

**SCALING UP THE ROLE OF PREDATION IN CARIBOU DECLINES
IN WEST-CENTRAL ALBERTA (REDWILLOW, NARRAWAY,
REDROCK PRAIRIE CREEK, A LA PÊCHE AND LITTLE SMOKY
RANGES)**

Interim Report, New Results Only
2012 AUPRF project status update



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Prepared For:

Petroleum Technology Alliance of Canada

Canadian Association of Petroleum Producers

Note: Further details on the project are in the enclosed proposal; titled:
Musiani & Hebblewhite PTAC- AUPRF Step 2 Proposal, Focus on Year 2013.

The core information on activities and key deliverables for Year 2011 can be found in:
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1.0 Preamble

This report relates to deliverables for the 1st half of Year 2012. This project is designed to last 1.5 more years. Therefore, other objectives will be addressed in subsequent reports. In addition, due to finalization of the project agreement, our funding started in spring 2011. Therefore our field activities occurred only for 6 months in 2011.

The core information on activities and key deliverables for Year 2011 can be found in:

DeCesare, N., C. Semeniuk, M. Musiani, M. Hebblewhite, J. Whittington, and A. Aivaz. 2012. Scaling Up the Role of Predation in Caribou Declines in West-Central Alberta (Redwillow, Narraway, Redrock Prairie Creek, A la Pêche and Little Smoky Ranges). Interim report to the Petroleum Technology Alliance of Canada (PTAC). 99 pages.

1.1 Project schedule including major milestones and timing

The table below lists major milestones obtained as scheduled, and their timing. Further details on scheduling of deliverables are in the enclosed proposal titled ‘Musiani & Hebblewhite PTAC-AUPRF Step 2 Proposal, Focus on Year 2013’, under “Deliverables to Project Steering Committee, PTAC/CAPP Project Manager (Mark Sherrington)”.

Major Milestones Of Project	2010 (Completed)	2011	2012	2013
1. Caribou, wolf, moose and grizzly bear GPS collaring & data collection	✓		✓ Bears	✓ Bears
2. Winter Kill-site field validation and modeling	✓			
3. Summer kill-site field validation	✓			✓ Bears
4. Summer kill-site modeling		✓	✓	✓ Bears
5. RSF Modeling – Moose	✓	✓		
6. Moose aerial surveys	✓			
7. Moose density modeling		✓	✓	
8. Hair gathering from bears, wolves, caribou and moose	✓	✓	✓	✓
9. Hair gathering from rarer species –e.g. snowshoe hare, mountain goats and sheep, and beaver		✓	✓	✓
10. Stable isotope analyses on hairs		✓	✓	✓
11. Analysis of diet overlap between predators, caribou and other prey (e.g. moose) from isotope data		✓	✓	✓
12. PhD theses completion		✓ UofC, UofM (two in Dec)	✓ UofC, UofM (two with revisions)	
13. Production of Scientific and Spatial Databases	✓	✓	✓	✓
14. Public communication and dissemination of research results		✓	✓	✓
15. Scientific Publications and Presentations at Conferences and at PTAC annual Forum		✓	✓	✓
16. Project status reports to CAPP Project Manager and PTAC (by Mar, Jun, Sep, Dec every year)		✓	✓	✓
17. Phase and Final Reporting to PTAC and Partners		✓ Jun, Dec	✓ Jun, Dec	✓ Jun, Dec
18. Reports on Research Applications: mitigation of impacts		✓ Dec	✓ Dec	✓ Dec
19. Final report of 3-year project (provided in addition to final reports of each year, above)				✓ Dec
20. Revision of final reports following its review by TSC members and external reviewers		✓ Feb	✓ Feb	✓ Feb

2.0 Animal capture and radio-collaring

We captured and radio-collared adult caribou and wolves to monitor movements and survival of individuals across the range of conditions present in the study area. Specifically, we used GPS-enabled collars (Lotek-2200, 3300S, 3300M, 4400S, 4400M, Lotek Wireless, Inc., Newmarket, Ontario, Canada; ATS-G2000, Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) to collect location data of high quality and quantity for multi-scale analysis of resource selection, predation and movement patterns.

Winter helicopter net-gunning was used to capture caribou and wolves (Andryk et al. 1983) and we supplemented these efforts with additional summer foot-hold trapping for wolves (Frame and Meier 2007). All animal capture procedures were approved by government and university animal care protocols and permitting processes (Table 2.1). Full details of animal capture protocols are available upon request from any project personnel.

Literature cited:

- Andryk, T.A.; L.R. Irby; D.L. Hook; J.J. McCarthy; G. Olson. 1983. Comparison of Mountain sheep capture techniques: helicopter darting versus netgunning. *Wildl. Soc. Bull.* 11:184-187.
- Frame, P. F.; Meier T. L. Field-Assessed Injury to Wolves Captured in Rubber-Padded Traps. *JWM* 71: (6) 2074-2078

Table 1. Research and collection permits, Canadian Rockies.

Alberta Sustainable Resource Development: Fish and Wildlife Division

Collection Licenses: #21803, #27086, #27088, #27090

Research Permit: #27085, #27809, #27812

Alberta Tourism, Parks, and Recreation

Research and Collection Permits: RC08WC014 & Wilka101-07



British Columbia Ministry of Environment: Permit and Authorization Service

Wildlife Act Permit VI08-31411

Park Use Permits: 101964



Parks Canada Agency

Research and Collection Permit: JNP-2007-952

Research and Collection Permit: LL-2010-4392



University of Montana

Animal Use Protocol: 056-06MHECS-010207

Animal Use Protocol: 059-09MHWB-122109



University of Calgary

Animal Use Protocol: BI-2007-57



3.0 Linking resource selection and predation risk to a demographic model of habitat quality

Abstract

Avoidance by caribou and increased wolf predation risk in disturbed areas indicate functional habitat loss for caribou, yet these patterns alone do not necessarily imply a demographic impact. Spatial analysis of factors influencing adult female survival indicated that caribou resource selection was broadly correlated with survival, but also that wolf predation risk was an additional mortality risk beyond that perceived by caribou. This failure of caribou to non-ideally avoid predation risk may explain multi-year declines for populations in west-central Alberta. Ultimately, if caribou conservation is to succeed, management must reverse the ultimate causes shifting the balance of apparent competition at both broad and fine scales across woodland caribou range.

Introduction

The relationship between environmental resources and individual fitness is central to ecology and evolution. As framed by niche theory, the fitness of individuals is a multi-dimensional function of the abiotic and biotic resources they experience (Hutchinson 1957). This conceptualization of the ecological niche as a fitness gradient across environmental conditions has since offered theoretical foundation for the spatially-explicit study of habitat quality as it relates to spatial heterogeneity in resources (Hirzel and LeLay 2008). However, quality is typically estimated according to spatial variation in the distribution or density of species rather than the more difficult to measure variation in demographic fitness indices. Thus, the inferred link between fitness-based habitat quality and density-based models such as species distribution models (Elith and Leathwick 2009) or resource selection functions (Manly et al. 2002) hinges on a positive relationship between the average individuals' selection of resources and the fitness benefits conferred by them (Pulliam 2000). Support for the selection-fitness relationship comes from theoretical expectation of animals that adaptively behave in ideal and free distributions (Fretwell and Lucas 1969). Selection of habitats that maximize fitness should be an evolutionarily stable strategy (Morris 2003), and one which collectively incorporates trade-offs between multiple niche dimensions such as food, density, competition, and predation (Grand 2002, Brown and Kotler 2004). Thus behavioral observation of species-habitat relationships provides one means of defining and delineating the spatial relationship between habitat and the dynamics of populations and communities (Fryxell and Lundberg 1998, Persson and De Roos 2003).

This theoretical selection-fitness relationship has been supported in only a handful of empirical studies where density- or selection-based measures correlate positively with fitness correlates (Morris and Davidson 2000, Bock and Jones 2004, McLoughlin et al. 2006, Pérot and Villard 2009, Gaillard et al. 2010). However, in other systems ideal or free behavior by animals may not be upheld, with implications for density-fitness relationships. Territorial behavior precludes free habitat selection (Fretwell and Lucas 1969) and likely increases occupation of suboptimal habitats, thus complicating interpretation of density with respect to habitat quality (Pulliam and Danielson 1991, Mosser et al. 2009). Animals may also have imperfect knowledge of habitat quality, particularly in the face of anthropogenic change (Kokko and Sutherland 2001),

making behavioral observations an inappropriate measure of fitness. Resource selection in such systems can portray a “non-ideal” yet still viable interpretation of habitat quality (Arlt and Pärt 2007), or can reflect ecological traps where animals prefer poor-quality, sink habitats (Battin 2004). Other behavioral constraints such as sociality (Pays et al. 2012) or site fidelity (Switzer 1993) may also prevent ideal and free habitat selection. Lastly, our ability to detect habitat-fitness relationships may be complicated by time-lagged effects (Van Horne 1983) or in appropriate treatments of scale (Gaillard et al. 2010) when measuring selection patterns.

Despite these complications, species distribution and resource selection models will remain a popular approach to define habitat quality because they facilitate multi-dimensional modeling of niche relationships with relatively accessible data (Beyer et al. 2010). When such studies are conducted, animals are assumed to behave ideally and the complex nuances of risk-forage trade-offs and inter-species interactions are integrated into a single selective response to habitat heterogeneity that maximizes fitness. Researchers have also paired resource selection studies with those of mortality risk, and subsequently described habitat quality by adjusting selection predictions with separately modeled risk correlates (Nielsen et al. 2006, Aldridge and Boyce 2008, Falcucci et al. 2009). However, it is theoretically unclear how selection and risk are expected to relate, given that if resource selection is adaptive behavior, selection should inherently balance risk avoidance with other factors. In some cases, selection behavior has been shown to include avoidance of risk (Mao et al. 2005, McLoughlin et al. 2005, Thomson et al. 2006). On the other hand, in maladaptive situations where selection patterns fail to represent fitness consequences, one might expect the measurement of risk alone to more accurately convey true demographic habitat quality (Latif et al. 2011). Ideally a fitness-based test of the importance of either resource selection or predation risk in driving population dynamics should concurrently test the relative effects of each in concert rather than assuming that either acts in isolation.

Here, we separately measure spatial patterns of both resource selection and predation risk and test their relationships with a key demographic fitness trait, adult female survival (Eberhardt 2002), for a threatened ungulate, woodland caribou (*Rangifer tarandus caribou*). Woodland caribou populations are currently suffering widespread range retraction (Schaefer 2003), population decline (McLoughlin et al. 2003, Environment Canada 2011), and local extirpations (Wittmer et al. 2010). In many cases the primary source of mortality and ultimately of population declines for caribou is predation from a predator with which they have evolved over millions of years, the wolf (*Canis lupus*; McLoughlin et al. 2005, Wittmer et al. 2005). Generally one would expect caribou to have adaptive resource selection patterns sufficient to minimize predation risk at sustainable rates (Ferguson et al. 1988, McLoughlin et al. 2010), though anthropogenic disturbances have recently altered the space use (James and Stuart Smith 2000) and community dynamics (DeCesare et al. 2010) of landscapes within which caribou and wolves coexist across their entire range (Environment Canada 2011). Landscape changes have also directly altered spatial variation in predation risk, specifically through their effects on wolf resource selection and thus the spatial risk of prey species encountering a wolf (Latham et al. 2011, DeCesare 2012). Caribou selection patterns are well studied and include avoidance behaviors that minimize predation risk (Rettie and Messier 2000, Gustine et al. 2006b, DeCesare et al. 2012b), yet widespread declines (Wittmer et al. 2010) in populations may imply that observed selection behavior is maladaptive. This species allows an informative test of the nature of selection- and risk-fitness relationships in a system where novel conditions may preclude caribou from effectively selecting high-quality habitats.

We assessed the relationship between adult female survival and predictive models of habitat quality based on caribou resource selection probability and wolf predation risk. We considered expectations under ideal free selection as a null hypothesis for this analysis, where resource selection should correlate with demographic fitness and where selection behavior should include and account for adaptive response to predation risk. The prediction under this “ideal selection hypothesis” (Fig. 1a) is a positive relationship between selection and survival and an insignificant relationship between risk and survival because animals’ behavior already includes sufficient risk avoidance to maximize fitness. We considered two alternative hypotheses that might describe different selection- and risk-fitness relationships given current conditions of caribou population decline in human-altered landscapes. First, we considered a “non-ideal selection” hypothesis (Arlt and Pärt 2007; Fig. 1b) under which selection would remain a favorable but incomplete form of maximizing fitness due to increased effects of predation risk beyond evolutionarily stable levels. In other words, this hypothesis suggests the risk-forage trade-off inherent within the selection patterns of individuals is imbalanced due to complicating factors such as novel changes to the spatial landscape of risk and/or fidelity and grouping behavior that preclude ideal free selection. Predictions under this hypothesis include both a positive correlation between selection and survival probability and a negative correlation between risk and survival, such that predation risk offers an additive source of mortality beyond that being accommodated by selection behavior alone. Lastly, we considered an “ecological trap hypothesis” (Fig. 1c) under which selection and risk would interact to drive maladaptive relationships with fitness. Predictions under the ecological trap hypothesis would include a risk dominated depiction of habitat quality where interaction between selection and risk drive an unsustainable and negative relationship between selection and fitness.

We test the relative support for each of these three selection-fitness hypotheses using Cox proportional hazards analyses (Therneau and Grambsch 2000). This provides an important test of ideal habitat selection in the face of human-mediated changes to the spatial risk pattern, but furthermore allows fitness-based estimation of habitat quality in a spatially explicit framework (Johnson et al 2004). We illustrate how such a fitness-based model can be extrapolated across our study area to define demographic habitat quality, based on adult female survival. Finally, given that population growth rates ultimately represent the mean fitness among individuals (Mills in press), we estimate variation in population growth rate according to selection and risk correlates in both environmental and geographic space, demonstrating the power of this technique for both conceptual and operational definitions of species habitat quality (Hirzel and LeLay 2008).

Materials and Methods

Study area and caribou populations

We studied woodland caribou survival in 5 spatially distinct local populations (A la Pêche, Little Smoky, Narraway, Redrock-Prairie Creek, and South Jasper) within west-central Alberta and eastern British Columbia, Canada. Caribou in our study area were partially migratory, exhibiting variation in migration tendency among populations (McDevitt et al. 2009). Migrations typically occurred between low-elevation foothills winter ranges and high-elevation mountainous summer ranges, though caribou also exhibited annually sedentary behavior within both mountain and foothills regions. Our study area included large networks of federal and provincial parks and protected areas, but a majority of lands were primarily managed by provincial governments for

multiple uses including forestry, oil, and natural gas industries. Resource extraction practices have left a substantial footprint in this study area in the form of early-seral stage forestry cut-blocks and linear forest-free corridors in the form of roads and seismic lines, each of which have been shown to impact caribou through changes to community dynamics of the greater large mammal predator-prey system (Dyer et al. 2001, Wittmer et al. 2007, DeCesare et al. 2012b).

Animal capture and monitoring

We deployed a combination of conventional very-high frequency (VHF; Lotek Wireless, Newmarket, Ontario, Canada) and global positioning system (GPS; Lotek GPS 1000, 2000, 2200, 3300, 4400, and 7000 models) telemetry collars during 1998–2011 on 468 adult female caribou using helicopter net-gunning (Table 1). Capture protocols were approved by the University of Montana Institutional Animal Care and Use Committee (Animal Use Protocol 059-09MHWB-122209), University of Alberta Animal Care Committee (Protocol SCHM-2005-61) and Parks Canada Animal Care Committee (JNP-2009-4052). Approximately 24% of the total monitoring time across all individuals included GPS data collected at 1-, 2-, 3-, 4-, or 6-hour intervals, while the remainder (76%) of monitoring time involved aerial telemetry of VHF telemetry collars at a median interval of 52 days. Across all populations and years we estimated an 88% mean probability of locating each individual during targeted VHF telemetry flights, which was found to have negligible effects on survival analyses (NJD, unpublished data). The fate of individuals was recorded with each telemetry location as either alive or dead. Animals that did not die during the study were right-censored and removed from the at-risk pool after their last known alive location in accordance with events such as collar removal, collar battery failure that prevented detection for a period of ≥ 2 years, or the end of the study.

Hypotheses of spatial habitat quality

We developed three candidate models to represent each of our three hypotheses concerning relationships between resource selection probability, predation risk and caribou survival (Fig. 1). First, we included in all models the possibility of weather effects in driving some among-year variation, as ungulate adult survival has been shown previously to vary with both summer and winter weather conditions (Wladji et al. 2002, Jacobson et al. 2004). Next, we did some preliminary analyses of the distinct selection-fitness and risk-fitness relationships, accounting for the possibility of both instantaneous and time-lagged effects of selection and risk on survival. We hypothesized that the resource conditions characterized by resource selection functions (both forage and risk) were likely to have both instantaneous and lagged effects on the hazard experienced by individuals (Gaillard et al. 2010). Exposure to different levels of habitat quality as measured by forage conditions may have a cumulative effect on hazard such that the seasonal average level of forage quality to which an individual is exposed may be more predictive than the instantaneous level of forage quality encountered at any given moment (Hebblewhite & Merrill 2011). Alternately, given that avoidance of risk is potentially also an underlying driver of resource selection patterns (McLoughlin et al. 2010), there may be an instantaneous effect of habitat quality on hazard as well. Prior to multivariable modeling, we tested whether the selection-fitness relationship was best described by seasonal average, instantaneous, or both scales of measuring resource selection probability for caribou (Gaillard et al. 2010). Spatial variation in wolf predation risk is perhaps most likely to have an instantaneous effect on the

relative hazard, though there is also some evidence to suggest accumulated exposure to predation risk may also induce indirect or lagged effects on animal condition and presumably hazard (Christianson and Creel 2010). Thus we compared among each seasonal and instantaneous treatments of predation risk with respect to caribou survival as well.

We then developed multivariable candidate models in accordance with our three hypotheses (Fig. 1), with specific statistical predictions for each: 1) the “ideal selection hypothesis” model included only a main effect of resource selection probability on survival and predicted a positive relationship between selection and survival, 2) the “non-ideal selection hypothesis” model included main effects coefficients for resource selection probability and predation risk, with the prediction that selection would correlate positively with survival while risk would correlate negatively; and 3) the ecological trap hypothesis model included main effects for weather, resource selection probability, and predation risk, as well as an interaction term for selection x predation risk, such that the relationship between selection and survival would vary under different risk scenarios (Fig. 1). We included and/or excluded the same variables characterizing weather in all models for a given season to equally account for its effect on the relative hazard among years while testing other covariates. Assuming the signs of model coefficients were also in agreement with our predictions (Fig. 1), we used Akaike information criteria (AIC) to evaluate the relative support for each hypothesis distinctly during summer and winter seasons.

Survival modeling

We used Cox-proportional hazards (CPH) modeling to assess the statistical support for each of our hypotheses concerning drivers of adult female caribou survival. Cox-proportional hazards models are semi-parametric regression models for survival data that specify a flexible and nonparametric baseline hazard function ($h_0[t]$) of the hazard over time, while at the same time parameterizing a function ($r[x,\beta]$) that describes proportional changes in the baseline hazard with changes in subject covariates (Hosmer et al. 2008). In total the hazard,

$$h(t, x, \beta) = h_0(t)r(x, \beta), \tag{3-1}$$

is a function of both changes in the baseline hazard over time and relative differences in hazard according to covariates. The relative effect of a unit change in a given covariate, i , on the hazard is assumed to be constant over time and can be estimated directly from each model coefficient (β_i) according to the hazard ratio (HR),

$$HR_i = \exp(\beta_i), \tag{3-2}.$$

We used a recurrent time of origin based on a biological year where May 1st of each year was set to a time of 1 and April 31st the following year to a time of 365. This method allows for continuous within-year variation in the hazard due to annually recurring phenomena such as seasonal variation in environmental conditions or life history, while facilitating the testing of effects of among-year variation such as weather variation on the relative hazard by pooling the at-risk sample of individuals across years (Fieberg and DelGiudice 2009). Because individuals were allowed to contribute multiple individual-years to the risk sample, we used robust “sandwich” variance estimation to account for within-individual correlation (Lin and Wei 1989, Cleves et al. 2010). We also stratified CPH analyses by caribou population, which allows for distinct baseline hazard functions among populations, but estimates a single population-averaged

coefficient or response to each covariate (Therneau and Grambsch 2000, Cleves et al. 2010). We estimated separate models for summer (1 May – 31 October) and winter (1 November – 31 April) seasons, and used AIC to evaluate sets of models within each season.

We conducted two tests of the assumption of proportional hazards for best models. We began with a link test, which re-estimates a CPH model using the linear and squared predicted values, and failure of this test is indicated by a statistically significant coefficient of the squared predictor (Cleves et al. 2010). We then plotted the scaled Schoenfeld (1982) residuals over time, wherein a nonzero slope over time can indicate a lack of proportionality (Grambsch and Therneau 1994, Cleves et al. 2010).

Survival covariates

Along with animal fate, each telemetry location was also associated with estimates of weather conditions, resource selection probability, and relative risk of wolf predation. We used weather data to capture potential among-year differences in the relative hazard due to weather conditions alone. We estimated seasonal averages for each year from 1998–2012 of maximum daily temperature (°C) and precipitation (mm) for the summer season and minimum daily temperature (°C) and snow on the ground (cm) for the winter season using Environment Canada’s National Climate Archive data for a weather station within the study area in Jasper, Alberta (52.93° N, 118.03° W).

To characterize preferred habitat as typically estimated using species distribution or resource selection modeling approaches, we used a previously developed scale-integrated resource selection functions (SRSFs; DeCesare et al. 2012*b*). These SRSFs were developed separately for each study population and season, as the integrated probabilities of resource use across first-, second-, and third-order scales of selection. We used previously developed seasonal predation risk models in the same study area to estimate spatial variation in wolf predation risk as a function of the integrated probabilities of both encountering a wolf and being killed given an encounter (DeCesare 2012).

Defining demographic habitat quality

To visualize the relative effects of covariates on seasonal survival probabilities, we predicted the cumulative survival probability from best seasonal model under 4 sets of conditions by varying resource selection probability and predation risk each between low and high levels. To approximate meaningful low and high values for each variable, we used the 5th and 95th percentiles of seasonal averages per set of locations for each individual-year. We also spatially extrapolated best seasonal predictive models for each population, j , by estimating seasonal survival rates to the end of each season ($S[t_e]$) as a function of each pixels’ attribute data according to:

$$S_j(t_e | \mathbf{x}) = (S_{0,j}[t_e])^{\exp(\mathbf{x}\beta_j)}, \quad (3-3)$$

where $S_{0,j}[t_e]$ is the baseline cumulative survival probability per population to the last day of each season, with different baseline estimates according to strata, j , or in this case populations (Cleves et al. 2010).

We used average recruitment estimates from age ratio surveys for the same 5 populations to further extrapolated survival models into projections of population mean fitness as driven predicted by resource selection and predation risk covariates. We followed methods of DeCesare et al. (2012a) to convert survival estimates from equation 3 and average recruitment estimates into estimates of population growth, or the mean fitness of individuals within a population (Mills in press). Because the annual period was divided equally into two seasons, we divided recruitment estimates in half to distribute the recruitment component of population growth equally across seasonal models. This additional step allowed us to spatially define population growth as a function of two commonly measured covariates, as well as to spatially extrapolate a raster of predicted population mean fitness across our study area, with immediate implications for critical habitat designation (Environment Canada 2011) and caribou conservation.

Results

Model selection results indicated strong support for the additive risk hypothesis that both resource selection and predation risk were important and non-interacting predictors of the relative hazard for adult female caribou (Table 1, Fig. 2). Though $\Delta AIC < 2$ for the ecological trap model for both seasons, the interaction term received no statistical support in either summer ($P=0.708$) or winter ($P=0.935$) seasons and can be considered an uninformative parameter; in this case low $\Delta AICs$ are simply a function of nested models differing in only 1 parameter (Arnold 2010). In accordance with the “non-ideal selection hypothesis” resource selection probability was negatively related to the mortality hazard (i.e., positively to survival) during both summer ($\beta = -34.364$, $P < 0.001$) and winter ($\beta = -22.509$, $P < 0.001$) seasons, and predation risk was positively related to the hazard (i.e., negatively to survival) in both summer ($\beta = 20.227$, $P < 0.001$) and winter ($\beta = 6.096$, $P < 0.001$) models (Table 2).

There was univariate support for relationships between the hazard and both seasonal average and instantaneous measures of resource selection probability and predation risk, though in multivariable models only a single treatment of each parameter remained significant (Table 2). In the best summer model, the seasonal average resource selection value for each individual-year was most predictive of mortality hazard, while in the best winter model the instantaneous, or per-location, value of resource selection probability was most predictive of changes in hazard. Predation risk was most predictive when measured instantaneously during both seasons. Weather parameters such as maximum temperature ($P=0.533$) and precipitation ($P=0.441$) during summer and minimum temperature ($P=0.116$) and snow ($P=0.212$) during winter did not have significant effects on the hazard as measured using seasonal averages for each year.

Predictions of seasonal survival rates varied from 0.660–0.996 during summer and from 0.820–0.985 during winter according to low (5th percentile) and high (95th percentile) values of average resource selection and predation risk values (Fig. 3). This amounted to a predicted range in annual survival from 0.541–0.981 between relatively hazardous areas with low selection probability and high risk and relatively safe areas with high selection probability and low risk, respectively. Spatially extrapolating the CPH models allowed the integration of baseline survival probabilities, relative selection probabilities, and relative predation risk into spatial depictions of survival-based habitat quality (Fig. 4). Furthermore, in combination with average estimates of recruitment these models allowed projection of population growth rate predictions in both environmental and geographic space as a function of these two key axes of species niches (Fig. 5).

Link tests of both summer ($P=0.720$) and winter ($P=0.990$) models showed insignificant squared predictors, and generally suggested that both models were specified correctly with little evidence for omitted variables. Scaled Schoenfeld residuals did not vary systematically over time and generally supported meeting the assumption of proportional hazards both summer and winter models.

Discussion

Resource selection and species distribution models hinge on an assumption that animals select habitat ideally and freely to maximize fitness with respect to forage, risk, and other niche dimensions. While such models have been predictive of fitness in some cases (Morris and Davidson 2000, McLoughlin et al. 2006, Pérot and Villard 2009), many studies in systems with high predation risk have revealed risk-induced breakdowns between habitat selection and realized quality (Nielsen et al. 2006, Latif et al. 2011). Additionally, recent evidence is mounting that anthropogenic effects can decouple selection-fitness relationships through changes in risk dynamics or to cues used by animals to select habitat (Kokko and Sutherland 2001, Battin 2004). We tested first whether resource selection models were predictive of demographic fitness in the form of adult female survival for woodland caribou. Indeed we found positive relationships between the predicted values of a scale-integrated resource selection function and the probability of survival across both winter and summer seasons. This result offered some support for our ideal free habitat selection hypothesis that selection was indicative of fitness benefits conferred by habitat.

The subsequent addition of predation risk into models allowed better explanation of spatial patterns of adult survival, suggesting that predation risk offered an additive source of hazard beyond that which was detected through resource selection alone. Similar to non-ideal selection originally posed by Arlt and Pärt (2007), we interpret this result to indicate a flaw in resource selection such that risk was not avoided in a matter representative of its impact on fitness. Non-ideal selection may be a symptom of recent, human-induced changes to spatial patterns in predation risk (DeCesare 2012) and the lag between present fitness outcomes of these novel features and their selective pressures on evolving animal behavior (Van Horne 1983). Non-ideal selection may also result from non-free selection by animals, such as caribou, with other constraints such as sociality (Pays et al. 2012) or site fidelity (Dalerum et al. 2007, Faille et al. 2010). In either case, predation risk represents an additive covariate of demographic habitat quality beyond that detectable through selection patterns alone.

We found no support for an ecological trap in this system, as shown by the lack of support for a statistical interaction between selection and predation risk. Thus predation risk induced a constant proportional decrease in fitness while not appearing to interfere with the generally positive selection-fitness relationship (Fig. 2). Ecological traps are often found where novel and risky conditions mimic those of high quality habitat, and as a result adaptive cues underlying habitat selection decisions become maladaptive (Schlaepfer et al. 2002). Classic examples include asphalt mimicking the cues used by mayflies to identify ponds for laying eggs (Kriska et al. 1998) or hawks using high prey density as cue to nest in urban areas which then convey high disease and collision mortality risk (Boal and Mannan 1999). Woodland caribou do not show active selection of risky areas, but rather have exhibited behavioral avoidance of risk across many study areas (Bergerud et al. 1984, Rettie and Messier 2000, Dyer et al. 2001, McLoughlin et al. 2005, Gustine et al. 2006 *b*, Bowman et al. 2010, DeCesare et al. 2012*b*).

Rather than novel sources or cues of risk, our results may simply reflect higher overall levels of risk in the same risky places, thus causing an imbalance between risk avoidance and other niche dimensions shaping caribou selection and demography.

The correlation between inherent animal preferences and our measurements of such using resource selection functions may vary with the greater abundance of animals occupying a given study area (McLoughlin et al. 2010). Theoretically, animals may use local variation in density to distribute themselves in a manner that facilitates equivalent fitness across all levels of habitat quality (Fretwell and Lucas 1969). This may preclude efforts to measure habitat quality as a function of adult survival as we do here because equal survival among individuals could be attainable across varying levels of inherent habitat quality as mediated by density. Caribou in our study area are known to occur at substantially lower densities than historically observed (ASRD and ACA 2010, Bradley and Neufeld 2012). Furthermore, because there is no evidence of negative density dependence on adult survival in declining woodland caribou populations (Wittmer et al. 2010, DeCesare et al. 2011), we expect few density-induced effects on local variation in fitness.

We also assessed the habitat-fitness relationship at multiple scales by estimating both among-individual seasonally averaged measures of selection probability and predation risk and within-individual instantaneous values at each telemetry location. Instantaneous variation in predation risk was found to be a better predictor of survival than the seasonal average risk exposure for each individual. This suggests that the most relevant variation in risk occurs locally, though the significance of seasonal averaged risk levels at the univariate level does lend some support to a cumulative risk effect (Christianson and Creel 2010). With regard to resource selection predictions, the seasonal average predicted values per individual were more predictive during summer whereas the instantaneous predicted values were more predictive during winter. This may reflect a greater role of predation risk in driving winter fitness and forage in driving summer fitness, though an opposite pattern has also been suggested for woodland caribou in British Columbia (Wittmer et al. 2006).

We focus on adult survival due to its high elasticity on population growth in ungulates, particularly those in declining populations (Johnson et al. 2010). However, recruitment may also explain much variation in ungulate population growth rates (Gaillard et al. 2000, Johnson et al. 2010). Demographic evaluation of habitat quality has shown both similar (Arlt and Pärt 2007) and discordant (Martin 1995) patterns of quality with respect to different vital rates. Our adult-based depiction of habitat quality (Figs. 4, 5) may not adequately account for important habitat components of juvenile survival. Complete representation of environmental and spatial gradients of fitness should integrate measures of habitat quality according to other life history parameters as well (Martin 1995). Regardless, in our populations calf survival is generally low and adult survival is both highly elastic and variable, inducing greater effect on population growth rates (DeCesare et al. 2012a). While studies of cause-specific mortality or human impacts on caribou calves have been rare (but see Gustine et al. 2006a), predator-caused mortality is usually an even more important source of mortality for neonatal and first-year calf survival in ungulates (Griffin et al. 2011). Therefore, we interpret our adult-female based spatial models of demographic habitat quality as important drivers of caribou population viability in our study area.

Predicted seasonal survival rates from our models suggest a wide range in habitat quality experienced by individuals according to their space use and underlying gradients of selection probability and risk of predation. Though Wald statistics suggested similar statistical evidence of the effect of both selection probability and predation, we used outer 5th and 95th percentiles of

seasonal averages to frame the observed bounds of selection probability and predation risk experienced by individuals. This spatial prediction suggested that variation between low and high selection probability more strongly dictated survival probability (Fig. 3). Predation risk appeared to induce a constant proportional decrease in survival probability across gradients in selection probability (Fig. 2), though this translated to a small absolute effect on survival probability in favorable habitat and a large absolute effect in poor habitat (Fig. 3).

Ultimately we used CPH modeling to facilitate the translation of resource selection and predation risk patterns into a survival-based estimate of demographic habitat quality. This achieves the high standard of translating gradients of environmental resources into a multi-dimensional, fitness-based model of the gradient in caribou niche space (*sensu* Hirzel and LeLay 2008). Furthermore, this technique allows the extrapolation of fitness predictions across geographical space (Figs. 4, 5), with great potential for conservation or management applications (Franklin et al. 2000, Johnson et al. 2004, Ezard, et al. 2008). Such a spatial model of demographic habitat quality may be used to inform delineation of management units such as critical habitat under endangered species legislation (Heinrichs et al. 2010) or linked with landscape scenario models to forecast relationships between landscape conditions and population viability (Carroll and Miquelle 2006, Rushton et al. 2006, Heinrichs et al. 2010). Overall, this work indicates both the strength and the limitation of commonly conducted resource selection or species distribution modeling wherein the basic density- or selection-fitness relationship is supported, but found to incompletely represent habitat quality as measured with fitness traits.

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4.0 Spatial relationships and resource partitioning of moose and woodland caribou in a human altered landscape

Abstract

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 (more than 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.

Introduction

Biologists need to understand the mechanisms leading to population declines, and potential complex interactions among these mechanisms, to manage and conserve species. Over the last century, humans have significantly impacted the global environment and thereby increased extinction rates well above natural background levels. 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 (Mills 2007). Caribou and reindeer (*Rangifer tarandus*) populations are declining throughout their circumpolar range due to changes in climate and human disturbance (e.g. implementation of infrastructure, mineral extraction or forest harvesting; Vors and Boyce 2009). For example, several studies describe how human landscape changes have led to shifts in the distribution of reindeer and caribou (Vistnes et al. 2001) or altered predator-prey relationships resulting in increased predation rates on reindeer and caribou (Seip 1992, Kojola et al. 2004), and thereby have directly or indirectly decreased population size of these habitat specialists (Nellemann and Cameron 1998). As in other parts of *Rangifer* range, conservation of woodland caribou (*Rangifer tarandus 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 (Government of Canada 2002). While widespread human landscape change (i.e. energy and forestry exploitation and

associated road and seismic line implementation) 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), necessitating a community approach to caribou conservation.

Changes in species composition and distribution may exacerbate population declines and extinction of threatened populations through apparent competition, the process by which two prey species can affect each other's fitness through their numerical response on a shared predator (Holt and Lawton 1994). Individual resource selection can lead to spatial and temporal segregation or differing diet preferences (Chesson and Kuang 2008) and thereby facilitate the coexistence of sympatric species. While moose (*Alces alces*) and woodland caribou (hereafter caribou) are sympatric throughout the boreal forest, they are hypothesized to coexist through resource partitioning (Boer 2007). The diet of caribou is comprised of terrestrial and arboreal lichens, especially during winter (Thomas et al. 1996). Consequently, caribou are strongly associated with large contiguous patches of low productivity, older seral conifer stands where lichen biomass is highest. In mountain regions, caribou generally select higher elevations and exhibit seasonal migration (Seip 1992). Moose are generalist browsers, mainly feeding on shrubs, and prosper in early succession vegetation communities (e.g. following fire or forest harvesting) that provide green forage (Peek 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).

The conversion of old-growth forests to young seral stands is hypothesized to increase the abundance of moose, the dominant prey for wolves (*Canis lupus*) throughout caribou distribution, and thereby increase wolf densities (Kojola et al. 2004, Wittmer et al. 2005). While wolves are responsible for the majority of adult female caribou mortality, also other predators, such as grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*) have been identified as effective predators for caribou and moose (Wittmer et al. 2005, Gustine et al. 2006). Additionally, research suggests that wolves and bears select for landcover types with high forage biomass (e.g. shrub communities, burns, logged areas; Mosnier et al. 2008, Gurarie et al. 2011) presumably to increase encounter rates with prey (Hebblewhite et al. 2005b). The combination of fragmentation of older forests preferred by caribou and increased densities of moose and predator populations may limit the realized niche, and hence distribution, of caribou (Seip 1992, James et al. 2004). Thus, understanding resource partitioning by moose and caribou in the context of spatial separation is key to evaluating the mechanisms of apparent competition.

Resource selection can be influenced by nutrition, behavior, competition or predation (Manly et al. 2002). Ungulates generally respond to their environment in a hierarchical fashion across spatial scales to limiting factors (Senft et al. 1987). In the context of the trade-off between predation risk and forage (Hebblewhite and Merrill 2009a), caribou select habitat to reduce predation at coarser scales and to maximize forage at finer scales (Rettie and Messier 2000, Polfus et al. 2011, DeCesare et al. 2012). In contrast, under the spatial separation hypothesis (Seip 1992), moose are generally associated with human resource extraction activities at coarser scales, but may also select for high browse landcover types at fine scales (Forbes and Theberge 1993). Thus, we can expect stronger differential resource use at coarser scales by caribou and moose and more similar use of environmental variables at smaller scales. Despite the importance of understanding the mechanisms of apparent competition for caribou declines, to date, direct comparisons of moose and caribou resource use are rare (Bowman et al. 2010).

Our goal was to determine the relationships between human disturbance and caribou and moose resource use, and to understand the effects on their resource partitioning and overlap at two spatial scales. We focused our efforts in a study area in west-central Alberta (AB) and east-central British Columbia (BC) which included 6 declining caribou populations (Alberta Sustainable Resource Development and Alberta Conservation Association [ASRD and ACA].2010). First, we

assessed resource overlap and partitioning between caribou and moose explained by human disturbance and other environmental variables at a coarser scale using redundancy analysis (RDA; ter Braak 1995). Second, we tested whether spatial separation between sympatric caribou and moose decreased at finer spatial scales in human altered landscapes by comparing resource use of sympatric caribou and moose using logistic regression (Latham et al. 2011) and overlap indices (Schoener 1974). Finally, the spatial separation hypothesis predicts increased risk of caribou mortality in areas of higher probability of moose occurrence (McLoughlin et al. 2005). We examined whether the majority of predation-caused mortalities of caribou occurred within moose, intermediate or caribou habitats.

Methods

Study Area

We assessed spatial relationships of caribou and moose in an approximately 54,000 km² study area in the foothills and mountains of west-central AB and east-central BC within the ranges of 6 declining spatially distinct woodland caribou herds: A La Peche herd (ALP), Red Rock Prairie Creek herd (RPC), Little Smoky herd (LSM), the Narraway herd (NAR), Redwillow (RW) and the Tonquin (TON) in Jasper National Park (Figure 1). Human landscape change varied throughout the study area with low human disturbance and a high proportion of protected areas, including Jasper National Park, the Wilmore Wilderness, Kakwa Wildland Park (AB) and Kakwa Provincial Park (BC) in the western part (Figure 1). The eastern part of the study area was characterized by provincial lands managed primarily for resource extraction, with correspondingly higher human disturbance in the form of oil and gas extraction and forestry exploitation with high densities of forest harvesting (mainly clearcut block harvesting) and linear developments (e.g., roads, pipelines, seismic lines). Anthropogenic impacts were greatest in the LSM caribou range (2012). Elevations followed an increasing gradient from east to west from about 500m to more than 3,000m.

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. Bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) inhabited the mountain region. In addition to wolves, other large predator species included black bear, grizzly bear, coyote (*Canis latrans*), cougar (*Puma concolor*), wolverine (*Gulo gulo*) and lynx (*Lynx canadensis*).

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 10 female and 7 male moose within and adjacent to caribou population home ranges (Figure 1). We radio-collared female and male moose to evaluate population-level habitat use and moose population overlap with female caribou. For threatened caribou populations, female caribou are the most relevant sex to study, because adult female caribou survival drives caribou population growth rates (DeCesare et al. 2011). Therefore, we used GPS collar (GPS 3300, 4400, LOTEK Engineering Ltd., 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 University of Montana Animal Care and Use Protocol 056-56MHECS-010207 and 059-09MHWB-122109, Alberta Sustainable Resource Development licenses #21803, #27086, #27088, #27090 and Parks Canada permit JNP-2007-952. Both moose and caribou GPS collars collected locations every 2 to 4 hours, which we re-sampled to

a consistent 4-hour relocation schedule. The majority of moose GPS collars were deployed for approximately 1 year, but caribou GPS data often spanned a longer time frame. Therefore, we limited caribou location data to one calendar year as well. Fix rate success of less than 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 need to 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. 2012).

Large-scale caribou-moose resource partitioning

We assessed niche separation and overlap by measuring the niche position of caribou and moose relative to each other at the scale of our study area 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 niche separation between species. Thus, the distribution of the two species along these environmental conditions can be considered as the realized niche within our study area (i.e., coarse scale). We overlaid a 500m² grid (largest extent of GIS data sets; Appendix A) onto our study area (n = 250,206) and assessed the presence of GPS locations from each species (presence/absence) in each cell. Continuous environmental variables were averaged within each grid cell. For categorical variables (i.e. landcover types) we estimated proportions within each grid cell in ArcGIS 9.3.1 (ESRI, Redlands, CA) and arcsine square root transformed them. We performed detrended correspondence analysis (DCA) to assess whether a linear response of species to environmental variables was expected (first axes length < 3). 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 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 1987). We 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 partition niche space and thus, should be associated with a unique set of environmental variables. First, we predicted that the species scores, i.e. the coordinates along the ordination axes specifying the position of the species in niche space, for moose and caribou would be strongly contrasting each other. 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 young seral stands and human disturbance (i.e. cutblocks, 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 partitioning

To evaluate resource partitioning of moose and caribou at a finer scale, i.e. when individuals of the two species occupied overlapping areas, we paired each moose with one caribou in their respective caribou herd home-range (95% fixed kernel) to maintain equal availability of resources to each pair. Because of moose collar failure in the RPC caribou herd we compared one caribou from this herd to the closest moose available (Figure 1). We used logistic regression (Hosmer and Lemeshow 2000) to model 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. 2011). We compared moose and caribou resource use in summer and winter. This analysis determined which covariates predicted spatial separation between moose and caribou resource use at smaller spatial scales, measured by the estimated β coefficients from logistic regression. We again, predicted that caribou would use higher elevations and lower human disturbance than moose. We used a random intercept ($\beta_0 + \gamma_0j$) for each caribou-moose pair 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 (Appendix A) previously reported to influence caribou and moose resource use. All covariates were screened for collinearity using the Pearson's correlation coefficient threshold of $|r| > 0.6$ (Hosmer and Lemeshow 2000), retaining the collinear covariate with the lower log-likelihood, highest coefficient of determination (pseudo R^2) and lowest p-values. We first conducted univariate logistic regression analysis, using a $P < 0.25$ on a Wald χ^2 -statistic as a cut-off for the inclusion in model building. To test whether coefficients were nonlinear we used Generalized Additive Models (GAMs; Hastie and Tibshirani 1990), and either transformed coefficients or used quadratics to capture non-linearity (Hosmer and Lemeshow 2000). 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). 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).

We estimated resource use overlap and thus, overlap of the realized niches (Hirzel and Le Lay 2008), between moose and caribou using Schoener's C (Schoener 1974), a symmetrical measure of overlap between species ranging from 0 (no overlap) to 1.0 (complete overlap). We used spatial distributions for each species predicted from the top caribou-moose logistic regression model. First, we created spatial predictive maps of caribou-moose resource use using ArcGIS 9.3.1 and classified each map into 10 equal-sized categories. These maps provided a relative index of caribou and moose resource use, where values closer to 1 indicated the highest relative probability of use by moose and conversely, values closer to 10 indicated the highest relative probability of use by caribou (Robinson et al. In press). We then calculated Schoener's overlap index in these 10 ranked resource use categories for moose and caribou telemetry locations. In this way, Schoener's overlap index provided a measure of the spatial distribution of caribou relative to moose (Abrams 1980). We predicted that increasing human landscape alteration decreases spatial separation between caribou and moose, and addressed this using the relationship between the Schoener's overlap indices for each caribou-moose pair versus the density of human disturbance measured as average clearcut density (at a radius of 3km as $\%area/100$; see landscape covariates section) 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 due to resource overlap.

Finally, 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). We classified areas as high overlap where both species were predicted to have intermediate relative probability of use (i.e. use of categories 4 - 7); caribou habitat was represented by categories 8 - 10 and moose habitat by categories 1 - 3. Long-term mortality data (1999-2009) were compiled by Alberta Fish and Wildlife Division and Parks Canada based on radio-collared (VHF and GPS) caribou. Radio-collared caribou were located at least every 3 months from a fixed-wing aircraft. Sensors of radio-collars indicated mortalities by altering their beacon frequency when the caribou was immobile for more than 8 hours. Animal mortalities were investigated on the ground as soon as possible to determine cause of death (Smith 2004). 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). 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 (bins 1-3), overlap (bins 4-7) and caribou (bins 8-10) habitat using a one-way chi-squared test.

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 land cover types (see Appendix A for details). To address impacts of human landscape alteration on caribou-moose resource partitioning, we used vector geodatabases to measure linear features (km/km²; roads, seismic exploration lines, rail roads, etc.) within 1 km circular neighborhoods surrounding each raster pixel (Appendix A). We characterized impacts from forest harvesting by clearcuts as a landcover class, as well as a relative index of clearcut density. To identify the relevant spatial scale at which clearcut density had the strongest effect on spatial caribou-moose relationships, we conducted circular neighborhood analysis for cut-block (proportionate area) density by measuring density surrounding each raster pixel at concentric radii from 75m to 10,000m (DeCesare et al. 2012). 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

Large-scale caribou-moose resource partitioning

We chose a linear response model for RDA, because the DCA first gradient lengths were all < 3 (ter Braak and Prentice 1988; ter Braak 1995), and performed analyses for both seasons. The matrix for the occurrence of the two ungulate species was significantly 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 show a distinct separation of the 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 (Figure 2).

During summer, the constrained variance of the species-environment relationship was largely explained by the first axis (approx. 21%), which showed opposite relative species scores (caribou: 2.43; moose: -2.45; Table 2) and thus, captured niche partitioning 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 disturbance (clearcuts, clearcut density, and density of roads and linear features) were correlated with moose presence (Table 2, Figure 2). The second axis (and therefore niche overlap between the species) was negatively related to muskeg (CC = -0.44) and open conifer (CC = -0.41), and positively related to slope (CC = 0.68) and mixed forests (CC = 0.27), but the proportion of variance explained by the second axis was very low (<0.1%).

During winter, the constrained variance of the species-environment relationship was largely explained by the first axis (approx. 15%), which also measured niche separation of the two species indicated by the opposite scores of 2.21 for caribou and -2.06 for moose (Table 2, Figure 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). The second axis was positively related to the density of linear features (CC = 0.75) and muskeg (CC = 0.47), and negatively related to slope (CC = -0.60), elevation and alpine shrub (CC = -0.34 for both variables). Similar to summer, the proportion of variance explained by the second axis, niche overlap, was very low (<0.1%).

Fine-scale caribou-moose resource partitioning

At a finer scale, we evaluated spatial partitioning with 14,420 caribou and 13,615 moose GPS locations in summer and 19,809 caribou and 20,437 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 1,165 (SE = 47.37) and 1,202 (SE = 38.44) respectively. In general, resource use by caribou and moose and the degree of spatial separation differed only slightly between seasons (Table 2, Figure 3). Caribou used significantly higher elevations than moose (the highest standardized z-values) during both season, although spatial separation due to elevation was weaker during winter. Moose also tended to use areas with increased human disturbance and green, broadleaved forage (NDVI; $z_{\text{std_NDVI}} = -1.00$ during summer and $z_{\text{std_NDVI}} = -1.26$ during winter), whereas caribou avoided these features relative to moose (Table 2). For example, the relationship between clearcut density and caribou resource use strongly negative during winter and summer ($z_{\text{std_ClearCutDens}} = -1.26$ in winter and $z_{\text{std_ClearCutDens}} = -0.90$ in summer). In general, caribou and moose differed in responses to human disturbance less in summer than winter. During winter, caribou used areas with higher probabilities of being covered by snow ($z_{\text{std_Snow}} = 2.41$) and occurred more often in open conifer ($z_{\text{std_OpenCon}} = 1.48$) and mixed-forsts ($z_{\text{std_Mixed}} = 1.14$) than moose. The most parsimonious generalized linear mixed models cross validated very 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 slightly higher ($C = 0.690$) in summer than in winter ($C = 0.672$). Overall, the proportion of overlap was high in all resource use categories (Figure 3). 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 (bins 8 -10) was higher (summer = 54% and winter=42%; Figure 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 under the spatial separation hypothesis, resource partitioning between moose and caribou decreased with increasing clearcut densities (Figure 4). This relationship was significant during summer ($R^2 = 0.35$, $F_{(1, 15)} = 8.15$, $P = 0.012$), but only marginally significant during winter ($R^2 = 0.17$, $F_{(1, 15)} = 3.12$, $P = 0.097$).

Finally, there were significant differences among the proportions of caribou mortalities falling into the caribou, moose and intermediate resource use categories during summer ($X^2_{(2, 57)} = 8.37$, $P = 0.015$). The greatest proportion of caribou killed by predators occurred where moose resource use was highest (53%; Figure 5). In winter most caribou mortalities occurred in caribou resource use categories (53%; Figure 5). However, this relationship was not quite statistically significant ($X^2_{(2, 49)} = 5.12$, $P = 0.077$). 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 significant only in summer (summer: $X^2_{(2, 26)} = 10.41$, $P = 0.002$; winter: $X^2_{(2, 18)} = 4.00$, $P = 0.135$).

Discussion

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 partition resources as expected under the spatial separation hypothesis, but we also showed that the strength of resource partitioning varies across different spatial scales and seasons, and can be affected by human landscape change. Results from the RDA suggested that caribou and moose clearly 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, niche overlap was indicated by the similar species scores for caribou and moose along the second axis, but was very weak (variance explained by the Eigenvalue <0.1%) during both seasons (Table 1). In contrast, at a finer scale, our analysis of sympatric caribou and moose pairs indicated substantial niche overlap in all 10 resource use categories (Figure 3), and increasing overlap with when increasing densities of human disturbance and at lower elevations, especially during summer (Figure 4). Finally, our results suggested that caribou experience increased mortality risk when their resource use overlaps with moose at finer spatial scales in summer.

Resource selection varies with scale and consequently, niche relationships between sympatric species may also differ 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 avoid predation risk strongest at coarse spatial scales and maximize forage at smaller spatial scales (Apps et al. 2001, Johnson et al. 2001, Polfus et al. 2011). In our study area DeCesare et. al. (2012) found that woodland caribou avoid clearcuts at coarse spatial scales (i.e. predator density in response to primary prey), before densities of linear features (i.e. increased predator kill rates), such as roads and seismic exploration lines, become predictive for caribou avoidance. Similarly, results from our analyses suggest that the minimal overlap between caribou and moose niches at the coarser spatial scale may be a demographic response if caribou mortality increases with clearcut density (Vors et al. 2007). Thus, caribou avoid the most limiting factor to fitness, i.e. overlap with moose at coarser scales (numeric response by predators), and maximize forage and avoid functional responses (i.e. increase predator kill rates) at finer scales (Rettie and Messier 2000, Johnson et al. 2001).

Generally, results from RDA and logistic regression were consistent with previous studies assessing caribou (Apps et al. 2001, Polfus et al. 2011) and moose resource use (Forbes and Theberge 1993, Bowman et al. 2010). Caribou associated with variables representing alpine and coniferous habitats and moose with variables representing deciduous foraging habitats at both scales of our analyses, but the magnitude of the predictor variables was scale- and season dependent. 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 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). Therefore, migratory strategies of caribou may constrain caribou to spatially separate at coarser scale during winter, but these habitat specialists may have adopted season dependent separation strategies which could differ with spatial scale (Ihl and Klein 2001). Spatial separation may be stronger at larger spatial scales during summer compared to winter while during winter, caribou increasingly separate from moose at finer spatial scales. Our results indicate such seasonal scale-dependent avoidance strategies by caribou by a much stronger avoidance of NDVI and clearcut densities by caribou compared to moose during winter at the finer scale, but not the coarser scale. Further, our results

indicate that snow may be a strong driver in the fine scale niche 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).

Selection coefficients from logistic regression and canonical coefficients from redundancy were consistent with the general consensus that caribou avoided human disturbance. For example, several studies have suggested that caribou avoid roads and seismic lines (Dyer et al. 2001, Vistnes and Nellemann 2001, DeCesare et al. 2012). Also, cutblocks in Ontario have significantly displaced caribou from harvested areas (Vors et al. 2007, Bowman et al. 2010). In our study area, DeCesare et al. (2012) reported long-term avoidance of clearcut density measured within 12 km radii. Habitat alteration in caribou range leads to the direct loss of habitat and can result in less contiguous caribou habitat that may be interspersed with habitat highly selected by primary prey species and loss of mature forests may restrict the ability by caribou to space out in the landscape (Wittmer et al. 2005). Consistent with the hypothesized effect of human landscape change on resource partitioning, we found increased general resource overlap of caribou and moose (Schoener's C) with increasing clearcut density (Figure 4).

Spatial 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 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. Similarly, Mysterud (2000) found that diet of moose and reindeer only overlapped by 0.6% in winter. However, in summer caribou may also feed on similar forbs and deciduous vegetation (Apps et al. 2001) as moose. Consequently, high fine-scale niche overlap during summer we observed can be explained by potentially overlapping forage and elevation preferences of the two species during summer (Seip 1992, Boer 2007). In contrast, we must assume that forage overlap did not result in similar niche 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 6 caribou herds we studied were altered by forestry based on satellite imagery (ASRD and ACA 2010).

Caribou survival and population growth may be significantly reduced in regions with increased disturbance 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. 2005a). Wittmer et al. (2005) reported that caribou killed by predators had proportionately less old forests and more mid-age forest in their home range compared to surviving caribou. Consistent with these conclusions, we reported higher mortality frequencies for caribou in moose resource categories during summer. 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, especially in the presence of linear features (Whittington et al. 2005, Gurarie 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). Lastly, while wolves are the main predator on caribou, also black and grizzly bears can be effective predators on caribou (Wittmer et al. 2005, Gustine et al. 2006). However, Latham et al. (2011) found that black bears do not hunt actively for caribou, but rather opportunistically kill them as they move between vegetation rich forage patches.

Although we feel confident in our conclusion that spatial separation between moose and caribou is decreased in landscapes with high human disturbance, 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, DeCesare et al. 2012). 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 and all female captured moose were pregnant at the time of capture determined by blood serum progesterone levels when blood samples were available (Haigh et al. 1993), suggesting high moose population viability in stark contrast to low caribou survival and 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 disturbance (Peek 2007). Further, we did not take within-population heterogeneity in resource use that may occur with partial migration (Hebblewhite and Merrill 2009b) into account. Some caribou migrated to higher elevations during summer, a mechanism of spatial separation (Seip 1992). Clearly, what appears to be an outlier in Figures 4 was caused by an animal in the LSM herd, the only sedentary herd in our study area. Thus, not only resource overlap may be elevated for non-migratory versus migratory animals, but also predation risk, if migration allows animals to escape from predation at broad spatial scales (Hebblewhite and Merrill 2009b). Therefore, further investigation of exclusively sedentary caribou and moose would be necessary to determine niche overlap during summer in the foothills.

Especially in human altered landscapes, species may be unable to adopt to novel mortality risks that were not present in their evolutionary history (Schlaepfer et al. 2002). Overall, our results supported the hypothesis that with the encroachment of human disturbance on the landscape, 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. Where wolf predation has been identified as one of the main limiting factors for caribou and reindeer population growth, management actions often include wolf culls to reduce predation pressure (Bergerud and Elliot 1986). However, wolf populations will quickly recuperate, unless moose density is also reduced due to rapid increases of moose following predator control and subsequent attraction of wolves from adjacent areas (Lessard et al. 2005). Also, conservation effort may be further complicated where both *Rangifer* and wolves are protected (Gurarie et al. 2011). Overall, predator control does not appear to be an effective long-term conservation strategy, if increased predation pressure is the 'symptom' of human disturbance (Vors and Boyce 2009). Failure to address the habitat-based root-causes of caribou declines, will likely result in continuous long-term caribou population decrease. 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). In our study, caribou used lower densities of roads and other linear features (DeCesare et al. 2012) compared to moose, suggesting that limiting the amount of linear features that potentially increase predation efficiency by predators (James et al. 2004) in caribou ranges is also important for caribou recovery. 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 effect persistence of globally declining caribou and reindeer (Vors and Boyce 2009). Integrating these global challenges in *Rangifer* conservation will be a challenging task determining the fate of this ecologically and economically important species.

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Appendix A: Description of GIS-Based spatial Landscape covariates

To address our research questions we used a suite of geographic information system (GIS) raster data sets characterizing habitat that caribou and moose used (Table A1). We used a digital elevation model (DEM) to estimate elevation (m) and slope (degrees). Vegetation was characterized by 13 categorical landcover layers, which were calculated on the basis of landcover type (10 classes; e.g., Upland Trees, Shrubs, Snow/Ice), forest canopy closure and tree species composition. These 3 layers were produced with Landsat 5 and 7 TM sensors (McDermid et al. 2005). Closed conifer was used as the reference category in habitat use models and thus always subsumed into the intercept. Alpine landcover types were delineated by estimating tree line, which was modeled through a curvilinear relationship between latitude and tree line along the north-south study area gradient following Paulsen and Körner (2001). Two landcover types, burns and cutblocks, were produced based on combined data from BC Ministry of Forests and Range Data Models (British Columbia Ministry of Sustainable Resource Management 2010), BC Forest Vegetation Composite Polygons and Rank 1 data (British Columbia Ministry of Sustainable Resource Management 2009), data from the Foothills Research Institute Grizzly Bear Program (FRIGBP) and the AB Sustainable Resource Development.

Normalized Differential Vegetation Index (NDVI) can be used as an index of vegetation productivity (greenness) to characterize green forage biomass (Pettorelli et al. 2005, Hebblewhite et al. 2008). We estimated NDVI during the growing season using 16-day composites derived from NASA's Moderate Resolution Imaging Spectroradiometer (MODIS, MOD13Q1; Huete et al. 2002). Hebblewhite et al. (2008) estimated the mean growing season from 3 May (Julian day 123) to 9 October (Julian day 282) near Banff National Park. Because the growing season decreases with increasing latitude, we estimated average NDVI based on these growing season dates, but used the closest day after 3 May and before 1 October (Julian day 129 and 273) at a 250m resolution for which MODIS data were available for our calculations. Percent snow cover was estimated from 8-day composites of maximum snow extent maps at a 500m resolution produced by MODIS satellites (MOD10A2; Hall et al. 2000). The number of days snow occupied a cell was divided by the number of days in the seasonal period to derive spatial models of percent snow cover. Season start and end dates were the same as for logistic regression models. For all habitat use analyses we calculated NDVI and snow cover values by using the layer of the corresponding year of the GPS locations. Spatial predictions were made using average NDVI and seasonal percent snow layers for winters 2007, 2008 and 2009 and for summers 2008 and 2009.

Besides forest harvesting impacts, human disturbance was further estimated from a variety of vector geodatabases of roads, seismic exploration lines, railways, pipelines and human trails (Alberta SRD –Resource Information Management Branch and digitized 2004 SPOT imagery and 1:250 000 NTS maps). We calculated density layers for roads and linear features (km/km^2) in the Spatial Analyst extension for ArcGIS® Desktop 9.3.1 software.

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Table A1. Description of covariates used in redundancy analyses and to determine differences in habitat use between moose and woodland caribou (data collected 2007 – 2010) in west-central Alberta and east-central British Columbia, Canada.

Covariate	Type	Resolution	Covariate Description
Human/Natural Disturbance			
Road Density	Continuous	30	Road density calculated for each cell (km/ km ²) in a 1 km radius based on a composite roads data layer.
Line Density	Continuous	30	Density of seismic exploration lines, hiking trails, railways and pipelines for each cell (km/ km ²) based on a composite linear features data layer (km/km ² in a 1km radius).
Cut-block	Categorical	30	Cut-blocks <60 years old.
Burn	Categorical	30	Burns <60 years old.
Cut-block density	Continuous	30	Density of cut-blocks (%area/100) within a 3km radius.
Topography			
Elevation	Continuous	30	Elevation in meters.
Slope	Continuous	30	Percent slope (0-89°).
Aspect	Continuous	30	S-N and W-E indices (-1 – 1)
Other Variables			
Closed conifer	Categorical	30	Closed conifer forest with ≥ 50% canopy closure and ≥ 70% coniferous. Reference category.
Open conifer	Categorical	30	Open conifer forest ≤ 50% canopy closure and ≥ 70% coniferous.
Mixed forest	Categorical	30	Mixed forest ≥ 30%, but < 70% coniferous.
Deciduous	Categorical	30	Deciduous dominated forest < 30% coniferous.
Herbaceous	Categorical	30	Grasslands below tree-line.
Herbaceous Alpine	Categorical	30	Grasslands above tree-line.
Barren	Categorical	30	Barren ground below tree-line.
Barren Alpine	Categorical	30	Barren ground above tree-line.
Muskeg	Categorical	30	Treed and herbaceous wetlands at all elevations.
Shrub Alpine	Categorical	30	Shrub communities above tree-line.
Shrub Alpine	Categorical	30	Shrub communities below tree-line.
Water	Categorical	30	Water at all elevations.
Glacier	Categorical	30	Permanent ice.
NDVI	Continuous	250	Mean of NDVI in non-forested habitats for growing season (-1 – 1).
Snow (s/w)	Continuous	500	Seasonal average a raster cell has been covered by snow estimated for summer (16 May–16 October) and winter (17 October–15 May).

5.0 In absentia of predators: identifying anthropogenic landscapes of fear and their effects on wildlife using a behavioral agent-based model

Abstract

Boreal woodland caribou (*Rangifer tarandus caibou*) populations in Alberta are under considerable pressure due, in part, to intense industrial development. In addition to the density-mediated effects of petroleum and forestry practices on population persistence, caribou can additionally perceive industrial features such as pipelines and roads (infrastructure), seismic lines, wellsites, and forestry cutblocks as threatening stimuli and respond accordingly, a phenomena referred to as the landscape of fear. Understanding how anthropogenic disturbances contribute to the way animals perceive and respond to their landscape of fear is essential to the development of strategies for wildlife management and conservation. Using a spatially explicit behavioral agent-based model (ABM), we took an inverse modeling approach in the form of a sensitivity analysis to gain insight into how caribou in west central Alberta differentially respond to industrial features and their attributes such as presence, density, age, and activity. The ABM encapsulates behaviorally mediated effects of predation risk, heterogeneous resource distribution, and species-specific energetic requirements, and produces insight into the context-dependent mechanisms driving habitat selection. The sensitivity analysis used an orthogonal, mixed-level screening design to develop different scenario arrangements of high-risk industry attributes, including a ‘no strong avoidance effect’. A multiple-response optimization approach was employed to identify industry type(s) and feature(s) with the greatest relative influence on caribou habitat use and spatial distribution. The resultant, optimized scenario was then evaluated by comparing simulated caribou movement patterns with those of actual caribou using GPS data from thirteen caribou radio-collars deployed over six winter months from 2004 to 2005, as well as with two null models using a pattern-oriented modelling approach. Results revealed that the presence of infrastructure and seismic lines, the density of cutblocks, and the activity status of wellsites all contributed to explaining caribou responses to industry. Moreover, caribou agents at the level of the individual were more sensitive to linear features than cutblocks or wellsites, but there was no clear substitution effect between features. Our findings suggest that different industries interact in a way to produce cumulative effects, as they jointly impact caribou spatial distributions and energetic reserves, even in the absence of direct predation.

Introduction

Measuring the impacts of anthropogenic activities on the responses of wildlife is crucial for their effective management and population persistence. Ever-increasing industrial disturbances are widely perceived to lead to negative consequences for wildlife beyond habitat loss alone, with one potential impact being the perception by animals of human activities as threatening stimuli (Beale 2007). In an attempt to elucidate the underlying processes driving habitat selection and movement of prey species, the ‘landscape of fear’ concept has been invoked as a behavioural mechanism explaining how perceived predation risk could alter an animal’s use of an area as it tries to reduce its vulnerability to predation (Laundré et al. 2001). Prey respond to spatial

variations in risk by altering their behavior (changes in vigilance, aggregation, and foraging) or their time allocation (avoiding high-risk areas through changes in habitat use and movement patterns; Laundré et al. 2010). If anthropogenic features and/or activities are also perceived as risks, contributing to the landscape of fear, they can similarly manifest in changes in habitat use, reduced foraging effort, increased energy expenditure in vigilance, altered movement patterns (Creel and Christianson 2008), and ultimately, diminution in reproduction and survival (Creel 2011).

In addition to spatial variation in predation risk caused either by natural predators or human activities, prey must usually also contend with more than just one source of predation. Similar to prey that share their landscape with multiple predators, wildlife exposed to different types of anthropogenic features can be affected by non-independent impacts. Indeed, recent meta-analyses of terrestrial (Mantyka-Pringle et al. 2012) and marine systems (Crain et al. 2008) revealed a significant overall synergistic interaction effect of multiple human stressors, indicating that cumulative effects of multiple factors will often be worse than expected based on single stressor impacts. Consequently, how animals perceive and respond to diverse anthropogenic features on the landscape is a critical component for wildlife management as it will impact their decisions of where to forage, how much energy to expend, and what habitats to use.

In Alberta, resource-based industries associated with the energy and forestry sectors have expanded dramatically over the last two decades into the threatened woodland caribou (*Rangifer tarandus*) habitat (ASRD 2010). This expansion has resulted in an increased network of rights-of-ways for seismic exploration, pipelines and roads, the latter of which are used by both forestry and oil and gas industries. In addition, forestry operations have created landscapes of early seral vegetation communities, effectively resulting in the loss of habitat of caribou-preferred lichen-bearing forests. Further evidence suggests that the decline of woodland caribou is partly based on an indirect interaction between caribou and resource-extraction industries that has enlarged the caribou's landscape of fear. Habitat change from forestry has increased predator biomass as dominant prey (such as elk, moose and deer) are attracted to the new vegetation land cover (Bergerud and Elliot 1986, Seip 1992, Wittmer et al. 2005). The linear features introduced onto the landscape aid in facilitating predator hunting and searching efficiency (Wittington et al. 2005). Resultantly, due to these higher levels of predation pressure, the evolved predator-defense strategies of caribou - avoidance/separation behaviours - can augment the allocation of habitat caribou deem as 'risky'/'fearful'.

Furthermore, research also suggests that caribou negatively perceive industrial development. Caribou can identify human activities and anthropogenic features both as disturbance and predation-risk events, either directly through physical footprint, or indirectly through sensory disturbance (Vistnes and Nellemann 2008). Caribou respond accordingly by attempting to minimize their exposure to them, similarly as they would to natural predators (Smith et al. 2000, Dyer et al. 2001, Polfus et al. 2011). Lastly, the winter season appears to play a confounding role on caribou risk perception, as overwintering caribou face the energetic costs of food availability, environmental conditions, predator avoidance, and disturbance. Winter is also the time of year when most industrial development occurs in the study area (Neufeld 2006). Caribou therefore need to tradeoff the energetic demands of resource acquisition with predator/disturbance avoidance, and the results of these decisions will affect their habitat use, spatial distributions, and resultant energetic expenditure.

To investigate the intrinsic (i.e., internal state), extrinsic (i.e., geographic space), and

behavioural (i.e., individual adaptive decisions) factors that influence caribou habitat selection and movement, we developed a spatially explicit agent-based model (ABM) to simulate winter habitat selection and use of woodland caribou in the Little Smoky herd in west-central Alberta (Semeniuk et al. 2012). The purpose of the ABM was to establish a behavioural and bio-energetic baseline of the underlying mechanisms driving female caribou movements across their landscape. Our findings suggested that when navigating their environs, caribou make context-dependent decisions, and respond to the pervasive predation risk of their environment when they can afford to (and in doing so, incur additional energetic costs). Energetic needs for daily maintenance and reproduction have priority. Furthermore, our model also revealed that while the perception of risk varies with spatial differences in habitat type or structure (i.e., extrinsically mediated risk response), the agent's internal state (e.g., energetic reserves) also affected its willingness to respond to landscape risk (i.e., internally mediated risk response). In our original model, we did not distinguish between forestry and oil-and-gas industrial features, although it was demonstrated that their effects are highly significant. However, caribou may respond differentially to these features with different degrees of sensitivity (Smith et al. 2000; Dyer et al. 2002).

In this paper, we take an inverse modeling approach in the form of a sensitivity analysis and use our ABM to infer knowledge about caribou responses to the different existing industrial features based on characteristics that may affect their relative perception: presence, age, density, and activity. The resultant, optimized scenario is then evaluated by comparing simulated caribou movement patterns with actual caribou data and with two null models of caribou movement based on random processes, using a pattern-oriented modelling approach. Our purpose is to identify industry type(s) and feature(s) with the greatest relative influence on caribou habitat use and spatial distribution using a multiple-response optimization approach. Combining a behavioral ABM with a methodology used to resolve unknown parameters allows for the identification of the intrinsic and extrinsic factors that drive habitat selection. Our ultimate goal is to create a comprehensive model that can assist further studies on how caribou may respond to continued industrial development and/or future mitigation measures.

Methodology

A detailed description of the study area, the geographic and biological datasets used to develop the ABM, and the model's implementation, calibration and validation processes can be found in Semeniuk et al. (2012). The following section provides a brief model overview and describes both the new data used in the ABM, the sensitivity analysis, and the patterns used to evaluate both the internal and external consistency of the model results.

Description of the study area

The Little Smoky (LSM) herd is located in the foothills of west-central Alberta, east of Grande Cache. The area of interest in this project is the official political and biological range delineation of the Little Smoky herd by the Alberta Fish and Wildlife Division (ASRD 2010) that covers an approximate area of 3,100 km² (Fig. 1). Because the Little Smoky is such a dynamically changing landscape due to industrial practices, we chose to confine our study to a single time period, and as such, all spatial and caribou data correspond to the winter 2004-2005. The LSM range has the highest level of industrial development of any caribou herd in Canada, with 95% of its range in proximity (500 m buffer) of anthropogenic activities (Environment Canada 2011). The site of four forestry management agreements and numerous petroleum-company operations

(WCCLPT 2008) generates an estimated 0.45 km/km² of infrastructure (roads and pipelines), 3.5 km/km² of seismic lines, and 9.1 ha/km² of cutblock densities in the LSM c. 2005. In addition to having the highest road and pipeline density of any caribou range in Alberta, it contains substantial industrial structures – i.e., 439 wellsites. At present, there is considerable development pressure from all fronts leading to the core of the range and increases in allocations to industrial users within caribou range (Robichaud 2009).

Model concept

The underlying premise of the model is that an individual's internal state influences how it perceives its environment and hence drives its decision-making process (Houston and McNamara 1992). The model consists of one category of agents, the caribou, represented as a cognitive entity. It has a mental representation of its environment, can plan its activities, and has a memory of profitable and safe patches in the study area. Specifically, the caribou agent can balance its needs to meet its daily energetic requirements and minimize its energetic loss in order to ensure its long-term goal of reproductive success. The caribou must also consider its predation risk since relatively safer locations are not always the most profitable in terms of energetic resources. Because the environment plays a critical role in the decision-making heuristics of caribou, the ABM includes a spatially explicit representation of the Little Smoky region to ensure biological and ecological realism.

Landscape representation

For integration with the ABM, four raster maps at a 45 m resolution are used to represent the physical environment where the caribou agents are located: (1) a forage-availability map, (2) an energetic-content map, (3) a predation-risk map, and (4) an elevation map. The forage-availability and predation-risk maps are both generated from a land-cover map and industrial-feature maps, and assigned ranked scores (Fig. 2). Energetic content is calculated from combining known caribou daily energetic intake rates and caribou-foraging time budgets with the relative forage-availability of each land-cover class (see Semeniuk et al. 2012 for more information). Lastly, the elevation map is represented by a digital elevation model (DEM).

To provide an environment to the agents and allow their movement, a virtual grid is overlaid on the four maps described above. Therefore each cell in the ABM spatial environment possesses four values accessible by the agent: a forage-availability score, an energetic content, a predation-risk score, and an elevation (m). Whereas forage-availability and predation-risk scores are fixed (it is just the agent's willingness to respond to them that varies), the energy content of the cells is depleted (and hence varies) when agents forage. The datasets used to create the forage-availability map, as well as the predation-risk maps used in the sensitivity analysis, are described below.

Sensitivity analysis

A schematic diagram representing the various steps involved in the dataset preparation, screening design, and evaluation for the sensitivity analysis is represented in Fig. 3 with each step presented in the following section.

Original datasets

A detailed description of the datasets used in the original ABM can be found in DeCesare et al. (2012) and Semeniuk et al. (2012). Briefly, a land-cover map at a 30 m spatial resolution, based

on Landsat 5 Thematic Mapper imagery acquired in 2005 was created to produce ten vegetation classes deemed to be biologically relevant to woodland caribou, ranging from closed conifer forests, to herbs and open water. The classes were ranked based on their forage availability (0 -5, with 5 representing highest availability) and their predation risk (0 – 5, with a score of 5 denouncing the highest risk) and these scores were used in the ABM environment. A raster-based elevation model (DEM) at 30 m resolution was used to represent landscape elevation and enable the calculation of movement costs of caribou agents associated with changes in elevation. The land-cover map and DEM, like all raster maps used in the ABM, were resampled at a 45 m resolution to increase computational performance while reflecting the biologically realistic size of the foraging patch of caribou (Bailey and Provenza 2008).

Updated and newly created datasets

Individual vector maps of roads, pipelines, seismic lines cutblocks, and wellsites were supplied by Alberta Sustainable Resource Development (ASRD) current to the year 2008. These maps included the location of industrial features and associated attributes, such as year of establishment (cutblocks) and activity status (wellsites); they were recorded over different sections of the study area in different monitoring years. To extract from the maps the industrial features appropriate for our year of study (winter 2004-2005) and to verify their accuracy, the presence of these features in the landscape was validated using a Landsat TM image from 2004. Any industrial features not present in the maps were digitized from the remote sensing image, and those not observed in the image were removed from the maps. As roads and pipelines are not distinguishable from one another in the 30 m resolution imagery, these two updated maps were merged to create a single infrastructure map.

The updated industrial-feature vector maps were used to generate raster layers at 45 m resolution for the production of both the forage-availability and predation-risk maps (Fig. 2). For the forage-availability map, each cell that contained the presence of an industrial feature was assigned a forage-availability score that ranged from 0 -1. For the predation-risk map, a four-step process occurred. First, multiple risk-attribute raster layers were created from the individual industrial-feature maps to represent conditions that could be perceived as risky by caribou, namely presence, density, age, and activity. ‘Presence’ indicates the presence of an industrial feature; ‘Density’ indicates areas of concentrated linear density for infrastructure and seismic lines (km/km^2), edge density for cutblocks (km/km^2), and number for wellsites ($\#/ \text{km}^2$); these values were calculated using the line and point density tools found in ArcMap 10 (ESRI) with a 1 km^2 search area. ‘Age’ is used to differentiate new (<10 years) from old (>10 years) cutblocks (Vors et al. 2007), and was generated from an age attribute of the vector map. ‘Activity’ is used to differentiate active from abandoned wells, based on an ‘activity status’ attribute on the vector map.

Second, these industrial-feature risk-attribute layers (ten in total) were each assigned a predation-risk score – either medium-high (4) or high (5). The specific attributes assigned a ‘5’ are feature presence, high density, young cutblocks, and active wellsites; and ‘4’ for low density, older cutblocks, and abandoned wellsites. The designation of ‘high’ density was guided by woodland-caribou literature sources. Infrastructure density was considered high for the LSM area when $>3.0 \text{ km}/\text{km}^2$ (McCutcheon 2006, Fortin et al. 2008), seismic line when $> 5.0 \text{ km}/\text{km}^2$ (WCCLPT 2008, McKenzie et al. 2012), cutblock edge when $>3.8 \text{ km}/\text{km}^2$ (Smith 2004, Faille et al. 2010), and wellsite density when $> 2 \text{ wells}/\text{km}^2$ (Hebblewhite 2008). In the absence of an industrial feature on the landscape, the risk value is the one assigned to the land-cover class. No

attribute was accorded a predation risk of 3 or lower since ample evidence suggests that the industrial features investigated in this study have an impact on caribou responses. Furthermore, our best-fit original caribou ABM was one that accorded risk scores of 4 and 5 to the presence of (unresolved) industrial features on the landscape. Once ranked, the raster layers were next arranged in various combinations via a screening design to generate different scenarios of industry-sourced landscapes of fear. Lastly, these scenarios were individually integrated with the land-cover map to produce different predation-risk maps for use in the ABM environment during the sensitivity analysis (Figs. 2 and 3).

Screening Design

Generating different arrangements of industry-sourced landscapes of fear for the predation-risk map consisted of using all industrial features (factors) in the represented landscape: infrastructure, seismic lines, cutblocks, and wellsites, and using a screening design to combine their attributes (levels) into various arrangements. The levels that were investigated are the following: for infrastructure and seismic lines, caribou sensitivities to presence and density were tested, for cutblocks – presence, density, and age were tested and for wellsites – presence, density, and activity status were selected. An additional level was added to each factor - a ‘no strong effect’, and assigned a risk of 4 - denoting that the feature in question is not deliberately avoided.

In order to avoid simulating through the whole spectrum of feature presence, density, age (cutblock), activity (wellsites), and ‘no strong effect’ arrangements, an orthogonal-array method was used to construct a mixed-level design to screen for caribou sensitivities that best encapsulate how they respond to industry. Two factors of 3 levels each and 2 factors of 4 levels were inserted into a L12 orthogonal screening design as shown in Table 1, and analyzed using JMP software (v.8.0, SAS Inc.). The goal of this method is to find factors and their levels that generate acceptable responses despite natural environmental variability. The screening design considers main effects and pairwise interactions, not higher-order ones. This is acceptable given the sparsity-of-effects principle, where a system is typically dominated by main effects at low-order interactions (Wu and Hamada, 2000 as cited in Dion et al. 2011). Individual factors and their interactions are therefore expected to have the most significant influence on the model output targets. Each of the scenarios generated represents industry-sourced predation risk and is integrated with the land-cover map into the predation-risk map used in the ABM to generate different landscapes of fear to which caribou agents are exposed.

Table 1. L12 design of experiment used in the sensitivity analysis: levels assigned to each scenario tested in the ABM simulation.

Scenarios	Infrastructure	Seismic lines	Cutblocks	Wellsites
1	Density	Density	Density	Activity
2	Density	Density	No Effect	Density
3	Density	No Effect	Presence	No Effect
4	Density	Presence	Age	Presence
5	No Effect	No Effect	Age	Density
6	No Effect	No Effect	Density	Presence
7	No Effect	Presence	No Effect	No Effect
8	No Effect	Presence	Presence	Activity
9	Presence	Density	Age	No Effect
10	Presence	Density	Presence	Presence
11	Presence	No Effect	No Effect	Activity
12	Presence	Presence	Density	Density

Output targets

As caribou agents move across the landscape, the ABM generates various behavioural, bio-energetic, and spatial metrics (patterns). Therefore, each scenario used in the ABM will produce output patterns that can be evaluated. To identify the most ecologically realistic scenario, meaningful patterns, referred to as ‘targets’, must be reproduced. Selected targets were therefore derived from radio-collared GPS location data of actual caribou. A total of 5225 location points were obtained for 13 female individuals from the Little Smoky in winter (November-April) 2004-2005. Using caribou GPS point samples, the spatiotemporal distribution of each caribou was built and stored within an ArcGIS database as timestamps corresponding to a 4-hour interval. Similarly, point locations for simulated caribou were sub-sampled at the same temporal resolution for comparative purposes.

The targets used in the sensitivity analysis are industry-related variables that comprise: (1) the median nearest distance (m) between caribou point locations and industrial features, (2) the median linear density of industrial features within 1km² of caribou point locations (km/km²), (3) the maximum wellsite density (#/km²) within 1km² of caribou point locations, (4) the association with young versus older cutblocks based on percent difference in the mean nearest distance to each, and (5) the association with active vs. abandoned wells based on percent difference in the mean nearest distance to each. These variables were purposely chosen since actual LSM caribou displayed responses that differed from random or exhibited meaningful patterns (Tables 2 and 3). For instance, LSM caribou have a higher observed association with older cutblocks and inactive wellsites despite the relatively fewer number and smaller areal coverage of older cutblocks and fewer numbers of abandoned wells in the LSM. To compare how well the different scenarios performed in reproducing real-life patterns, we extracted the same five output variables from each of the twelve scenarios run. Two regulating criteria were further added as additional target variables to identify biologically unrealistic model runs: individual-MCP (minimum convex polygon; i.e., the average caribou’s spatial extent – 270 km²; Semeniuk et al. 2012), and the cumulative seasonal energy lost by the caribou agent (a normal range should be between 710 – 947 MJ; Bradshaw et al. 1998, Semeniuk et al. 2012; Table 3).

Table 2. Target-variable outputs (and units) extracted from actual LSM-caribou, ABM scenarios, and the null models for use in the sensitivity-analysis evaluations. Also included is the response function needed to be achieved by the simulated caribou when model outputs were on average either lower, the same, or higher than the actual targets to attain a best-fit optimization.

Output targets	Response Function	Notes
Nearest median distance (km)		
infrastructure	Maximize	
seismic line	Minimize	
cutblock	Match	
wellsite	Match	
Median density (km or well km ⁻²)		Values are for non-zero instances for comparative purposes
infrastructure	Minimize	
seismic line	Maximize	
cutblock	Maximize	
wellsite	Minimize	Maximum density used since too little variation between simulations otherwise
% Difference in association with cutblock age	Match	Older cutblocks are in closer proximity to LSM caribou
% Difference in association with wellsite activity	Match	Abandoned wellsites are in closer proximity to LSM caribou
Seasonal energy loss (MJ)	Match	Used to identify unrealistic outputs
Mean spatial extent (km ²)	Maximize	Used to identify unrealistic outputs

Internal and external consistency evaluations

To identify the arrangement of industry-feature attributes that best reproduces the multiple targets generated by actual caribou, a multi-response optimization technique known as the ‘desirability function’ was used (Obermiller 2000). This technique allows for the simultaneous optimization of several targets. In essence, the desirability function is a transformation of the target variable to a 0 to 1 scale. This transformed response, called d_i , can take on different functions depending on whether the target value should be maximized, minimized, or a combination between the two options (see Table 2 for the response functions used in this analysis). A value of 0 represents a completely undesirable response and 1 represents the most desirable response. In order to simultaneously optimize several responses (k), each of these d_i are combined using the geometric mean to create the overall desirability (D).

For k responses: $D = \sqrt[k]{d_1 * d_2 * \dots * d_k}$ (5.1)

Using the product of the desirability functions insures that if any single desirability is 0 (undesirable), the overall desirability is 0. Thus, the simultaneous optimization of several responses has been reduced to optimizing a single response: the overall desirability, D (Obermiller 2000). Employing the maximizing desirability feature in JMP's Prediction Profiler allowed the determination of the conditions that simultaneously achieved the ten response target values and/or stayed within the specification ranges. This internal consistency evaluation allows for the investigation of any non-independent industry impacts. Because only a subset of combinations is evaluated (albeit orthogonal in design), the analysis employed can moreover allow for an optimized, 'best-fit' combination to emerge. If this is the case, the emergent scenario must then be evaluated for its ability to reproduce the multiple targets.

Once an optimal configuration had been elucidated, it is then tested for external consistency – i.e., the ability of the optimal scenario to predict other caribou patterns not used in the sensitivity analysis and directly unrelated to industry responses. In particular, optimized caribou sensitivities were assessed for their capability to reproduce other observed caribou patterns of habitat selection such as the combined MCP of individuals (i.e., herd spatial extent), and its degree of spatial overlap with that of actual caribou.

An additional evaluation was performed on the best-fit, optimized scenario: how well it reproduced the patterns used in both the internal and external consistency evaluations in comparison to two null models: (1) target responses generated by a random distribution of points ($n = 5225$, comparable to the number of caribou GPS point locations) within the spatial extent of the collared caribou's distributions, and (2) target responses generated by a recreation of the original caribou ABM (but with updated industrial feature datasets). In this latter model, a risk of '4' or '5' is randomly assigned to the presence of industrial features regardless of density, age or activity. This further evaluation provides a more rigorous assessment of model fit.

Description of the agent

Figure 4 illustrates the sequence of steps involved in the caribou agent's decision making as implemented in the ABM. At each time step, the agent first assesses its energetic state; it determines whether it has reached its daily energetic requirements (22-33 MJ day⁻¹, McEwan and Whitehead 1970, Boertje 1985) and by what magnitude, and whether it will have enough energetic reserves (and by what magnitude) to have a successful birth at the end of the season (710 - 947 MJ, Bradshaw et al. 1998; 'A' in Fig. 4). At this stage it also senses the immediate risk in its environment as well as the forage availability ('B'). It then determines which fitness-maximizing goal is most important to trade off against the others, and does so by assessing which goal has reached a minimum threshold. Based on this decision-making heuristic ('C'), the agent either forages, ruminates, or moves to a new location ('D'). The agent then updates its energy reserves, both gained and lost through its actions ('E'), and commits to memory any profitable or safe locations encountered ('F'). Each step is described in detail in Semeniuk et al. (2012), with a presentation of the parameter values used to parameterize and calibrate the model.

Assessing intrinsic factors

Based on an assessment of its internal energetic reserves, a caribou agent can find itself either at the low end or below its energetic thresholds, within threshold range, or at the high end or above

its thresholds. The agent can also forecast how much energy will be lost by season's end based on its current energy-loss rate. The actual lower and upper threshold ranges remain inexplicit, so as not to unduly influence the agent's decision-making. If the resultant agent activity culminates in at least an average of 22 MJ accumulated per day, for instance, this behaviour is more 'emergent' than if the agent was given explicit instructions to achieve at least 22 MJ day⁻¹.

Assessing extrinsic factors

The caribou agent can sense the riskiness of its environment up to 1 km in radius, and responds to this risk at two scales: within a 500 m buffer (i.e., during intra-patch foraging), or between 500 - 1000 m (when assessing whether adjacent foraging areas are equally or more safe for inter-patch travel). These buffers correspond to known average avoidance distances of caribou to industrial features (Dyer et al. 2002; Weclaw and Hudson 2004) and predator perception ranges of ungulates (Laporte et al. 2010). When sensing its environment, if there are any features (industry or other) within its perception range with a predation risk score of 5, the agent accords a risk of 5; otherwise, it assesses the mean predation risk of its surrounding habitat. This means that if a high-risk feature is present within the detection radius or annulus, the caribou agent will assess its environment as being of high risk, regardless of the surrounding habitat, and respond by minimizing its exposure to the feature (i.e., by moving away), should its energetic reserves be sufficient. A risk of 5 is considered high, 3-4 is medium, and 1-2 is low. Caribou agents can also perceive food availability in their environment at two scales: intra-patch forage, corresponding to eight neighbouring cells, and within a 450 m in radius for area-restricted (i.e., inter-patch) searches (Johnson et al. 2002). In addition, caribou agents are also capable of assessing the elevation of their current location, as well as that of their immediate surroundings so that they may choose the cells with minimal elevation when deciding to travel at low energetic cost.

Movement-ecological rules

The caribou agent engages in four different types of movement, reflecting different scales of habitat selection: local, intra-patch foraging; inter-patch foraging, also known as 'area-restricted searching'; random taxiing to an unknown location; and revisiting a previously-visited patch randomly drawn from memory. These movements take place at different spatial scales, and range from 45 m and 450 m up to 6 km in distance per movement type. When movement, agents can either select cells of lower relative predation risk or elevation, depending on their energetic vs. predator-avoidance needs.

Behavioural-decision rules

As the agent's goal is to find an optimal balance between its daily energetic requirements, its longer-term reproductive energy requirements, and its predation-risk minimization, the following rules generally apply in governing which action the agent will undertake. If the agent is highly energetically stressed predation risk becomes irrelevant (even if high), and the agent attempts to find a profitable patch in which to forage, at the lowest travel cost. Oppositely, for an energetically flush agent, predation risk takes precedence, and the agent will seek out as safe or safer locations in which to forage, if necessary. The more energetically stressed, the less willing an agent is to taxi long distances, and will tend to rely more on previously-visited sites in which to forage (i.e., access memory). Lastly, a foraging agent foraging will not only reduce the energetic content of the cell it occupies, but will no longer feed within it during the same feeding bout.

Sources of biological information necessary for the caribou ABM parameterization, calibration and evaluation include caribou agents' bio-energetic functions, spatial memory, and learned decision-making processes. The values for these variables were either derived or obtained from an extensive literature review (Semeniuk et al. 2012).

Simulation framework

The ABM is run with one agent and is assumed to be 132 kg in weight, pregnant, and expected to lose mass over the course of winter (Bradshaw et al. 1998). Accordingly, at the start of simulation, the agent's cumulative energetic loss is set at 0. The simulation is also begun with the agent at a daily energy intake of 0. Because caribou have distinct summer and winter habitat requirements (including forage), the agent also begins the simulation with no winter locations stored in its memory. Lastly, the start coordinates for the agent corresponds to one of the thirteen initial locations of the actual GPS-collared LSM caribou. To account for environmental stochasticity and for variability in the model outputs, runs are replicated five times per 13 'caribou', for a total of 65 runs per scenario. The simulation results correspond to the average or median of the values obtained in these replicates.

The model has a reporting mechanism describing the instances of various events at each time step of 30 min. on a 3,100 km² grid surface (1786 x 1619 45-m cells). The time and areal step are appropriate temporal and spatial resolutions to capture the variability of foraging behaviours that are characteristic of ungulates at the spatial level of the food patch (Owen-Smith et al. 2010). Important outputs of the model include the spatial distribution of the caribou agents, which is represented as a series of point locations (*x*, *y* coordinates and time stamp) and sub-sampled at 4-h. The model also reports the cumulative amount of energy lost at the end of the simulation. The ABM simulates over a period of 180 days, the span of winter in Alberta. The simulation model was developed using the platform NetLogo v. 4.1.2 (Wilensky 1999), and verified for proper programming functioning through progressive debugging and uncertainty testing.

Table 3. Sensitivity-analysis outputs (range)¹ in comparison to the optimized multiple response², random points in herd MCP and simulation with industrial features randomly allocated predation-risk scores (null models), and actual caribou values. Shaded values denote instances where the optimized scenario is an improvement over the null models. IS = infrastructure; SL = seismic lines, CB = cutblocks; WS = wellsites= C.

	Median nearest distance (m)				Median Density (km or well / km ²)				% difference CB age association	% difference WS activity association	Individual spatial extent (km ²)	Seasonal energy loss (MJ)
	IS	SL	CB	WS	IS	SL	CB	WS (max.)				
Simulated models' range ¹	1528-1613	133-174	3221-4392	1724-2058	1.01-1.07	2.41-3.1	1.61-2.69	3-4	18.0-60.1	-23.6-24.4	164-262	0-873
Optimized model ²	1449	133	4095	1790	1.03	3.18	1.60	4	41.0	20.0	288	865
Random points	1231	104	4043	1701	1.07	3.07	2.95	4	24.0	15.5	NA	NA
Random industrial-feature allocation	1356	132	3866	1767	1.07	3.11	2.33	4	25.0	15.0	253	859
Actual caribou (quartiles, range)	1524 (689-2315)	118 (53-204)	4012 (2365-7991)	1327 (830-2231)	0.91 (0.55-1.18)	3.12 (2.1-4.3)	2.43 (0.75-4.30)	3	52.0	18.0	270 (250-290)	825 (710-947)

1. Range of outputs from 12 responsiveness scenarios derived from L12 screening design.
2. Optimal multiple response: Infrastructure = Presence; Seismic lines = Presence; Cutblocks = Density; Wellsites = Activity.

Results and Discussion

In the simultaneous optimization of all target responses, maximum desirability was achieved when the presence of infrastructure and seismic lines, the density of cutblocks, and the activity status of wellsites were concurrently considered (Fig. 5). The optimized scenario was not one of the twelve explicitly modeled during the screening-design process. We therefore simulated this scenario and compared its output with (i) the twelve other design scenarios; (ii) two null models based on a simple, random allocation of points within the LSM, and the original ABM with randomly assigned industry risk; and (iii) with actual caribou values (Table 3). There was no possibility of confounding effects by cell number/raster map overwhelmingly driving the results: the allocation of cells in the ‘presence’ and ‘high density’ datasets were similar. Furthermore, the activity-wellsite dataset, with the fewest number of pixels, was still able to influence the outcome of the multiple optimization procedure.

Each industrial feature was perceived by caribou to be of high risk – ‘no strong effect’ was never selected during the optimization procedure to maximize overall desirability, ‘D’. The simulation results further demonstrate that the optimized multiple-response scenario performs well overall, and outperforms either of the null models more often than the reverse (Table 3). The improvement of this optimization scenario over the original ABM is not so drastic as to change the reproduced fundamental patterns that had matched well with actual caribou behavioural patterns derived from the GPS-collar data. Indeed, most patterns remain unchanged, as expected: closed conifer forests, muskeg/wetlands and open conifer forests were still the land-cover classes used most frequently by agents; caribou agents continued to use lower elevations in late winter with reduced daily step-lengths; and the single daily peak in activity levels remained unaffected (present values not reported, although see Semeniuk et al. 2012).

One of the more dramatic changes between the null model meant to represent the original ABM and the current optimized scenario, however, is the spatial extent and overlap of the simulated agents in comparison to actual caribou c. winter 2004-2005. Caribou agents, in their quest to minimize their exposure to the selected industrial features and their attributes, reproduced individual-agent MCPs still within the observed actual-caribou range (250-290 km²), but did so with a smaller and restricted herd range than the null model, converging more accurately to the areal coverage used by actual caribou (Table 4). This external-consistency validation reinforces the assertion that the fit of the model is more realistic and has been improved upon over the original ABM.

Table 4. External consistency: validation of the optimized scenario using patterns not directly related to industrial features. Shaded values denote instances where the optimized scenario is an improvement over the null model based on the original ABM with randomly assigned predation risk.

Spatial-distribution Patterns	Actual (n = 13)	Optimized scenario (n = 65)	Null model: original ABM (n = 65)
Herd MCP (km ²)	1867	2417	2865
Proportion Spatial Overlap	1	0.754	0.644

This realism extends not only to LSM-specific caribou but is also consistent with what is known about caribou sensitivities to industrial features in general. In a broad resource-selection study that crossed multiple hierarchical spatial scales, DeCesare et al. (2012) found woodland caribou herds in western Canada to be responsive to cutblocks at first- and second-order selection, respectively - the population and individual home ranges. They attribute their findings to predator numerical responses associated with this industrial feature. In particular, cutblocks represent more ideal habitat for alternate ungulate prey species, thereby increasing their biomass, which in turn drives an increase in predator numbers. In essence, avoidance of forestry cutblocks is akin to caribou spatially separating themselves from predators, the initial anti-predator strategy used by caribou when selecting habitat. This behavior will then influence the type of habitat in which caribou choose to reside at the home-range level. Within an individual caribou’s home range, DeCesare et al. (2012) found caribou to be sensitive to linear density (when compared to forestry cutblocks) at third-order caribou selection (i.e., the individual). They explain this phenomenon with disturbance features that are linked to predators’ functional response – in other words, once established in the area, caribou then respond to features that, should predators be encountered, can enhance predator hunting efficiency such as facilitated sight lines and ease of movement generated by linear features on the landscape. In a more herd-specific habitat-selection study on the Little Smoky and A La Pêche herds in west central Alberta, Neufeld (2006) found, using a resource-selection model, that caribou occupancy in winter habitat was influenced only somewhat weakly by the proportion of 1km² area that is cutblock, that there was no effect of wellsite distance or density, but there existed a strong effect of distance to seismic lines (but not density).

The results of the caribou ABM sensitivity analysis are consistent with these statistical findings: our agents represent a herd already ‘established in an area’, and were found to be less responsive to cutblocks and active wellsites (Table 5.1). As can be observed in Figure 5, the density of cutblocks deemed ‘high’ tend to form a contiguous movement barrier in the northern portion of the herd range. Agents, therefore spending more of their time in the central area, are exposed to a higher frequency of occurrence of infrastructure and wellsites (seismic lines are ubiquitous). Indeed, at the scale of the individual, caribou agents were most sensitive to linear

features that included seismic lines, roads and pipelines, as these were the features most often encountered (Table 5.1). Our results resultantly validate a consistent trend in that industrial features contribute to a caribou’s landscape of fear at the individual level. No one industrial feature is substitutable for another when invoking anti-predator responses in caribou – there is no redundancy (Table 5.2). They interact in a way to produce cumulative effects, as can be evidenced in their ability to jointly impact a variety of caribou responses even in the absence of direct predation. These impacts extend to the extent to which caribou distribute themselves on the landscape, and on their energetic reserves (the caribou agent’s seasonal energy loss was slightly higher when compared to the null ABM model; Table 3). Consequently, both the ability of the caribou ABM to reproduce actual caribou behaviours without explicit guidance, and the success of the inverse modeling approach in elucidating caribou responsiveness, speaks to the strength of the ABM as an effective habitat-selection model.

Table 5. Relative target sensitivity within the optimized responsiveness scenario: (1) percent change in overall ‘desirability’ fit (*D*) when alternative levels are chosen within each target feature, one at a time, and (2) overall ‘desirability’ fit (*D*) standardized to 1, when one target is set to its maximized level and other targets are set to ‘No strong effect’ (i.e., substitution effect). Shaded cells correspond to maximized-desirability levels. Sub-optimal desirability calculations performed by the Prediction Profiler in JMP 8.0 (SAS Inc.)

Target variable	Level	(1) % change from overall fit	(2) Substitution effect fit (<i>D</i>)
Infrastructure	Presence	0.00	Approaches zero
	Density	-98.84	
	No strong effect	-89.16	
Seismic lines	Presence	0.00	0.17
	Density	-91.64	
	No strong effect	-99.99	
Cutblocks	Presence	-57.43	Approaches zero
	Density	0.00	
	Age	-63.55	
	No strong effect	-30.28	
Wellsites	Presence	-25.80	Approaches zero
	Density	-63.42	
	Activity	0.00	
	No strong effect	-57.94	

The approach undertaken to determine caribou sensitivities conveys many advantages. First, it simultaneously incorporates behaviorally mediated effects of predation risk, resource distribution, and species-specific energetic requirements. Second, it produces insight into the context-dependent mechanisms driving habitat selection. Our agents have been imbued with

fitness-maximizing behaviours that allow them to decide when to tradeoff the costs of predation risk with the benefits of continued foraging, using realistic behavioural-ecological and movement-ecology rules. Third, the ABM infers the responsiveness of caribou to their landscape of fear. Using a sensitivity analysis as an inverse modeling approach, it relies on a bottom-up approach where the data guide the optimization process. An *a priori* imposition can be unreliable when applied to conditions that differ from the ones considered for parameterization. Similar in vein, the multiple-response optimization approach also prevents over-fitting. This denotes that because not any one target is being fit perfectly (although it can occur), the generalization capacity of the model will not be lost, and will be labile enough to be easily transferred to other situations – in particular, to future scenarios of industrial development within LSM.

Each of the deliverables described is challenging to achieve using statistical approaches alone. Woodland caribou are oftentimes studied remotely, through the use of telemetry studies that produce locational data. As such, traditional methods to ‘measure’ an animal’s perceived landscape of fear – for example, direct observations of behavioural responses (vigilance, group-size effects, giving-up densities, fitness-costs of movement) or hormonal responses (stress) are not always possible (although see Willems and Hill 2009, and Wasser et al. 2011, respectively). Statistical analyses are therefore performed on either density/abundance estimates or the ratio between used and available habitats to infer adaptive habitat selection and habitat quality. Despite the prevalence of these species distribution models (SDMs) in applied ecology, a review of recent papers cautions using a statistical description that implicitly captures these “habitat use” processes as they are statistically associated with the predictor variables, but may not be so biologically (Semeniuk et al. 2011). In essence, while habitat availability has been typically related to the selection order of concern (Johnson 1980), availability is also restricted to movement capacity of animals as well as their behavioural state (Martin et al. 2008). A lack of this insight into the mechanisms that govern animal movement and habitat selection can have consequences on the predictive success of SDMs in determining range limits and habitat suitability.

In contrast, agent-based models are designed to describe organisms, their individual characteristics, fates, and interactions with other individuals and with their environment (Imron et al. 2011). They are often validated using patterns with characteristic, non-random, identifiable states of the system under investigation (Grimm et al., 1996, Grimm and Railsback 2012). ABMs can be seen as a complementary approach in the study of habitat selection – indeed, the convergence of our model results with other studies demonstrates its ability to reproduce actual phenomena. ABMs can therefore be used as an effective tool for understanding and forecasting animal habitat selection and use. This methodology can subsequently enable the exploration of how wildlife might respond to future changes in environmental conditions - an inquiry of utmost importance for wildlife conservation and management.

Conclusion

Woodland caribou of the boreal ecotype in Alberta are currently designated as *threatened* under Alberta’s *Wildlife Act* due to their reduced distribution, a decrease in the number and size of populations, and threats of continued declines associated with human activities (ASRD 2010). Annual population growth rates and calf recruitment of caribou have been shown to be highly impacted by a combination of natural and anthropogenic disturbances (Sorensen et al. 2008, Environment Canada 2011). Consequently, the Canadian Federal Government has undertaken a scientific assessment to inform the identification of critical habitat for the woodland boreal

population (Environment Canada 2008, 2011). The range of local caribou populations has been identified as the appropriate scale at which to address critical habitat, and critical habitat is subsequently defined as the percentage of range needed to maintain or return that herd at or to a self-sustaining rate. While conservation measures should focus on critical habitat designation beyond range boundaries to ensure caribou spatial persistence, the reality is that within the province of Alberta at least, industrial development will continue. Consequently, habitat protection outside of range delineations is but one strategy, and must also accommodate the possibly encroaching anthropogenic activities into ranges that currently still house caribou. The implications for actual caribou are significant: any future increase in actual and functional habitat loss (i.e., removal of prime caribou habitat and increased industrial development) can energetically tax caribou as they respond to risk effects imposed by their landscape of fear combined with reduced forage availability. Because relatively small shifts in mass result in relatively large changes in caribou parturition rate (Cameron and Ver Hoef 1994), caribou fecundity can be negatively impacted. In essence, our agent caribou experienced an average mass loss of 18% (using calculations presented in Bradshaw et al. 1998), approaching the 20% failed-reproduction threshold. The attention to biological realism, in combination with our validated sensitivity analysis, provide confidence in the predictive ability of the ABM to explore caribou spatial distribution and bio-energetic expenditure to future changes in the LSM landscape - an asset to conservation planning, and the next focus of our research.

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