

Resource separation analysis with moose indicates threats to caribou in human altered landscapes

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Species recovery is often impeded by inadequate knowledge on mechanisms of community interactions that cause and exacerbate species endangerment. Caribou and wild reindeer *Rangifer tarandus* are declining in many regions of their circumpolar range likely because of human-induced landscape changes. In general, their niche specialization enables *Rangifer* to survive in nutrient-poor habitats spatially separated from other ungulates and their shared predators. Research has indicated that shifts in primary prey distribution following human landscape alteration may result in spatial overlap with *Rangifer*. We studied overlap relationships of woodland caribou *R. t. caribou* and moose *Alces alces*, quantified by their differential use of environmental resources, and evaluated the role of human landscape alteration in spatial separation in south-western Canada. Anthropogenic conversion of old-growth forests to early seral stands is hypothesized to decrease the spatial separation between caribou and moose, the dominant prey for wolves *Canis lupus*, contributing to increased caribou mortality. Redundancy analysis (RDA) was first used to examine coarse scale resource separation across our study area. Second, at a finer spatial scale, we used logistic regression to compare resource- and spatial separation of sympatric pairs of 17 moose and 17 caribou. Finally, we tested if the frequency of predator-caused caribou mortalities was higher in regions with higher moose resource use. Although environmental resource separation was strong at the coarser scale, we observed substantial spatial overlap (> 50%) at the finer scale. In summer we reported a significant positive relationship between spatial overlap of moose and caribou and the degree of human landscape alteration. Most importantly, locations of caribou mortalities corresponded with areas of high resource use by moose in summer. Thus, consistent with the spatial separation hypothesis, our research suggests that early successional forest stages may decrease spatial separation between caribou and moose, resulting in increased mortality risk for threatened caribou.

Over the last century humans have significantly impacted the global environment, leading to dramatic changes in species distributions and increased extinction rates well above natural background levels (Chapin et al. 2011). Ecosystem functions and processes are commonly influenced by interactions among species and human-induced changes of systems such as competition and trophic interactions can have wide-ranging ecosystem effects. Direct (e.g. habitat loss or over-exploitation) and indirect (e.g. changes in community interactions) mechanisms often act concurrently and their combination can drive vulnerable populations towards extinction (Brook et al. 2008). Therefore, conservation biologists need to understand the mechanisms leading to population declines, and complex interactions among those mechanisms to manage and conserve species. Unfortunately, how human landscape alteration can affect spatial overlap of species and their use of resources, and thus competitive interactions, often remains unstudied in many systems. For example, interactions of

species in the same trophic level can lead to declines when indirectly mediated by a shared predator (DeCesare et al. 2010). Apparent competition is the process by which two prey species can affect each other's growth rates through their contribution to the numerical response of a shared predator (Holt and Lawton 1994). Examples for declining species due to human-induced apparent competition include Vancouver Island marmots *Marmota vancouverensis* (Bryant and Page 2005), Sierra Nevada bighorn sheep *Ovis canadensis californiana* (Johnson et al. 2012) or the extinct Macquarie Island parakeet *Cyanoramphus novaezelandiae erythrotis* (Taylor 1979).

One of the most important relationships that permit species coexistence is the differential use of physical and biological components (i.e. resources), which places sympatric species into specific habitats (Rosenzweig 1981). Following Hutchinson (1957), in the absence of inter-specific interactions (e.g. predation and competition) a species can occupy a geographical region where the abiotic

conditions (e.g. climate) are suitable for its survival and reproduction, called the fundamental niche. Whenever species coexist in geographical space, a species occupies only a proportion of its fundamental niche due to interspecific interactions, which is called the realized niche. The behavioral process of habitat selection (Johnson 1980) often leads to spatio-temporal separation among species (Chesson and Kuang 2008) due to differing resource preferences (e.g. diet), facilitating their sympatric coexistence through the differentiation of their realized niches. Therefore, community studies often focus on assessing environmental gradients of resources, linking resource variables at used (e.g. global positioning (GPS) collar data) or occupied locations in geographic space (i.e. habitat) to realized niches in environmental space (Hirzel and Le Lay 2008). The arrangement of resources in geographic space may determine species distribution and the degree sympatric species' realized niches overlap or separate. In sufficiently heterogeneous habitats, apparently competing prey species may be able to spatially separate and thereby avoid shared predation by isolation in spatial refuges due to this differential resource selection (DeCesare et al. 2010). Lastly, it is commonly assumed that a species' resource selection and therefore, its geographical distribution, is in close relationship with its ecological requirements that permit positive population growth (Hirzel and Le Lay 2008). However, especially in the face of human landscape alteration, animals may occupy suboptimal habitat where death rates may exceed birth rates (Pulliam 2000).

An example for the importance of human-altered resource distribution driving species declines are caribou and many wild reindeer *Rangifer tarandus* populations, which are decreasing throughout their circumpolar range coincident with landscape alteration (e.g. implementation of infrastructure, mineral extraction or forest harvesting; Vors and Boyce 2009). A growing body of literature describes how human landscape changes have led to shifts in the distribution of reindeer and caribou (Vistnes et al. 2001) or altered predator-prey relationships (Seip 1992, Kojola et al. 2004) and thereby have directly and indirectly decreased population size of these habitat specialists (Nellemann and Cameron 1998). As in other parts of *Rangifer* range, conservation of woodland caribou is amongst the most pressing conservation challenges in Canada. In 2000, boreal and southern mountain woodland caribou were federally listed as threatened under the Canadian Species at Risk Act (SARA). Although human landscape change has been identified as the ultimate cause for woodland caribou declines (McLoughlin et al. 2003), the proximal mechanisms are hypothesized to be mediated by changes in predator-prey dynamics in the large mammal community in which caribou occur (James et al. 2004). This necessitates a spatial community approach to caribou conservation.

While moose *Alces alces* and woodland caribou *R. t. caribou* (hereafter caribou) are sympatric throughout the boreal forest, they are hypothesized to coexist through their differential use of resources (Boer 2007). For example, caribou diet is comprised of terrestrial and arboreal lichens, especially during winter (Thomas et al. 1996), and caribou select large contiguous habitat patches of low

productivity, older seral conifer stands where lichen biomass is highest. In mountain regions, such forests are generally at higher elevations and caribou often exhibit seasonal altitudinal migration (Seip 1992). Moose, in contrast, are generalist browsers of early succession shrubs that prosper following fire or forestry (Peek 2007). Despite this broad forage separation, their diet often overlaps in summer when both species consume forbs and deciduous plants (Boer 2007). The spatial separation hypothesis suggests that the niche specialization by caribou enables them to survive in nutrient-poor habitats at low densities, spatially separated from other ungulates and their predators, which reduces the negative effects of apparent competition and increases survival (Bergerud and Page 1987, Seip 1992). However, the conversion of old-growth forests to early seral stage forests is hypothesized to increase the abundance of moose, the dominant prey for wolves *Canis lupus*, and thereby increase wolf densities (Kojola et al. 2004, Serrouya et al. 2011). Predation by wolves is a leading cause of caribou mortality (Wittmer et al. 2005), and wolves (as well as other predators) select for land-cover types with high ungulate forage biomass (e.g. shrub communities, burns, logged areas; Mosnier et al. 2008, Gurarie et al. 2011) to increase encounter rates with prey (Hebblewhite et al. 2005). Thus, understanding how the realized niches of moose and caribou differ in the context of spatial separation is key to evaluating the mechanisms of apparent competition.

We aimed to determine the relationship between the separation of realized niches of moose and caribou and human landscape alteration by relating data of used animal locations to environmental covariates (Chesson and Kuang 2008). As noted above, the geographic distribution of a species may not always reflect its ecological requirements (i.e. population growth may be negative; Hirzel and Le Lay 2008). While we did not assess growth rates of moose and caribou populations, we will use the term 'resource separation' as a proxy for separation of realized niches herein. Further, because ungulates respond to limiting factors in their environment in a hierarchical fashion across spatial scales (Senft et al. 1987), hierarchical approaches should also be considered when comparing realized niches of sympatric species (Ihl and Klein 2001). First, we tested for resource separation by assessing the structure of the caribou and moose realized niches explained by environmental variables at a coarser scale across caribou herds within our study area using redundancy analysis (RDA; ter Braak 1995). We expected substantial resource separation at this coarser scale, because research has shown that caribou exhibit stronger sensitivity to human landscape alteration at coarser spatial scales (e.g. landscape scale versus within-home range scale according to Johnson 1980, Polfus et al. 2011, DeCesare et al. 2012b), while moose are expected to select browse-rich habitats often associated with human resource extraction activities (Boer 2007). Second, we tested whether both resource and spatial separation between sympatric caribou and moose was lower at finer spatial scales in human altered landscapes by comparing resource use of sympatric individual caribou and moose with logistic regression (Latham et al. 2011a) and overlap indices (Schoener 1974). In contrast to the coarse scale,

we expected greater resource overlap of paired (i.e. sympatric) caribou and moose in regions with high human landscape alteration, due to the limited capability of caribou to space away and avoid resource overlap with moose at these finer scales (Bergerud and Page 1987). Moreover, we expected resource overlap to be higher during summer due to increased forage overlap between moose and caribou (Boer 2007). Finally, the spatial separation hypothesis predicts increased risk of caribou mortality in areas of higher probability of moose occurrence (McLoughlin et al. 2005). Therefore, we also examined the relationship between predation-caused mortalities of caribou and spatial predictions of the probability of resource use by moose and caribou in geographical space.

Methods

Study area

We assessed spatial relationships of caribou and moose in an approximately 36 000 km² study area in the foothills and mountains of west-central AB and east-central BC within the ranges of six declining spatially distinct woodland caribou herds: A La Peche (ALP), Red Rock Prairie Creek (RPC), Little Smoky (LSM), the Narraway (NAR), Redwillow (RW) and the Tonquin (TON) in Jasper National Park (Fig. 1). Human landscape change varied throughout the study area with low human landscape alteration and a high proportion of protected areas in the west. The eastern part of the study area was characterized by provincial lands managed primarily for resource extraction, with correspondingly higher human landscape alteration in the form of oil and gas extraction and forestry exploitation and therefore high densities of forest harvesting (mainly clear-cut block harvesting) and linear developments (e.g. roads, pipelines, seismic lines). Anthropogenic impacts were greatest in the LSM caribou range. Elevations followed an increasing gradient from east to west from about 500 to > 3000 m. Lower elevations were characterized by mixed-wood forests, comprised mainly of trembling aspen *Populus tremuloides*, lodgepole pine *Pinus contorta*, white spruce *Picea glauca*, and black spruce *Picea mariana*; while the western forests in the mountain region, were dominated by lodgepole pine and Engelmann spruce *Picea engelmannii*. Moose and white-tailed deer *Odocoileus virginianus* comprised the majority of the ungulate population, whereas elk *Cervus canadensis*, mule deer *Odocoileus hemionus* and woodland caribou were less common. Further, bighorn sheep *Ovis canadensis* and mountain goats *Oreamnos americanus* inhabited the mountain region.

Animal capture

We captured and radio-collared moose via net-gunning (Barrett et al. 1982) in winters of 2007/2008 and 2008/2009. We used data from Global Positioning System (GPS) collars (ATS G2000 GPS collars; Advanced Telemetry Systems, Isanti, MN, USA) deployed on ten female and seven male moose within and adjacent to caribou population home ranges (Fig. 1). We radio-collared female and male

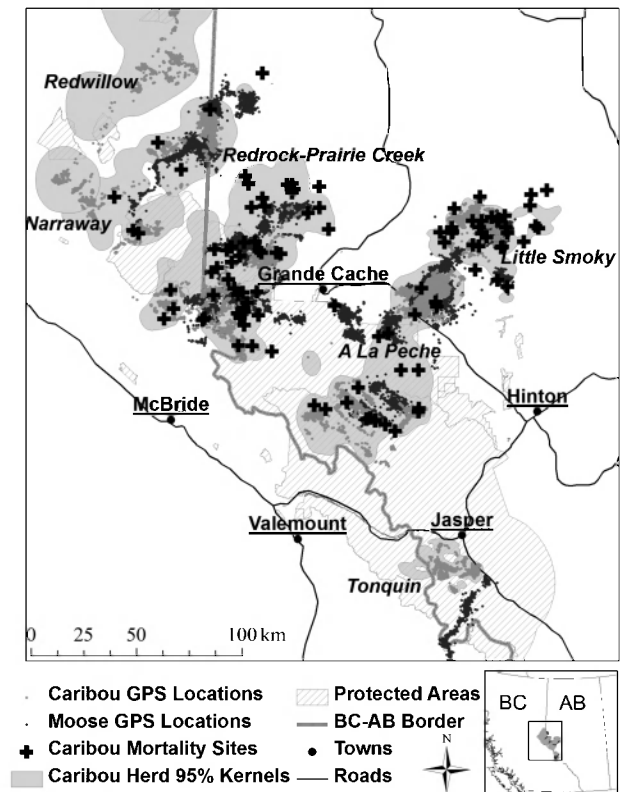


Figure 1. Study area in west central Alberta (AB) and east central British Columbia (BC). In this study we used global positioning (GPS) collar data from 17 moose and 17 caribou. Moose GPS collars were deployed between winters 2007/2008 and 2009/2010 within or adjacent to caribou herd home ranges. GPS locations from caribou were collected between winters 2006/2007 and 2009/2010.

moose to evaluate population-level habitat use and moose population overlap with female caribou. For threatened caribou populations, female caribou are most relevant for monitoring population growth rates (DeCesare et al. 2012a). Therefore, we used GPS collar (GPS 3300, 4400, LOTEK Engineering, Newmarket, ON, Canada) data from 17 female caribou, captured using the same methods as described above for moose. Net-gunning protocols were approved by the Univ. of Montana Animal Care and Use Protocol 056-56MHECS-010207 and 059-09MHWB-122109, Alberta Sustainable Resource Development licenses no. 21803, 27086, 27088, 27090 and Parks Canada permit JNP-2007-952. Both moose and caribou GPS collars collected locations every two to four hours, which we re-sampled to a consistent four-hour relocation schedule for one year. Fix rate success of < 90% can cause habitat-induced bias in resource selection studies (Frair et al. 2004). In our study, fix-rates for moose and caribou were 92.4 and 90.3% respectively. As a result, we did not correct for habitat-induced fix-rate bias. We conducted all analysis for two seasons, summer and winter. Woodland caribou within our study area are partially migratory (McDevitt et al. 2009), and we defined summer (16 May–16 October) and winter (17 October–15 May) seasons according to nonlinear regression analysis of mean migration dates (DeCesare et al. 2012b).

Coarse-scale caribou–moose resource separation

We first assessed resource separation of caribou and moose populations by measuring the realized niche position as a function of a suite of environmental covariates for caribou and moose used locations across our study area (i.e. similar to the second order scale described by Johnson (1980)) using the ordination method of stepwise redundancy analysis (RDA; ter Braak 1995, Bowman et al. 2010). In RDA, the ordination axes for the species matrix are constrained to be linear combinations of the columns of the environmental matrix to obtain the best linear combinations of environmental variables that maximise resource separation between species. Thus, the distribution of the two species along these environmental gradients can be considered as the realized niche within our study area (i.e. coarse scale). We overlaid a 500×500 m sampling grid (largest resolution of GIS data sets; Supplementary material Appendix 1, Table A1) onto our study area and assessed the presence of GPS locations from each species in each grid cell. Because RDA excludes null values (i.e. grid cells without observations), the sample size for RDA was constituted by all grid cells used by at least one species ($n_{\text{summer}} = 6175$, $n_{\text{winter}} = 7309$). Continuous environmental variables (Supplementary material Appendix 1, Table A1) were averaged within each grid cell. For categorical variables (i.e. landcover types) we estimated proportions within each grid cell in ArcGIS Desktop 9.3.1 software (ESRI, Redlands, CA) and arcsine square root transformed them. Monte Carlo permutation tests were used to assess the significance of constraints (999 permutations, $\alpha = 0.05$; ter Braak 1992). Then, we produced seasonal ordination biplots to represent the moose and caribou assemblage and environmental resource covariates in realized niche space (ter Braak 1995). We assessed the fraction that constrained variance represented of all covariances between species and environment (ter Braak 1995) and reported canonical coefficients (CC) to address the influence of environmental variables in structuring the ordinations.

Based on the spatial separation hypothesis, caribou and moose should separate niche space across our study area and thus, should each be associated with a unique set of environmental resource covariates. First, we predicted that the species scores, i.e. the coordinates along the ordination axes specifying the position of the species in realized niche space, would be strongly contrasting. We also expected the axis separating caribou and moose in niche space to be dominant over the axis associating the two species. With respect to specific covariates, we predicted that caribou would be associated with higher elevations and older forest structures, while moose would group with variables representing early seral forest stands and human landscape alteration (i.e. clear-cuts, burns and NDVI). These analyses were performed by the R 2.13.1 software with the package 'vegan' 2.00-0 (Oksanen et al. 2011).

Fine-scale caribou–moose resource and spatial separation

To evaluate separation of moose and caribou resource use at a finer scale, we paired each caribou with one

sympatric moose in or near its respective caribou herd home-range (95% fixed kernel) to maintain equal availability of resources to each pair (i.e. similar to third order scale described by Johnson (1980)). We used logistic regression (Hosmer and Lemeshow 2000) to model seasonal (i.e. summer and winter) differences in the resource use of moose and caribou, where caribou used locations were coded as 1 and moose used locations as 0 (Latham et al. 2011a). This analysis determined which covariates predicted similarities and differences in resource use between paired caribou and moose at smaller spatial scales, measured by the estimated β coefficients from logistic regression. Negative coefficients indicate less use by caribou compared to moose and positive coefficients indicate more resource use by caribou compared to moose. We again, predicted that caribou would use higher elevations and lower human landscape alteration than moose. A random intercept ($\beta_0 + \gamma_0$) for each caribou–moose pair was used to account for differences in sample sizes of GPS locations of individual animals using generalized linear mixed-effects models (GLMM; Gillies et al. 2006).

We employed a manual stepwise model selection process described by Hosmer and Lemeshow (2000) and considered candidate covariates (Supplementary material Appendix 1, Table A1) previously reported to influence caribou and moose resource use. All covariates were screened for collinearity using the Pearson's correlation coefficient threshold of $|r| > 0.6$, retaining the collinear covariate with the higher log-likelihood, highest coefficient of determination (pseudo R^2) and lowest p-values. Further, non-linear covariates were transformed upon visual inspection (Hosmer and Lemeshow 2000). We first conducted univariate logistic regression analysis, using a $p < 0.25$ as a cut-off for the inclusion in model building. Retained covariates entered the multivariate logistic regression modeling process to build a small subset of biologically sensible candidate models (Hosmer and Lemeshow 2000). We selected the top model using Akaike's information criterion (ΔAIC ; Burnham and Anderson 2002). We reported standardized Wald statistics (z_{std}), where we divided the Wald statistic for each variable by the average of the absolute values of all Wald statistics estimated for all predictor variables included in the top model (DeCesare et al. 2012b). These standardized Wald statistics allowed us to compare the direction and strength of resource variable use by the two ungulate species relative to each other between seasonal models and variables. Like β -coefficients, positive or negative values of z_{std} indicate resource use for increasing or decreasing values in the predictor variable by caribou relative to moose, respectively. Statistical analyses were carried out in STATA 11.0 (StataCorp 2007). To assess the predictive capabilities of caribou–moose resource selection models, we conducted k-fold ($k = 5$) cross validation (Boyce et al. 2002).

Models estimating resource separation by species in environmental space, are commonly used to predict the spatial separation in geographical space (i.e. habitat; Hirzel and Le Lay 2008, Latham et al. 2011a). We measured spatial separation of resource use by moose and caribou based on fine-scale logistic regression (described above) by translating environmental patterns of resource use (realized niche) into spatial predicted values (geographical space);

Hirzel and Le Lay 2008). To do this, we developed spatial raster maps at a 30 m resolution based on top logistic regression models that predicted the probability that a pixel was used by caribou or moose using ArcGIS 9.3.1. Values closer to 0 indicated the highest relative probability of use by moose and conversely, values closer to 1 indicated the highest relative probability of use by caribou. We then classified the predicted probabilities of moose/caribou use across the study area into 10 equal-sized categories (Boyce et al. 2002). Finally, we counted the frequency of GPS locations by each species in each resource use category. As an index of resource separation between moose and caribou we calculated Schoener's overlap index in these 10 ranked resource use categories for animal locations of individual pairs moose and caribou. In this way, Schoener's overlap index provided a measure of the spatial distribution of each caribou relative to its paired moose (Abrams 1980). We predicted that human landscape alteration is positively correlated with resource overlap between caribou and moose. We tested our prediction by regressing the Schoener's overlap index for each caribou-moose pair versus the intensity of human landscape alteration measured as the proportionate area density of clear-cut forest per unit area (at a radius of 3 km as % area/100; see landscape covariates section; hereafter referred to as 'clear-cut density') at caribou GPS locations. Because the diet of caribou and moose can overlap in summer when both species consume forbs and deciduous vegetation (Boer 2007), we predicted that spatial separation would be lower in summer.

Mortality consequences of spatial caribou-moose overlap

We tested whether caribou mortalities occurred with higher frequency in areas of high overlap between moose and caribou or in higher quality moose habitat as expected under the spatial separation hypothesis (McLoughlin et al. 2005) using a one-way chi-squared test. In our spatially predictive maps developed above, we classified areas as caribou habitat where caribou had a high relative probability of use (categories 8-10); moose habitat was represented by categories 1-3 and habitat where both species were predicted to have intermediate relative probability of use by categories 4-7. Long-term mortality data (1999-2009) were compiled by Alberta Fish and Wildlife Division and Parks Canada based on radio-collared (very high frequency and GPS) caribou. Mortalities used in this analysis were identified as wolf ($n = 32$), grizzly/black bear ($n = 5$), unknown confirmed predator ($n = 9$) and unknown mortality ($n = 72$), totaling 59 per season. Confirmed non-predatory mortalities (e.g. road kill or avalanches) were excluded. The large number of unknown mortality causes likely resulted from delays in mortality site investigation due to the remoteness of the study area. While we can assume that the majority of caribou mortalities were predator-caused (Wittmer et al. 2005), we also tested mortality using only confirmed predator-killed caribou ($n = 44$). We tested the null-hypothesis that caribou mortalities were not significantly different in moose

(categories 1-3), overlap (categories 4-7) and caribou (categories 8-10) habitat. The expected frequency distributions for the chi-squared tests were estimated based on the relative proportions of used caribou GPS locations in each category.

Landscape covariates

We estimated caribou and moose resource use with spatial covariates, including elevation, slope, aspect, percent snow cover, normalized difference vegetation index (NDVI) and landcover types (see DeCesare et al. 2012b and Supplementary material Appendix 1 for details). To address impacts of human landscape alteration on caribou-moose resource separation, we used vector geodatabases to measure linear features (km km^{-2} ; roads, seismic exploration lines, rail roads, etc.) within 1 km circular neighborhoods surrounding each raster pixel (Supplementary material Appendix 1). We characterized impacts from forest harvesting by clear-cuts as a landcover class, as well as a relative index of clear-cut density. To identify the relevant spatial scale at which clear-cut density had the strongest effect on spatial caribou-moose relationships, we conducted circular neighborhood analysis for clear-cut (proportionate area) density by measuring density surrounding each raster pixel at concentric radii from 75 to 10 000 m. Then, we fit univariate logistic regression models using density estimates measured at the varying radii and identified the most predictive radius of caribou resource use relative to moose using AIC (Burnham and Anderson 2002).

Results

Coarse-scale caribou-moose resource separation

We chose a linear response model for RDA, because the DCA first gradient lengths were all < 3 (ter Braak 1995), and performed analyses for both seasons. The matrix for the occurrence of the two ungulate species was related to the set of predictor variables (summer: $F_{22, 6175} = 76.55$, $p = 0.005$; winter: $F_{22, 7307} = 59.82$, $p = 0.005$). For both seasons, the biplots showed a separation of the realized niche positions of caribou and moose and especially in winter, the amplitude of environmental variables describing caribou occurrence clearly indicated the niche specialisation by caribou (Fig. 2). During summer, the constrained variance of the species-environment relationship (approx. 21%) was largely explained by the first axis, which showed opposite relative species scores (caribou: 2.43; moose: -2.45; Table 1) and thus reflected resource separation between the two species. Environmental variables that were negatively correlated with axis 1 were associated with moose and vice versa; environmental variables positively correlated with axis 1 were associated with caribou. Elevation ($CC = 0.78$), snow ($CC = 0.77$) and alpine shrub ($CC = 0.54$) were strongly positively correlated with ordination axis 1, explaining caribou presence. In contrast, NDVI ($CC = -0.49$), closed conifer ($CC = -0.33$) and mixed forests ($CC = -0.32$), but also human landscape alteration (clear-cuts, clear-cut density, and density of roads and linear

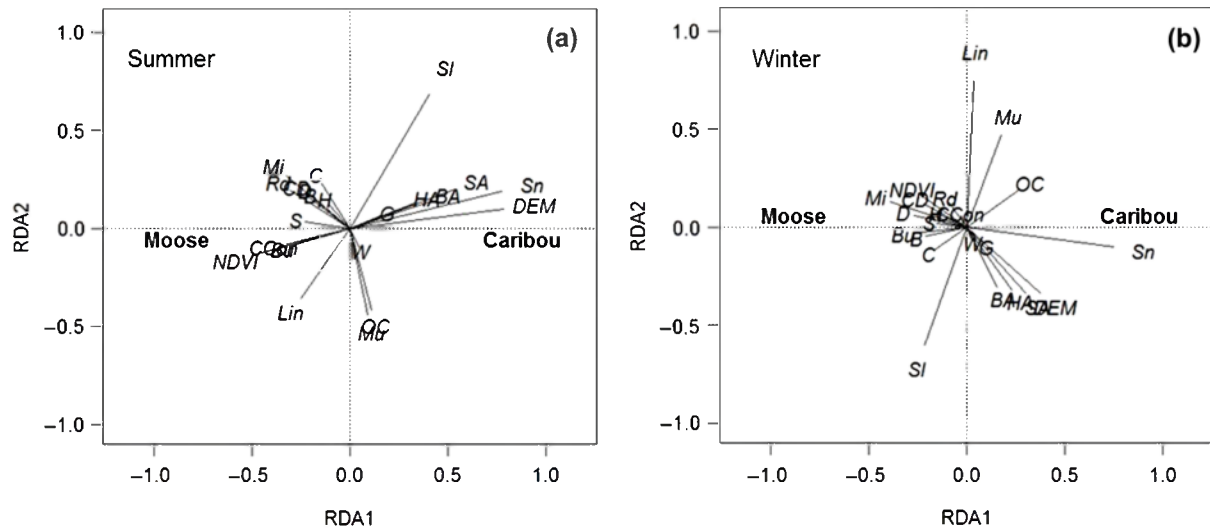


Figure 2. Ordination biplots for environmental matrices and the occurrence of moose and caribou (based on global positioning system (GPS) collar locations) in 500 m² grid cells for summer (16 May–16 October) and winter (17 October–15 May). Acronyms are explained in Table 1. GPS collars were deployed on 17 moose and 17 caribou between winters 2007/2008 and 2009/2010 in west-central Alberta and east-central British Columbia, Canada.

Table 1. Summary of redundancy analysis (RDA) between the presence of moose and caribou (i.e. global positioning system (GPS) collar locations) and a set of environmental variables in west-central Alberta and east-central British Columbia for summer (16 May–16 October) and winter (17 October–15 May). Eigenvalues, percentage and proportion of constrained variance and canonical coefficients of constraining variables are listed for the first two axes. GPS collars were deployed on 17 moose and 17 caribou between winters 2007/2008 and 2009/2010 in west-central Alberta and east-central British Columbia, Canada.

	Summer		Winter	
	Axis 1 association	Axis 2 separation	Axis 1 association	Axis 2 separation
Eigenvalues	0.11	2.25E-04	0.08	7.88E-04
Percentage of constrained variance over total variance	0.21	4.50E-04	0.15	1.58E-03
Proportion of constrained variance explained by ordination axes	0.98	0.02	0.99	0.01
Species scores (caribou)	2.43	-0.11	2.21	0.21
Species scores (moose)	-2.45	-0.11	-2.06	0.23
Constraining variables	Canonical coefficients			
Elevation (m; DEM)	0.78	0.10	0.38	-0.34
Slope (SI)	0.40	0.68	-0.21	-0.60
Snow (Sn)	0.77	0.19	0.75	-0.10
Linear feature density (km 10 km ⁻² ; Lin)	-0.25	-0.35	0.04	0.75
Road density (km 10 km ⁻² ; Rd)	-0.30	-0.20	-0.09	0.12
Clear-cuts (% area/100 within r = 3 km; CD)	-0.23	0.17	-0.22	0.12
Barren (B)	-0.16	0.14	-0.21	-0.05
Barren alpine (BA)	0.42	0.14	0.16	-0.30
Burn (Bu)	-0.29	-0.09	-0.27	-0.03
Closed conifer (CCon)	-0.33	-0.08	-0.03	0.06
Cut (C)	-0.15	0.23	-0.16	-0.11
Deciduous (D)	-0.19	0.16	-0.27	0.06
Glacier (G)	0.16	0.07	0.08	-0.08
Herbaceous (H)	-0.11	0.12	-0.13	0.06
Herbaceous alpine (HA)	0.33	0.13	0.23	-0.32
Mixed (Mi)	-0.32	0.27	-0.39	0.13
Muskeg (M)	0.09	-0.44	0.17	0.47
Open conifer (OC)	0.11	-0.41	0.27	0.19
Shrub (S)	-0.23	0.04	-0.16	0.02
Shrub alpine (SA)	0.54	0.20	0.30	-0.34
Water (W)	0.05	-0.10	0.03	-0.07
NDVI	-0.49	-0.14	-0.23	0.16

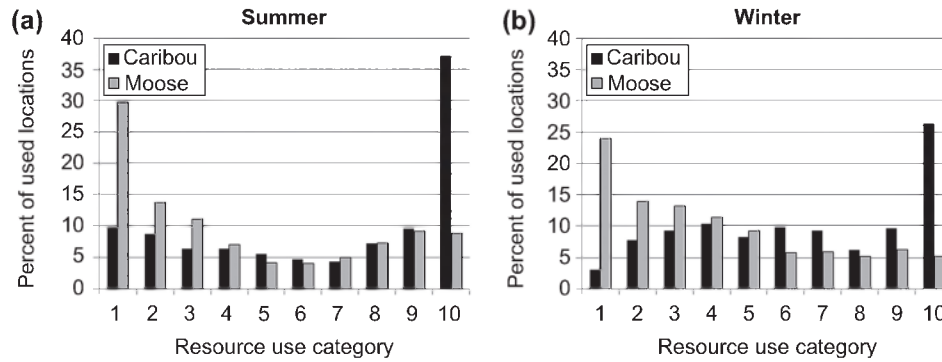


Figure 3. Frequency of occurrence of woodland caribou ($n = 17$) and moose ($n = 17$) global positioning collar (GPS) location data in 10 equal sized bins predicted from the most parsimonious generalized linear mixed models with a random intercept during summer (16 May–16 October; (a)) and winter (17 October–15 May; (b)) in west-central Alberta and east-central British Columbia, Canada. Values closer to 1 indicate high relative probability of use by moose and conversely, values closer to 10 indicate high relative probability of use by caribou. Areas with high shared use of both species indicate low resource separation. GPS collars were deployed between winters 2007/2008 and 2009/2010.

features) were correlated with moose presence (Table 1, Fig. 2). The second axis (and therefore resource overlap between the species) explained a very low proportion of variance ($< 0.1\%$). Thus, indicating that our set of variables better explained the separation between species than their overlap. Similarly, during winter, the constrained variance of the species–environment relationship (approx. 15%) was largely explained by the first axis ($> 99\%$), which also measured resource separation of the two species indicated by the opposite scores of 2.21 for caribou and -2.06 for moose (Table 1, Fig. 2). Variables that were strongly related to the presence of caribou were snow ($CC = 0.75$), elevation ($CC = 0.38$) and alpine shrubs ($CC = 0.30$), while moose were associated with mixed forests ($CC = -0.39$), NDVI ($CC = -0.23$), burns and deciduous forests ($CC = -0.27$ for both variables).

Fine-scale caribou–moose resource and spatial separation

At a finer scale, we evaluated resource separation with 14420 caribou and 13615 moose GPS locations in summer and 19809 caribou and 20437 moose locations in

winter from 17 individuals of each species. The average number of locations per caribou and per moose in summer was 848 ($SE = 37.58$) and 801 ($SE = 14.09$), and in winter 1165 ($SE = 47.37$) and 1202 ($SE = 38.44$) respectively. In general, resource use by caribou and moose and the degree of resource separation differed only slightly between seasons (Table 2, Fig. 3). Caribou used higher elevations than moose (also, the highest standardized z -values) during both season, although resource separation due to elevation was weaker during winter. Moose also tended to use areas with increased human landscape alteration and green, broad-leaved forage (NDVI; $z_{std_NDVI} = -1.00$ during summer and $z_{std_NDVI} = -1.26$ during winter), whereas caribou avoided these features relative to moose (Table 2). For example, the relationship between clear-cut density and caribou resource use was strongly negative during winter ($z_{std_ClearCutDens} = -1.26$) and summer ($z_{std_ClearCutDens} = -0.90$). In general, caribou and moose differed in responses to human landscape alteration less in summer than winter. During winter, caribou used areas with higher probabilities of being covered by snow ($z_{std_Snow} = 2.41$) and occurred more often in open conifer ($z_{std_OpenCon} = 1.48$) and mixed-forsts ($z_{std_Mixed} = 1.14$) than moose. The most parsimonious generalized linear mixed models cross validated very

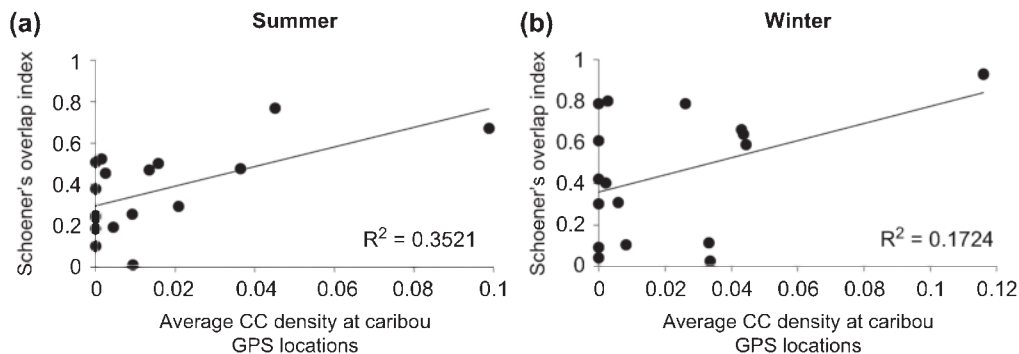


Figure 4. Schoener's overlap index values, where values closer to 0 indicate low overlap between caribou and moose resource use and values closer to 1 indicate high overlap, versus proportionate area density of clear-cuts (CC) measured within 3 km radii (% area/100) for summer (a) and winter (b).

well, confirming their predictive capacity with average Spearman's rho of 0.86 ($p = 0.002$) during summer and 0.98 ($p < 0.0001$) during winter.

Schoener's overlap index was high in all 10 resource categories in both seasons (Fig. 3; $C_{\text{summer}} = 0.690$, $C_{\text{winter}} = 0.672$), indicating high resource overlap. The proportion of caribou locations falling into moose resource categories (categories 1–3) was higher during summer (25%) than during winter (20%), but also the proportion of caribou locations falling into caribou resource use categories (categories 8–10) was higher (summer = 54% and winter = 42%; Fig. 3). Consequently, the proportion of caribou locations falling into intermediate resource categories (i.e. categories 4–7) was lower during summer (21%) than during winter (38%). As predicted, spatial separation between moose and caribou was negatively correlated with clear-cut density (Fig. 4). This relationship was significant during summer ($R^2 = 0.35$, $F_{(1, 15)} = 8.15$, $p = 0.012$), but not during winter ($R^2 = 0.17$, $F_{(1, 15)} = 3.12$, $p = 0.097$).

Mortality consequences of increased caribou–moose overlap

We observed differences among the proportions of caribou mortalities falling into the caribou, moose and intermediate resource use categories during summer ($\chi^2_{(2, 59)} = 23.70$, $p < 0.0001$). The greatest proportion of caribou killed by predators occurred in categories of highest moose resource use (53%; Fig. 5). In winter, the relationship between resource use categories and the frequency of caribou mortalities was not statistically significant ($\chi^2_{(2, 59)} = 9.36$, $p = 0.406$). The analysis exclusively with predator-caused mortalities broadly confirmed this pattern with 65, 12 and 23% of the mortalities occurring in moose, intermediate and caribou resource categories, respectively in summer and 11, 44 and 44% in winter. Again, the relationship was only significant in the summer (summer: $\chi^2_{(2, 26)} = 22.69$, $p < 0.0001$; winter: $\chi^2_{(2, 18)} = 0.42$, $p = 0.807$).

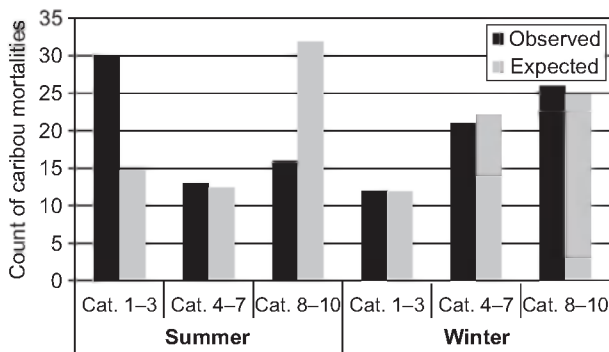


Figure 5. Observed woodland caribou mortalities in categories (cat.) of the relative probability of resource use by caribou relative to moose, where cat. 1–3 have the lowest probability of use by caribou, but the highest by moose, cat. 4–7 have intermediate probabilities of use by both species and cat. 8–10 have highest probabilities of use by caribou, while lowest for moose. For further explanation, please see the methods section.

Discussion

Conservation biologists often need to understand complex ecological interactions to identify threats for declining species and prescribe management actions to reverse declines. In this study, we present an example for comparative analyses of resource use and spatial overlap between a threatened species (caribou) and a generalist species (moose), thriving in human altered landscapes. Surprisingly, despite the often suggested importance of understanding the mechanisms of apparent competition for caribou declines, direct comparisons of moose and caribou resource use are rare. In this example, we showed that human landscape alteration was positively correlated with resource overlap of coexisting species, which may be especially important in systems of shared predation. Woodland caribou isolate themselves from other more abundant primary prey species and their shared predators to reduce the negative effect of predation (Bergerud and Page 1987, Seip 1992). Our results confirmed that caribou and moose generally use different resources as expected under the spatial separation hypothesis, but we also showed that the strength of resource separation varies across different spatial scales and seasons, and the geographical realization of resource separation could be influenced by the intensity of human landscape change.

Resource selection varies with scale and consequently, niche relationships between sympatric species may also change at different scales (Ihl and Klein 2001). Scale-dependent resource selection has been demonstrated for caribou in previous studies. For example, several researchers concluded that caribou broadly select resources to minimize predation risk at coarse spatial scales and maximize forage benefits at smaller spatial scales (Rettie and Messier 2000, Apps et al. 2001). Our RDA suggested that caribou and moose separated through their asymmetric occurrence in the multidimensional space of environmental variables at coarse spatial scales in both seasons, and thus, occupied contrasting realized niches (Hirzel and Le Lay 2008). This niche separation was indicated by the opposite species scores for the first axis and that almost all of the total variance was explained by the Eigenvalue of the first axis (>99%; Table 1). At this coarse scale, resource overlap, indicated by the similar species scores for caribou and moose along the second axis, was weak (variance explained by the Eigenvalue <0.1%) during both seasons (Table 1). Nonetheless, at a finer scale, our analysis of sympatric caribou and moose pairs indicated substantial spatial overlap due to similar use of environmental resource variables in geographical space in all 10 resource use categories (Fig. 3). Further, we observed a positive relationship between resource use overlap and intensity of human landscape alteration, especially during summer (Fig. 4). Finally, our results suggested that caribou also experience increased mortality risk when their resource use overlaps with moose at finer spatial scales in summer, coincident with similar forage requirements during this season. Thus, caribou may avoid the most limiting factor to fitness, i.e. overlap with moose at coarser scales (i.e. numeric response by predators), but maximize forage at finer scales which could result in spatial overlap with moose especially in summer (Rettie and Messier 2000, Apps et al. 2001).

Table 2. Model coefficients (β), standard errors (SE) and standardized Wald statistics (z_{std}) from the most parsimonious generalized linear mixed models with a random intercept describing differences in habitat use by woodland caribou (dependent variable = 1) and moose (dependent variable = 0) in west-central Alberta and east-central British Columbia, Canada. Habitat use was compared during summer (16 May–16 October) and winter (17 October–15 May) and from 2007 to 2009. Closed conifer was the reference category for land-cover types.

	Summer			Winter		
	β	SE	Z_{std}	β	SE	Z_{std}
Elevation (100 m)	0.63	0.011	4.19	0.38	0.010	2.67
Aspect west-east	-0.24	0.024	-0.73	-	-	-
Aspect north-south	-	-	-	0.17	0.019	0.61
Aspect north-south squared	-	-	-	-0.28	0.037	-0.52
Snow (winter)	-	-	-	9.92	0.277	2.41
Linear feature density (km km ⁻²)	-0.22	0.021	-0.78	-	-	-
Road density (km km ⁻²)	-0.61	0.069	-0.65	-0.10	0.048	-0.14
Clear-cuts (% area within 3 km radius)	-2.95	0.242	-0.90	-3.55	0.189	-1.26
Barren	-	-	-	-1.23	0.153	-0.54
Burn	-1.05	0.110	-0.71	-1.94	0.162	-0.80
Cut	-	-	-	-1.40	0.114	-0.83
Deciduous	-	-	-	-1.19	0.128	-0.62
Herbaceous	-0.73	0.136	-0.39	-1.04	0.124	-0.56
Herbaceous alpine	0.22	0.092	0.18	-	-	-
Mixed	-1.18	0.089	-0.97	-1.29	0.076	-1.14
Muskeg	0.78	0.069	0.83	-	-	-
Open conifer	0.43	0.054	0.59	0.93	0.042	1.48
Shrub	-	-	-	-0.54	0.041	-0.90
NDVI	-2.32	0.171	-1.00	-3.84	0.205	-1.26
Model intercept	-7.92	0.543	-1.08	-11.63	0.469	-1.66

In our study, caribou associated with variables representing alpine and coniferous habitats and moose with variables representing deciduous foraging habitats at both scales, but the magnitude of the predictor variables was scale- and season dependent. These differences may arise because of differences in migratory strategies between sympatric ungulates. For example, as predicted by the spatial separation hypothesis (Seip 1992), elevation was one of the main factors separating caribou and moose niches, but its effect strongly varied with season. In our study area, five out of six caribou populations are partially migratory (i.e. only part of the population migrates; McDevitt et al. 2009) and individuals may leave high elevation mountain summer ranges to exploit mature and old conifer forests in the foothills during winter, reflected by the weaker coefficients for elevation during winter compared to summer at both scales (Table 1, 2). As a result, migration may constrain caribou from spatially separating at coarser spatial scales during winter, but interestingly, caribou seem to separate from moose at finer spatial scales during this season, possibly because of large forage differences between moose and caribou during this season (Boer 2007). Thus, caribou may have adopted seasonal separation strategies which could differ with spatial scale (Ihl and Klein 2001). Our results indicate such seasonal scale-dependent avoidance strategies by caribou by a much stronger avoidance of NDVI and clear-cut densities by caribou compared to moose during winter at the finer scale, but not the coarser scale. Further, our results suggest that snow may be a strong driver in the fine scale resource separation during winter that allows caribou to spatially separate from sympatric moose. Caribou are well adapted to harsh winter conditions and their large, crescent-shaped hooves and long legs allow them to dig through snow to access lichen, and ease locomotion

over snow (Klein et al. 1987). In contrast, moose movements have been found to be impeded at snow depths exceeding 60 cm, because of the associated high energy cost for this larger bodied ungulate (Renecker and Schwartz 2007).

There is a general consensus that caribou avoid human landscape alteration in the literature and our selection coefficients from logistic regression and canonical coefficients from RDA were consistent with previous studies. Nevertheless, studies assessing how landscape alteration may affect resource use overlap between sympatric moose and caribou are rare (Bowman et al. 2010). For example, several studies have suggested that caribou avoid roads and seismic lines (Dyer et al. 2001, Vistnes and Nellemann 2001). Also, clear-cuts in Ontario have significantly displaced caribou from harvested areas (Vors et al. 2007, Bowman et al. 2010). Habitat alteration in caribou range leads to the direct loss and fragmentation of caribou habitat with that preferred by other ungulate species (Wittmer et al. 2005). In agreement with the hypothesized effect of human landscape change on resource separation, the two ungulate species in our study had higher resource use and spatial overlap (Schoener's *C*) in regions with increased clear-cuts per unit area (Fig. 4).

Overlap of sympatric prey species can result in concurrent occurrence of exploitative (shared resources consumption) and apparent competition (shared predators; Holt and Lawton 1994). However, the degree of overlap between species does not necessarily equal the amount to which they compete with each other, but rather the degree co-existing species are similar in their environmental resource use (Sale 1974). In general, direct habitat loss is unlikely to limit forage for woodland caribou because most populations are hypothesized to be well below the forage carrying capacity (McLoughlin et al. 2003, Wittmer et al.

2005). Although we did not specifically assess diet composition and foraging by moose and caribou, habitat use of both species seemed to indicate that exploitative competition between the two species is unlikely, especially during winter. In a stable isotope diet study conducted by Ben-David et al. (2001) in Alaska, moose and caribou stable isotope ratios were significantly different from each other in late summer–autumn and winter. However, in early and mid summer caribou may also feed on similar forbs and deciduous vegetation (Apps et al. 2001) as moose. Consequently, high fine-scale resource overlap during summer we observed can be explained by potentially overlapping forage and elevation preferences of the two species during summer (Boer 2007). In contrast, we must assume that forage overlap did not result in similar resource overlap in winter at finer scales, but rather the limited availability of undisturbed caribou habitat as previously suggested (Wittmer et al. 2005). For example, between 23 and 38% of the winter or permanent ranges of five caribou herds we studied were altered by forestry based on satellite imagery (Alberta Sustainable Resource Development and Alberta Conservation Association [ASRD and ACA] 2010). In summary, while interpretation of resource (niche) overlap indices as measures of competition between species has been subject to debate (Abrams 1980), we feel that our use of overlap indices rather as a measure for the distribution of moose and caribou with respect to resources is a good approach to measure spatial overlap.

Caribou survival and population growth may be significantly reduced in regions with increased landscape alteration and thus, increased spatial overlap between caribou, primary prey and wolves (McLoughlin et al. 2005, Vors and Boyce 2009). For example, the abundance of wolves is predominantly determined by the biomass of their ungulate prey and therefore, should be more abundant in landscape impacted by human alteration (Hebblewhite et al. 2007). Our results suggested higher mortality frequencies for caribou in moose resource use categories during summer. Similarly, overlapping resource use by caribou and moose may also be the reason for increased predator-caused caribou mortalities in caribou home ranges that had proportionately less old forests and more mid-aged forest compared to surviving caribou, reported in a study by Wittmer et al. (2007). Further, wolves have been shown to use roads and other linear features as travel routes that can increase predation efficiency. In that way, wolves might dominate the scale at which moose and caribou partition resources due to increased range and speed of movements in human altered landscapes, especially in the presence of linear features (Gurarie et al. 2011, Whittington et al. 2011). We would expect this effect to be strongest during the snow free period when movement rates of wolves are highest, which may be the reason why caribou mortalities were significantly higher in moose resource use categories during summer in comparison to winter (functional response by wolves).

Although we feel confident that spatial separation between moose and caribou is lower in landscapes with human landscape alteration, some characteristics of our study design may affect our results. In general, resource selection studies should be interpreted cautiously because of the common assumption that resource selection is directly

linked to fitness, which cannot be generalized (van Horne 1983). Furthermore, while high levels of overlap in resource use are often used to infer competition (Sale 1974), it is essentially the ratio of the density of consumer individuals (i.e. moose and caribou) relative to the resource base (i.e. habitat) that determines the strength of competitive interactions (Abrams 1980). In our study area, caribou populations experience negative growth rates in landscapes altered by humans (Vors and Boyce 2009). In contrast, we observed only one death of a total sample of 33 radio-collared moose that were monitored for at least one year each. Further, moose are expected to persist in high densities in regions with improved forage following clear-cutting (Lavsund et al. 2003), suggesting high moose population viability in stark contrast to caribou population declines. Thus, despite the untested assumption about moose density relating to highly selected moose habitats, our results are indicative for higher moose density in caribou ranges as a result of increased human landscape alteration (Peek 2007). Also, we did not take within-population heterogeneity in resource use that may occur with partial migration into account. But, we can expect that not only resource overlap may be elevated for non-migratory versus migratory animals (Seip 1992), but also predation risk, if migration allows animals to escape from predation at broad spatial scales (Hebblewhite and Merrill 2009). Therefore, further investigation of exclusively sedentary caribou and moose would be necessary to determine niche overlap during summer in the foothills. Lastly, Latham et al. (2011b) described the potential role of distribution shifts of white tailed deer in response to human landscape alteration as primary prey species for wolves in north-eastern AB and suggested that also management of white tailed deer populations need to be considered if the aim is to conserve caribou populations in AB. In this study, we only present research on the relationship between moose and caribou, but of course community interactions are complex and other factors such as climate (e.g. rain on snow events) or other primary prey and predators may play an important role in our and other study areas and should be evaluated (Vors and Boyce 2009).

Especially in human altered landscapes, species may be unable to adapt to novel mortality risks that were not present in their evolutionary history (Schlaepfer et al. 2002). With the encroachment of human landscape alteration, caribou refugia from moose, and hence predators like wolves, are compromised and their spatial separation strategy may be less effective. This could potentially result in destabilizing the relationship between predators and prey as predicted by the spatial separation hypothesis. However, predator control does not appear to be an effective long-term conservation strategy, if increased predation pressure is only the ‘symptom’ of human landscape alteration (Vors and Boyce 2009) or possibly wolves are also protected (Gurarie et al. 2011). Failure to address the habitat-based root-causes of caribou declines, will likely result in continuous long-term caribou population decrease. Thus, if the goal is long-term recovery of caribou populations (ASRD and ACA 2010), the integrity of caribou refugia (old coniferous forest in our study area and throughout the boreal forest) and the connectivity between these refuges in already compromised caribou ranges should be maximized

(Wittmer et al. 2005, Vors et al. 2007). We described spatio-temporal changes in the distribution of prey species, but other factors, such as changes in plant phenology or extreme weather events due to climate change can affect persistence of globally declining caribou and reindeer (Vors and Boyce 2009). Integrating these global changes in wild *Rangifer* conservation will be a challenging task determining the fate of this ecologically and economically important species. As in other biomes, also the absence of changes in policy and human behavior will continue to alter biodiversity in the boreal forest biome.

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Supplementary material (Appendix E7733 at <www.oikosoffice.lu.se/appendix>). Appendix 1.