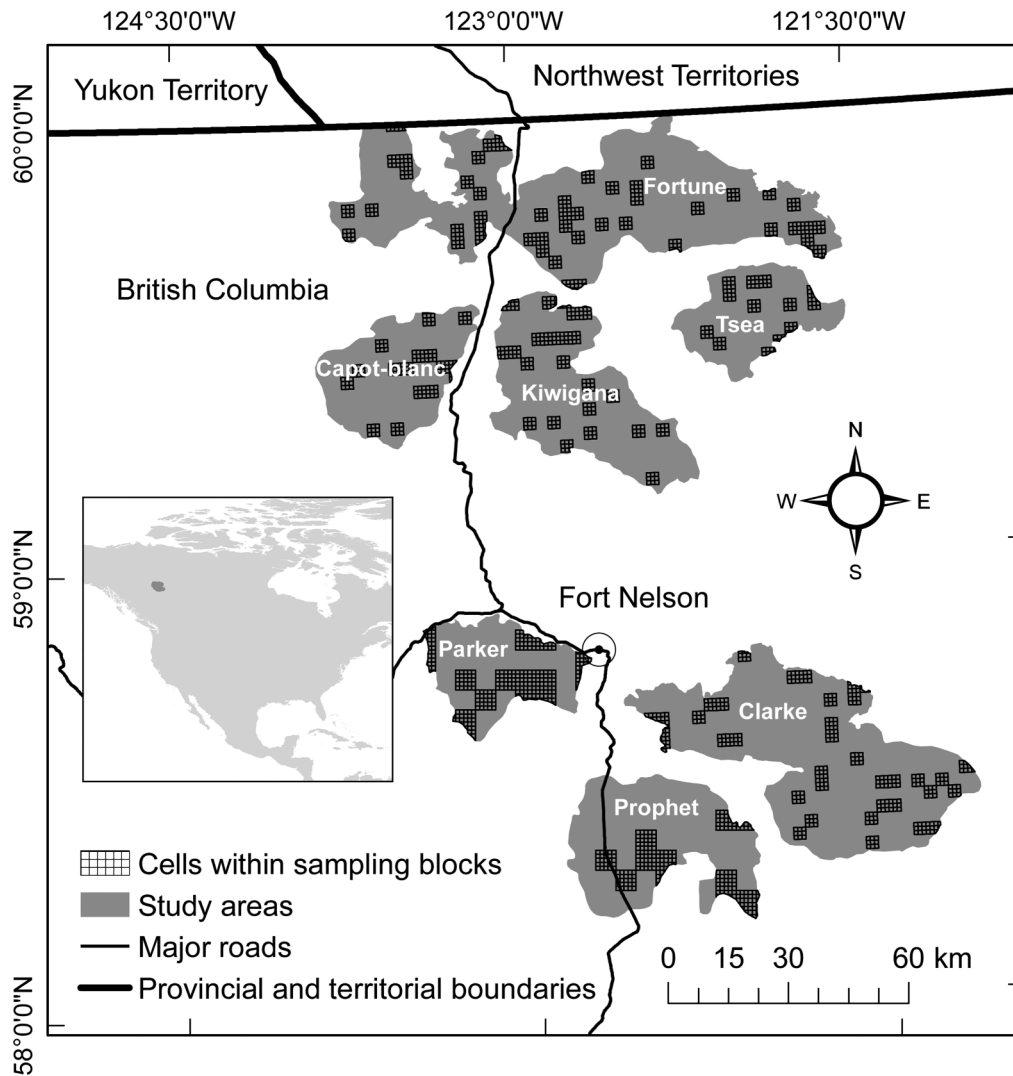
Received 20 November 2017. Accepted 11 January 2018.

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Fig. 1. Blocks sampled for North American beaver (*Castor canadensis*) lodges and winter food caches during fall 2011 and 2012 within seven study areas (Capot-blanc, Clarke, Fortune, Kiwigana, Parker, Prophet, and Tsea) in northeast British Columbia, Canada. Cells within sampling blocks depict the post-sampling division of blocks into 1 km × 1 km cells for the purpose of analyses.



damming and deepening and lengthening canals (Hood and Larson 2015) eases the difficulty in transporting the primary contents of winter food caches, deciduous trees (Slough 1978), and provides a refuge from terrestrial predators (Gable et al. 2016).

Previous studies associated beaver occurrence with greater amounts of open water (Johnston and Windels 2015) and deciduous vegetation (Howard and Larson 1985). The availability of forage (deciduous and aquatic vegetation) is also related to local beaver abundance (Slough and Sadleir 1977; Fryxell 2001). Abandoned lodges are often located in ponds with decreased forage quality (Townsend 1953; Beier and Barrett 1987) and less open water (Cunningham et al. 2006), which is a result of unmaintained dams that no longer impound water. Beaver lodge abandonment and recolonization, however, is dynamic and likely depends, in part, on forage quantity and forage resilience (i.e., ability to regenerate following browsing) (Fryxell 2001). Distance to “source” colonies (colonies where recruitment exceeds mortality), however, might also be important by subsidizing “sink” colonies (mortality exceeds recruitment) and quickening the recolonization of abandoned colonies via immigration (Fryxell 2001).

The influence of predators on beaver occurrence remains uncertain. Where predators occur, beaver foraging strategies reflect a trade-off between maximization of energy and minimization of

predation risk (Baisey and Jenkins 1995; Smith et al. 1994). Potvin et al. (1992) observed a negative correlation between beaver and gray wolf (*Canis lupus* Linnaeus, 1758) densities in Quebec, Canada. Similarly, wolf predation was suggested to be a stabilizing force for beaver abundance on Isle Royale, USA (Romanski 2010). Other studies, however, suggest that even high levels of wolf predation are insufficient to limit beaver population growth (Theberge and Theberge 2004; Sidorovich et al. 2017) and range expansion (Gable and Windels 2017).

Our goal was to evaluate the impact of predation risk on beaver occurrence in northeast British Columbia (BC), Canada, while accounting for habitat quality and the potential influence of anthropogenic disturbance. Recent natural gas development in northeast BC has resulted in an extensive network of roads and seismic lines (3–10 m wide cleared, linear paths created during natural gas exploration). These disturbances, along with the additional roads contributed by forestry activities, might influence beaver occurrence by degrading beaver habitat. We built models to predict the occurrence of beaver colonies and evaluated landscape features surrounding locations containing active and inactive colonies. Consistent with previous research, we predicted that habitat quality would be positively associated with beaver occurrence and that active colonies would be located in areas with

Table 1. Classification of vegetation classes (DeMars 2015) and water using an enhanced wetland classification (EWC) from Ducks Unlimited Canada (2013) and disturbance classes using DataBC layers from the Province of British Columbia (2016).

Vegetation class	Source: layer	Description	Percentage of landscape
Conifer swamp	EWC: conifer swamp	Mineral soils or peatlands with >60% tree cover, primarily black spruce (<i>Picea mariana</i>) and white spruce (<i>Picea glauca</i>)	8
Deciduous swamp	EWC: shrub swamp, hardwood swamp, mixed-wood swamp	Mineral soils with pooled water and >25% deciduous tree cover, primarily paper birch (<i>Betula papyrifera</i>) and balsam poplar (<i>Populus balsamifera</i>)	11
Nutrient-poor fen	EWC: graminoid-poor fen, shrubby-poor fen, treed-poor fen	Peatlands with 25%–60% tree cover, primarily black spruce, tamarack (<i>Larix laricina</i>), and bog birch (<i>Betula pumila</i>)	20
Nutrient-rich fen	EWC: graminoid-rich fen, shrubby-rich fen, treed-rich fen	Peatlands with bog birch, willow (<i>Salix</i> spp.), and alder (<i>Alnus</i> spp.)	6
Treed bog	EWC: treed bog, open bog, shrubby bog	Bogs with black spruce and <i>Spaghnum</i> moss	16
Upland conifer	EWC: upland conifer	Mineral soils with >25% tree cover, primarily black spruce, white spruce, and lodgepole pine (<i>Pinus contorta</i>)	10
Upland deciduous	EWC: upland deciduous, mixed-wood upland	Mineral soils with >25% deciduous tree cover, primarily trembling aspen (<i>Populus tremuloides</i>) and paper birch	19
Open water	EWC: open water	Water	2
Other	EWC: upland other, cloud shadow, anthropogenic	Rocky uplands, areas obscured by clouds in imagery, and anthropogenic features, including houses, roads, and well pads	3
New cutblock	DataBC: forest openings	<15-year-old cutblocks	1
Old cutblock	DataBC: forest openings	~16- to 40-year-old cutblocks	1
New burn	DataBC: historical fire perimeters	<15-year-old burns	2
Old burn	EWC: burn	~16- to 40-year-old burns	1

higher habitat quality in comparison to inactive colonies. We also predicted that areas with a higher probability of wolf use would be negatively correlated with beaver occurrence. We did not anticipate that anthropogenic disturbance would be correlated with beaver occurrence, because the total area of disturbed vegetation is relatively small (<1% of study areas) in northeast BC, despite the widespread nature of roads and seismic lines. This is the first research to explore the potential impact of wolves and natural gas development on beaver occurrence. Our study illuminates factors limiting the distribution of beavers and allows a better prediction of beaver occurrence across boreal ecosystems.

Materials and methods

Study area

The vast peatland complexes (bogs and fens), riparian areas, and deciduous and mixed-wood uplands of northeast BC (DeLong et al. 1991) span an area of moderate topography (214–1084 m above sea level). Dominant tree species include black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) and white spruce (*Picea glauca* (Moench) Voss), trembling aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), balsam poplar (*Populus balsamifera* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), and paper birch (*Betula papyrifera* Marshall) (DeLong et al. 1991). The climate consists of long, harsh winters and short summers (DeLong et al. 1991). Commercial logging in BC has endured since the 1800s and continues to contribute resource roads, but the recent expansion (<25 years) of natural gas development in northeast BC has led to high road (0.79 km/km²) and seismic line (1.84 km/km²) densities, along with well pads and pipelines. The expanded anthropogenic footprint coincided with the decline of BC's threatened boreal caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) population (Culling and Cichowski 2017) and resulted in the need for a better understanding of predator-prey interactions. Seven study areas (Capot-blanc, Clarke, Fortune, Kiwigana, Parker, Prophet, and Tsea) were selected that correspond to existing ef-

Table 2. Competing multinomial logistic regression models for active and inactive North American beaver (*Castor canadensis*) colony occurrence in northeast British Columbia, Canada, evaluated using Akaike's information criterion corrected for small sample sizes (AIC_c).

Model	k	Log-likelihood	AIC _c	ΔAIC _c
Habitat quality	16	-838.8	1710.1	0.0
Habitat quality and mean wolf RSF	18	-837.9	1712.2	2.1
Habitat quality and max. wolf RSF	18	-838.0	1712.5	2.5
Habitat quality and disturbance	20	-838.6	1717.9	7.8
Mean wolf RSF	8	-884.1	1784.4	74.3
Max. wolf RSF	8	-912.9	1841.9	131.8
Disturbance	10	-932.7	1885.5	175.4

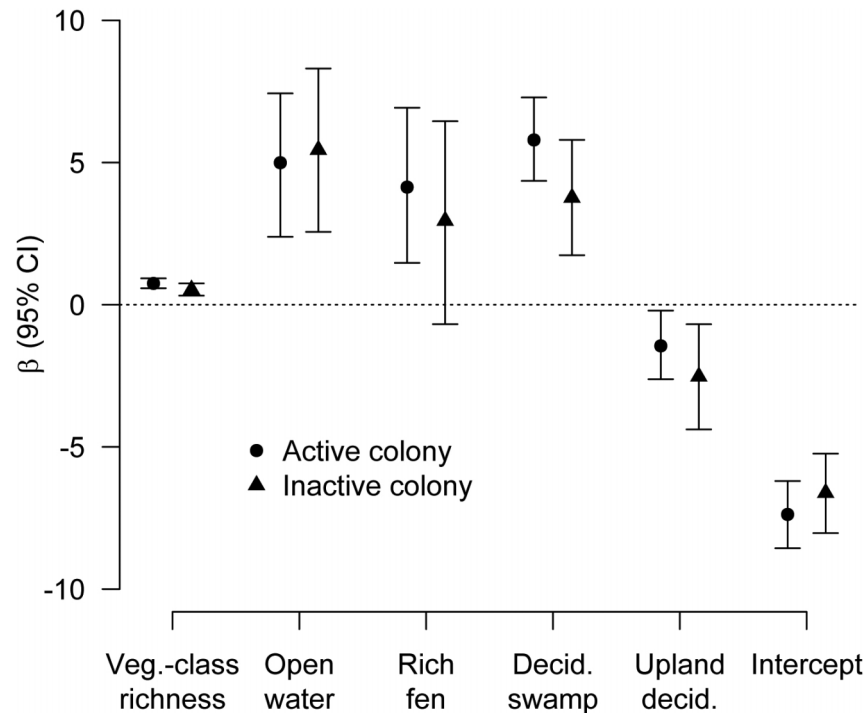
Note: Wolf resource selection function (RSF) indicates the inclusion of mean and maximum (max.) values for each cell of the relative probability of wolf use predicted using a previously developed RSF (Mumma and Gillingham 2017). *k* is the number of parameters and disturbance is anthropogenic disturbance.

forts researching other prey and predator species in northeast BC (Fig. 1). Since 1926, trapping in BC has been regulated through the assignment of spatially separated traplines (~2900 across the province) to licensed individuals (Hatler and Beal 2003). Beavers fall into the category of a class 1 furbearer, indicating that they can be managed on a trapline basis and that individual trappers are allowed to determine appropriate trapping intensity to sustain harvestable populations (Hatler and Beal 2003). Beaver densities and the number of beaver harvested each year are unknown within our study areas. Wolf densities (7.4/1000 km²) have only been estimated within the Clarke study area (Serrouya et al. 2016).

Aerial surveys

Data was provided by the BC Ministry of Forest, Lands, and Natural Resource Operations and Rural Development (FLNRORD). A grid of 5 km × 5 km sampling blocks were overlaid across the Parker and Prophet study areas (Fig. 1), and 10 and 8 blocks, respectively, were randomly selected for aerial surveys (Thiessen

Fig. 2. Coefficients (β) and 95% confidence intervals (CI) for the most parsimonious multinomial logistic regression model predicting active and inactive colony occurrence of North American beaver (*Castor canadensis*) for 1 km \times 1 km cells in northeast British Columbia, Canada. Covariates include vegetation-class (veg.-class) richness, as well as the proportions of open water, nutrient-rich fen (rich fen), deciduous (decid.) swamp, and upland deciduous.



and DeMars 2012). Logistical restraints limited the percentage of blocks surveyed to \sim 20% of each study area. Blocks overlapping study area boundaries were clipped and, when applicable, combined with adjacent partial blocks. In early November 2011, before freeze-up, a helicopter was flown at a mean height of 100 m and water bodies, wetlands, and water courses were surveyed for beaver lodges and winter food caches (Thiessen and DeMars 2012). When multiple lodges were in close proximity (<10 m), they were treated as a single beaver colony and the approximate centroid of lodge locations was recorded. Active beaver colonies were distinguished by the presence of a winter food cache (Slough 1978) adjacent to a lodge, consisting of a collection of primarily deciduous branches stored beneath the water. When occupying water courses, beavers often forgo lodge building and instead opt to construct bank dens. Given that bank dens are difficult to detect, the presence of a winter food cache was used to identify locations with active beaver colonies. This approach, therefore, did not allow the identification of previously occupied (inactive) bank dens. In early October 2012, 3 km \times 3 km blocks were overlaid across five additional study areas (Fig. 1) and randomly selected blocks (Capot-blanc: 15 blocks; Clarke: 33 blocks; Fortune: 45 blocks; Kiwigana: 22 blocks; Tsea: 11 blocks) were surveyed.

Data analysis

To correct for differences in sampling block size between years, we divided survey blocks into 1 km \times 1 km cells in ArcGIS (ESRI 2015). Using lodge and winter-cache locations, we assigned each cell to one of three categories (active colony, inactive colony, or absent). Active colony cells contained at least one active lodge or at least one active location (presence of winter food cache) along a water course, whereas inactive colony cells only contained inactive lodges. Absent cells lacked both active (lodge with winter food cache or winter food cache along water course) and inactive colonies.

Next, for each cell we estimated landscape covariates associated with habitat quality, risk of wolf predation, and anthropogenic disturbance. We reclassified a boreal vegetation layer (30 m \times 30 m pixel; Ducks Unlimited Canada 2013) using the methods of DeMars (2015) into conifer swamp, deciduous swamp, nutrient-poor fen, nutrient-rich fen, treed bog, upland conifer, upland deciduous, and other, which included several nonhabitat classes (e.g., anthropogenic, rock) (Table 1). We also classified open water and new (16–40 years) and old (≤ 15 years) cutblocks and burns (Province of British Columbia 2016; Table 1). Deciduous vegetation is an important food source for beavers (Busher 1996; Salandre et al. 2017) and has functioned as an indicator of habitat quality in other studies (Fryxell 2001; Severud et al. 2013a). Hence, we determined the proportion of three vegetation classes known to contain deciduous trees for each 1 km \times 1 km cell. Nutrient-rich fen primarily contains bog birch (*Betula pumila* L.), willows (species of the genus *Salix* L.), and alders (species of the genus *Alnus* Mill.) (Table 1). Deciduous swamp is composed of $>25\%$ deciduous tree cover, mostly consisting of paper birch and balsam poplar (Table 1). Upland deciduous is also composed of $>25\%$ tree cover, with trembling aspen and paper birch predominating (Table 1). We also estimated the proportion of open water. Beavers are associated with landscape heterogeneity (Wright et al. 2002); therefore, we quantified vegetation-class richness (number of vegetation classes/cell) for each cell. We used a resource selection function (for details see Mumma and Gillingham 2017) previously developed during spring (16 May – 15 July) to predict the relative probability of wolf use for 25 random locations within each cell (excluding open water). A resource selection function (RSF) uses model coefficients to relate a suite of landscape covariates to the relative probability of use. We then identified the mean and maximum (max.) predicted probability of wolf use across random locations for each cell. We used road (Province of British Columbia 2016) and seismic line layers (British Columbia Oil and Gas

Commission 2016) to characterize disturbance by calculating the density (km/km²) of roads and seismic lines for each cell. We did not evaluate the influence of cutblocks and burns because they are less widespread in northeast BC compared with anthropogenic linear features.

We used mixed-effects multinomial logistic regression to model beaver occurrence, with the package MCMCglmm (Hadfield 2010) in program R (R Core Team 2015). This modelling framework is an extension of logistic regression that permits the modelling of >2 discrete outcomes. Each cell i has a set of M covariate values X_i ($X = X_1, X_2, \dots, X_M$) that are related to the probability (π_i) of K outcomes via a set of outcome-specific coefficients β_k . In our case, we predicted the probability of a cell containing an active colony (eq. 1) and inactive colony (eq. 2), whereas the K th outcome (absent) served as the reference (eq. 3) and the K probabilities of each cell summed to one.

$$(1) \quad \pi_{i1} = \frac{\exp(\beta_1 X_i)}{1 + \sum_{k=1}^{K-1} \exp(\beta_k X_i)}$$

$$(2) \quad \pi_{i2} = \frac{\exp(\beta_2 X_i)}{1 + \sum_{k=1}^{K-1} \exp(\beta_k X_i)}$$

...

$$(3) \quad \pi_{iK} = \frac{1}{1 + \sum_{k=1}^{K-1} \exp(\beta_k X_i)}$$

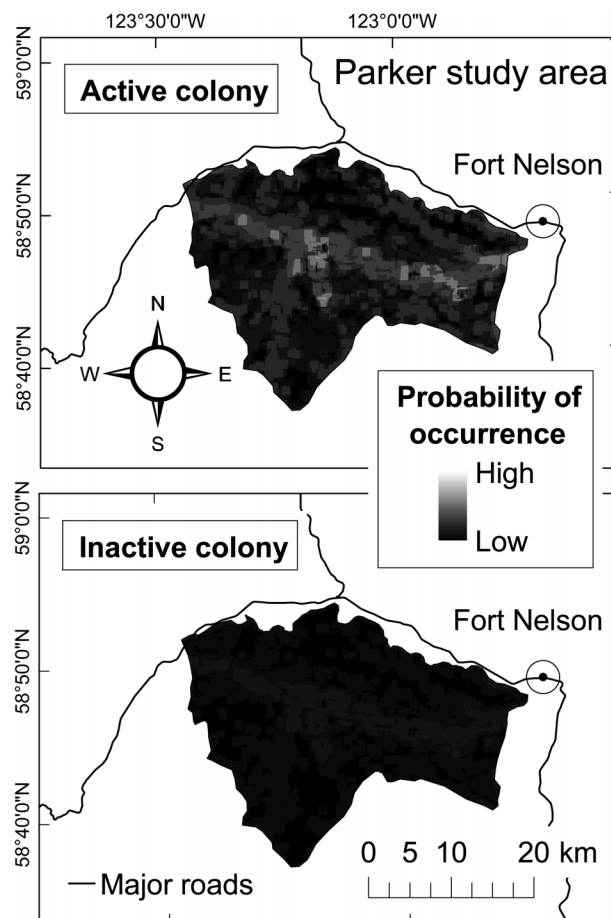
We built competing models theorized to influence beaver occurrence representing our individual hypotheses (habitat quality, predation risk (i.e., mean wolf RSF and max. wolf RSF), and disturbance) and combinations of these hypotheses (habitat quality + mean wolf RSF, habitat quality + max. wolf RSF, and habitat quality + disturbance). The most parsimonious model was identified using Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). Each model included survey block as a random effect to account for spatial autocorrelation between cells of the same block. We used the relative operating characteristics (ROC) test to assess model fit (Mason and Graham 2002; package ROCR: Sing et al. 2005) for each outcome.

The model with the lowest AIC_c value was used to predict the probabilities of occurrence for active colonies (i.e., lodge with winter food cache or winter food cache along water course) and inactive colonies across each study area to allow for a visual comparison of the predicted distributions of active and inactive colonies. We also compared landscape covariates (i.e., habitat quality, predation risk, and anthropogenic disturbance) of active colony and inactive colony cells using two-sample t tests for unequal variances ($\alpha = 0.05$; Welch 1947).

Results

Aerial surveys detected a winter food cache (active colony) at 446 (52%) out of 862 total colonies (active and inactive). The number of colonies/km of shoreline was 0.44 and 0.88 for active colonies and total colonies, respectively. The number of colonies/km² was 0.30 and 0.59 for active colonies and total colonies, respectively. Dividing our 144 complete and partial survey blocks resulted in 1467 (1 km × 1 km) cells. Three hundred and ten of these cells contained at least one active colony or winter food cache (active colony cells) and 110 contained only inactive colonies

Fig. 3. The predicted probabilities of containing an active or inactive North American beaver (*Castor canadensis*) colony for each 1 km × 1 km cell within the Parker study area in northeast British Columbia, Canada.

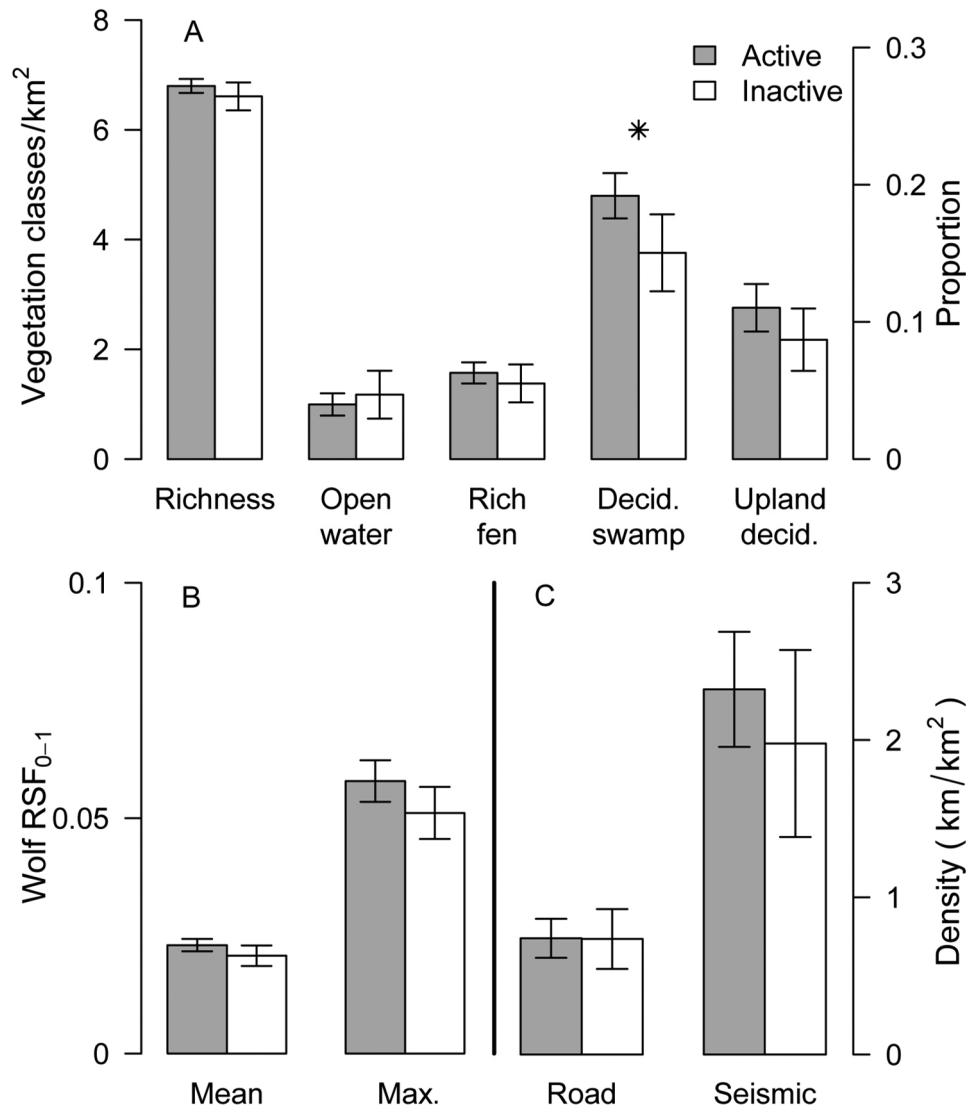


(lodges without winter food cache). Habitat quality was the most parsimonious model predicting beaver occurrence and included vegetation-class richness and the proportions of open water, nutrient-rich fen, deciduous swamp, and upland deciduous (Table 2). The model was predictive with ROC values for individual outcomes ranging from 0.72 to 0.75. Both active colony and inactive colony occurrence was positively related to vegetation-class richness and the proportion of open water, nutrient-rich fen, and deciduous swamp, and negatively related to the proportion of upland deciduous (Fig. 2). The models containing wolf use or disturbance covariates were less supported than the habitat-quality model (Table 2). Models combining habitat-quality and wolf-use covariates were the second (habitat quality + mean wolf RSF) and third (habitat quality + max. wolf RSF) most parsimonious models and demonstrated some support ($>4 \Delta AIC_c$; Table 2). Coefficients for habitat-quality covariates in the combined models (Supplementary Table S1)¹ were similar to coefficients in the habitat-quality-only model (Fig. 2). Wolf-use coefficients in the combined models were positively correlated with beaver occurrence (Supplementary Table S1).¹

To further examine beaver occurrence, we used the habitat-quality model to predict the probabilities of occurrence for active and inactive colonies. The predicted probabilities of active colonies and inactive colonies demonstrated similar trends, but the

¹Supplementary tables are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2017-0327>.

Fig. 4. Comparing habitat quality (A), risk of gray wolf (*Canis lupus*) predation (B), and anthropogenic disturbance (C) covariates of 1 km × 1 km cells containing active and inactive North American beaver (*Castor canadensis*) colonies in northeast British Columbia, Canada, using two-sample *t* tests for unequal variances ($\alpha = 0.05$; Welch 1947). The asterisk (*) indicates a significant difference. Mean and maximum (max.) values of the relative probability of wolf use were estimated for each cell. The relative probability of wolf use (standardized between 0–1) was predicted for 25 random locations within each cell (excluding open water) using a previously developed wolf resource selection function (RSF) (Mumma and Gillingham 2017). Deciduous = decid.



probability of containing an active colony was generally higher than the probability of containing an inactive colony (Fig. 3). The only landscape covariate to demonstrate a significant difference ($t_{[190.4]} = 2.5$, $p = 0.012$; Supplementary Table S2¹) between cells containing active and inactive colonies was the proportion of deciduous swamp (Figs. 4A, 4B, 4C) — the proportion of deciduous swamp was greater in active colonies.

Discussion

Our analyses indicated that habitat quality (related to vegetation classes) drives beaver occurrence in the boreal landscapes of northeast BC. Our habitat-quality model was the most parsimonious (Table 2), and active and inactive colonies were positively associated with vegetation-class richness, open water, nutrient-rich fen, and deciduous swamp (Fig. 2). A negative relationship was observed between occurrence and upland deciduous, which likely reflects the drier nature and lower damming potential (Cunningham et al. 2006) of upland habitats. The proportion of

deciduous swamp was also higher in areas with active colonies compared with inactive colonies (Figs. 4A, 4B, 4C). Our analyses did not provide evidence that wolf use or recent disturbances, as indexed by anthropogenic linear features, decreased the likelihood of beaver occurrence (Table 2, Supplementary Table S1¹).

Previous research reflects the influence of habitat quality on beaver colonization, abandonment, and behaviour. During colonization, high-quality sites are occupied first and less likely to be abandoned (Cunningham et al. 2006). Other studies have linked forage availability (Beier and Barrett 1987) and composition (aspen stands are more prone to depletion) to abandonment (Slough and Sadleir 1977) and to beaver colony size (Fryxell 2001). Poor habitat also has been associated with reduced body condition (Smith and Jenkins 1997) and decreased productivity (Severud et al. 2013b), which increases the likelihood of lodge abandonment (Fryxell 2001). Furthermore, beaver foraging strategies reflect an energy maximization strategy (Gallant et al. 2016) through the selection of high-value forage species, while accounting for the energetic

costs associated with food-item size and the risks (predators) associated with increasing distance from water (Fryxell and Doucet 1993; Gerwing et al. 2013).

Risk of wolf predation did not correspond to lower beaver occurrence in our analyses. Models including wolf use, in addition to habitat-quality covariates, were less supported than our habitat-quality-only model (Table 2), and in contrast to our predation risk hypothesis, wolf use was positively correlated with beaver occurrence (Supplementary Table S1).¹ This suggests that wolves might be selecting for locations where beavers occur in snow-free months, but fail to negatively impact beaver occurrence. Although some studies suggest that wolves reduce beaver densities (Potvin et al. 1992; Romanski 2010), other studies infer that predators are incapable of limiting beaver population growth despite high levels of predation (Theberge and Theberge 2004; Sidorovich et al. 2017). Predation risk is also demonstrated to impact the foraging behaviour of beavers (Smith et al. 1994), although the strength of this effect is theorized to be of less importance than the energetic costs of foraging (Salandre et al. 2017). Given the scale of our analyses (colony level), predation-caused changes in beaver abundance could have gone undetected. Wolves might impact beaver abundance through a reduction in the number of beavers per colony, but have no influence on colony occurrence, contingent upon predation rate, colony productivity, and immigration from other colonies.

Our most parsimonious beaver occurrence model (habitat quality) closely aligned with wolf resource selection patterns. In spring, wolves selected for vegetation-class richness, locations near water, nutrient-rich fen, and deciduous swamp, and avoided upland deciduous (Mumma and Gillingham 2017). These similar patterns between beaver occurrence and wolf selection are consistent with wolves occupying locations near lodges in snow-free months to capitalize on a readily available food source, beavers (Gable et al. 2016), but low fix rates for many of our wolf collars prevented us from investigating this further. We also do not know the importance of beavers as a food item for wolves in this system. Indeed, wolves might be selecting these locations for reasons other than or in addition to beaver availability. Future research should seek to identify the importance of beavers in wolf diets across systems and use high fix rate collars to examine the behaviour of wolves near beaver colonies. Of particular interest would be multiyear studies examining wolf space use in relation to beaver colony locations to evaluate if fluctuations in local colony abundance correspond to wolf presence.

Despite widespread disturbances in northeast BC, we found no evidence that roads and seismic lines were impacting the distribution of beaver. The preservation of aspen stands is a means of assuring high-quality beaver habitat (Slough and Sadleir 1977) and permanent anthropogenic features, such as roads, have the potential to reduce aspen and other high-value tree species. However, the total area of disturbed vegetation resulting from anthropogenic linear features is small (<1% of study areas) in northeast BC. In addition, it is unclear if anthropogenic disturbance degrades habitat or improves habitat through the creation of early seral vegetation. Landriault et al. (2009) reported that post-clearcut shorelines (20–35 years following forest harvesting) were a good predictor of activity at a beaver lodge. This suggests that cutblocks adjacent to water have a successional trajectory that ultimately provides high-quality habitat.

At the scale of our analyses (1 km × 1 km cells), we assumed that the factors influencing beaver occurrence would be consistent for water bodies, wetlands, and water courses. Our sample size, however, prohibited us from evaluating that assumption. Likewise, the sampling scheme did not permit us to detect abandoned bank dens along water courses, and although our sampling spanned 2 years, each study area was only sampled once, thus precluding an evaluation of temporal changes in colony status (active or inactive). An additional limitation was our inability to determine

the probability of detection for lodges and winter food caches. Although we think that the detection of colonies was likely high, given our sampling method (Johnston and Windels 2015), we concede that we likely marked some active colonies as inactive because of inconspicuous or absent winter food caches.

Following years of excessive harvest, North American beaver populations have largely recovered and again exert a large influence on their surroundings (Rosell et al. 2005). Here, we increased our knowledge of beaver ecology across a portion of the northern boreal forest. For the study populations, occurrence was largely explained by habitat quality. Neither the threat of wolf predation, nor widespread industrial activity from natural gas development, influenced beaver occurrence. However, development of oil and gas reserves in the boreal forest is continuing and climate change may further influence the distribution and population dynamics of beavers. Therefore, monitoring should continue (Jarema et al. 2009).

Acknowledgements

We acknowledge the BC Oil and Gas Research and Innovation Society for funding this study. We thank C. Thiessen, M. Anderson, and Diversified Environmental Services for sampling design and data collection. We also thank D. Seip, M. Watters, and S. Wilson for their roles in facilitating this research. We thank the BC Oil and Gas Commission, Research and Effectiveness Monitoring Board, Qwest Helicopters, and Bailey Helicopters for logistical and field support, and thank Ducks Unlimited Canada for allowing use of their boreal vegetation layer. We also thank the two anonymous reviewers for their insightful comments.

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