A Bayesian approach to evaluating habitat for woodland caribou in north-central British Columbia[1]

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Abstract: Woodland caribou (*Rangifer tarandus caribou* (Gmelin)) populations are in decline throughout much of their range. With increasingly rapid industrial, recreational, residential, and agricultural development of caribou habitat, tools are required to make clear, knowledgeable, and explainable management decisions to support effective conservation of caribou and their range. We developed a series of Bayesian belief networks to evaluate conservation policy scenarios applied to caribou seasonal range recovery areas. We demonstrate the utility of the networks to articulate ecological understanding among stakeholders, to clarify and explicitly depict threats to seasonal range. We also show how simulated forecasts of spatially explicit seasonal range can be compared with landscape potential with range under assumed conditions of natural disturbance. These tools have provided opportunities to operationally define and measure conditions for recovery of caribou in north-central British Columbia.

Résumé : Les populations de caribou des bois (*Rangifer tarandus caribou* (Gmelin)) sont en déclin dans la majeure partie de leurs aires naturelles. Avec l'expansion rapide des activités industrielles, récréatives, résidentielles et agricoles dans l'habitat du caribou, des outils sont nécessaires pour prendre des décisions d'aménagement claires, bien documentées et explicables, et ainsi aider à la conservation du caribou et de ses aires naturelles. Nous avons développé une série de réseaux de croyances bayésiens pour évaluer des scénarios de politiques de conservation applicables aux quartiers de recouvrement saisonniers du caribou. Nous démontrons l'utilité de ces réseaux pour articuler la compréhension écologique chez les décideurs, pour clarifier et décrire de façon explicite les menaces dans les quartiers saisonniers et pour montrer comment des prévisions simulées de la répartition saisonnière spatialement explicite peuvent être comparées au potentiel du paysage et à la répartition saisonnière, dans des conditions présumées de perturbations naturelles. Ces outils ont fourni des opportunités de définir opérationnellement et de mesurer les conditions nécessaires au recouvrement du caribou dans le centre-nord de la Colombie-Britannique.

[Traduit par la Rédaction]

Introduction

Woodland caribou (*Rangifer tarandus caribou* (Gmelin)) are threatened throughout the Southern Mountains National Ecological Area in British Columbia (Thomas and Grey 2001). Population declines (Bergerud 1974) and reduced distribution of caribou since the early 1900s (Spalding 2000) have contributed to their current threatened status. Because British Columbia is a signatory on the National Accord for the Protection of Species at Risk,[3] the threatened status of caribou is a significant conservation issue (British Columbia Forest Practices Board (BCFPB) 2004). Founded on information concerning the interactions among road building, timber harvest, other ungulates, predators, and caribou mortality, the government of British Columbia (British Columbia Ministry of Sustainable Resource Management (BCMSRM) 1999, 2000) developed three strategies to conserve habitat for caribou in north-central British Columbia: (*i*) protect portions of caribou range by prohibiting industrial development (BCMSRM 2000); (*ii*) in unprotected areas, set limits on the total allowable impact to caribou range due to industrial development (BCMSRM 1999); and (*iii*) where timber harvesting occurs within caribou range, promote "large-patch" forest management (e.g., Racey et al. 1999). Large-patch management is intended to spatially concentrate forest harvest thereby leaving larger patches of undisturbed caribou range (BCMSRM 2000).

To aid implementation of these management strategies and to support development of caribou recovery plans, we modeled caribou seasonal ranges using Bayesian belief networks (BBNs). Bayesian modeling in ecology is not new and has proven useful in other resource management issues

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particularly when empirical approaches (i.e., solution characterization) were intractable (Reckhow 1999; Marcot et al. 2001; Rowland et al. 2003; Peterson and Evans 2003; Poirazidis et al. 2004). Bayesian modeling is probabilistic, and therefore, can include data and other sources of information even though either may be incomplete. Results are characterized by measurable uncertainty allowing for risk assessments and other forms of decision analysis. Therefore, the approach is consistent with at least some properties of formal decision-making and forwards a problem-solving technique to support critical decisions about recovery of caribou. We used a BBN approach even though caribou are generally well studied and our knowledge is supported by a broad foundation of empirical data. The probabilistic nature of BBNs allowed us to address the fact that most research on caribou was collected during a period of population decline; specific empirical results are not readily generalized to new ecological settings (spatially or temporally); and the response of caribou to proposed management strategies has not been thoroughly investigated. We used a BBN approach even though data-based models are more broadly accepted in the scientific literature because we could: efficiently capture the current knowledge about caribou, their habitat, and potentially threatening human-related activities; present this information to stakeholders in a manner that was understandable, explicit, and transparent regarding the information sources and assumptions; and establish a framework for assessing relative differences among alternative future conservation policies. The focus of the work was to develop a tool that would assist the management decision-making process rather than predict ecological consequences (Bunnell 1989). In addition to assisting decision-making, our use of BBNs offered the extended benefit of having formal and explicit hypotheses that can be evaluated and tested through more traditional statistical methods. Our objectives were to (*i*) construct BBNs of seasonal range use by caribou according to how this was understood by experts, (*ii*) formalize relationships between range quality and potential threats to caribou range, and (*iii*) evaluate the relative efficacy of conservation of caribou and their seasonal ranges under alternative management scenarios.

Study area and management situation

Spanning the boundary between the Northern and Southern Mountains National Ecological Areas, the Mackenzie, and Fort St. James Forest Districts are adjacent forest management units extending over 6.1×10^6 and 3.1×10^6 ha and with annual allowable timber volume harvests of 3.1×10^6 and approximately[4] 3.7×10^6 m^3, respectively. Five threatened caribou herds occur in these management units, four of which were the focus of our study: the Chase, Scott, Takla, and Wolverine herds. We delineated four recovery planning areas for these herds encompassing historic and current range use by caribou and allowing for spatial connectivity among herds. Current range use by caribou was determined based on relocation of radio-collared caribou observed from 1996 to 2000. Spatial connectivity was included by using land-use planning zones that encompassed potential, but currently unoccupied, range between herds.

The Wolverine recovery planning area was 844 312 ha in rolling high-elevation foothills and included four major watersheds of the Omineca, Manson, Klawli, and Germansen rivers (Fig. 1). The Scott recovery planning area was 594 894 ha due east of the Wolverine recovery planning area and was situated along the floodplain of the historic watercourse of the Parsnip River (now the Williston Reservoir). The Chase recovery planning area was 1 733 038 ha situated in steep mountainous terrain and had three major watersheds including the Ingenika, Osilinka, and Mesilinka rivers. The Takla recovery area was 492 051 ha due west of the Wolverine recovery area and surrounded a large freshwater lake.

Valley bottoms and midslopes of the four recovery areas are dominated by relatively cool and dry, or cool and moist, macroclimates of short growing seasons leading to boreal ecosystems of white (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) BSP). Large-scale and frequent wildfires were characteristic prior to fire-control policy (Delong 2002). Common in these ecosystems are large, relatively flat areas of well-drained fluvial deposits, which in combination with frequent and large fires gave rise to large areas of even-aged lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) dominated forest stands. Generally, a cold moist macroclimate with long, cold winters characterize upper slopes where Englemann spruce (*Picea engelmannii* Parry ex Englem.) dominates. At the northern extent of the Chase recovery area, deciduous shrubs can dominate these upper slopes. Alpine tundra prevails above treeline throughout the study area.

The Wolverine, Chase, and Takla herds have an estimated 460 (Wilson et al. 2004*a*), 550 (Zimmerman et al. 2002), and 125 (Wilson et al. 2004*b*) caribou, respectively. No formal population estimate has been made for the Scott herd, but anecdotal reports range from a few individual animals to, on one occasion, a group of 23 animals.

Although the life history and range use of caribou vary widely across their geographic range (Heard and Vagt 1998), caribou use lodgepole pine forests at middle to low elevations during fall and winter at the northern extent of their distribution in the Southern Mountains National Ecological Area (Johnson et al. 2004*b*). This winter range is typically found on relatively flat terrain, and therefore, is also easily developed for residential, agricultural, recreational, and industrial use. Disturbance of caribou range in north-central British Columbia is mostly from road building and timber harvesting. Where timber harvesting occurs in caribou range, the resulting early seral forests support abundant moose (*Alces alces* (Linnaeus, 1758)) (Franzmann and Schwartz 1998), which leads to increased densities of wolves (*Canis lupus* Linnaeus, 1758) (Messier et al. 2004) interspersed throughout the older, unharvested forest. Compounding this spatial distribution of increased wolves is the development of roads that provide wolves' ease of travel and an increase in their hunting efficiency (James and Stuart-Smith 2000). The increased predation effect on caribou, indirectly caused by logging, has been demonstrated by Wittmer et al. (2005).

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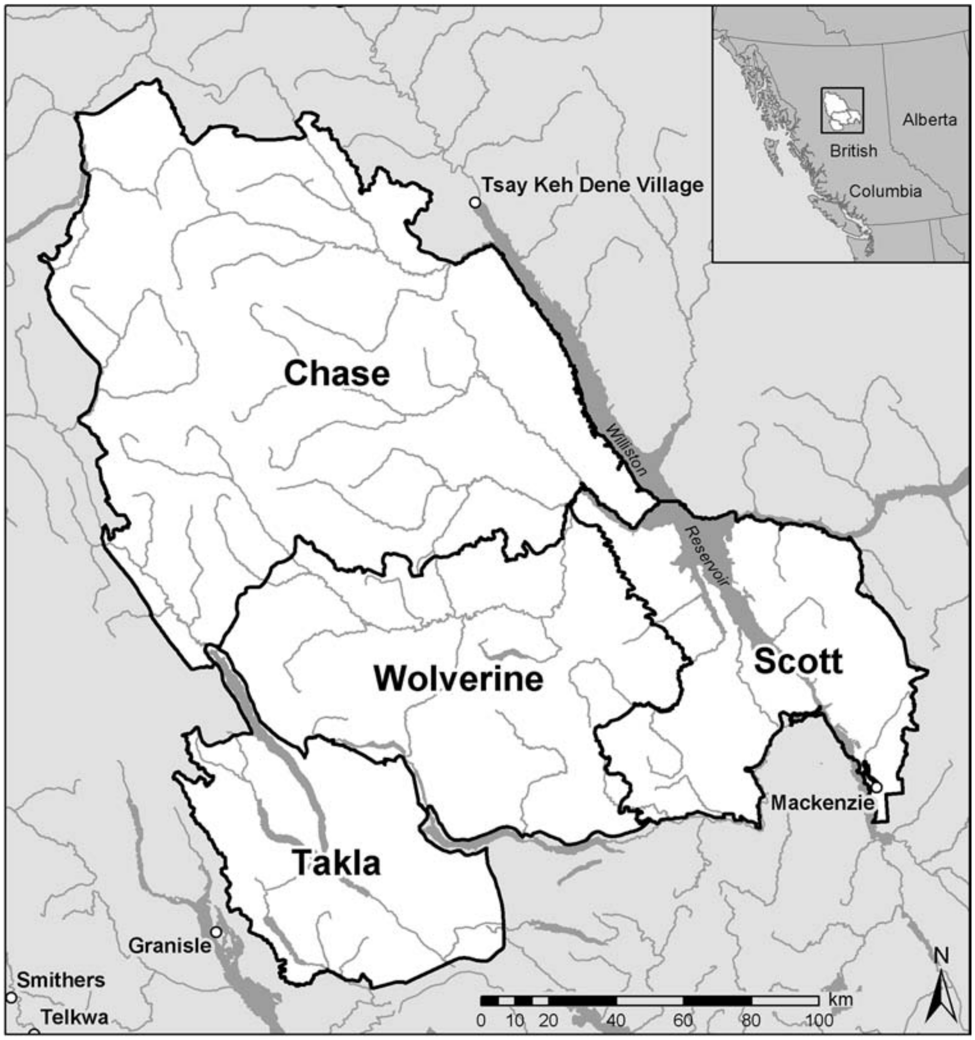
[4] The lead author calculated this figure as a direct proportion of the annual allowable cut (9.1×10^6 m^3) for the larger Prince George Timber Supply Area (7.6×10^6 ha) within which the Fort St. James Forest District occurs.

Fig. 1. Location of recovery planning areas for the Chase, Wolverine, Takla, and Scott woodland caribou herds in north-central British Columbia.



Whether wolves prey primarily on moose and kill caribou incidentally (Messier 1995), whether wolves switch to caribou as easier prey (Dale et al. 1995; Messier 1995), or whether wolves continue an original selection for caribou and use moose as an alternate prey (Messier 1995; Ballard et al. 1997), caribou populations experience greater mortality than they would without moose interspersed throughout the habitat. When moose are abundant, wolves do not experience negative feedback from declining caribou populations (Messier et al. 2004).

In contrast with the rest of the Southern Mountains National Ecological Area, our study area had relatively large, unmanaged forests with extensive industrial development beginning only after construction began on the W.A.C. Bennett hydroelectric dam in 1961. Subsequent flooding of the Finlay, Peace, and Parsnip rivers created British Columbia's largest body of freshwater, which has likely been a barrier to caribou migration and contributed to reductions of caribou, particularly in the Scott recovery planning area. Prior to hydroelectric and forest development, the area was occupied primarily by Sekani (Tsay Keh Dene and Kwadacha) First Nations and by gold miners occupying small communities in the Wolverine and Takla herd areas. First Nations reported historic seasonal use of the area by wolves and described an increase in the abundance of wolves and their more persistent presence following the first appearance of moose in the early 1920s. With the recent mountain pine beetle (*Dendroctonus ponderosae* Hopkins, 1902) epidemic (Eng et al. 2005), the amount of road building and timber harvest in the pine–lichen habitat areas is anticipated to increase.

Methods

Alpha- and beta-level BBN construction

In general, BBNs consist of nodes and linkages, where nodes represent environmental correlates, disturbance factors, and response conditions (see Marcot et al. 2006, for descriptions of terms and components of BBNs). All nodes are linked by probabilities. Input nodes (the range and environmental prediction variables) contain marginal ("prior") probabilities of their states determined from actual existing conditions; intermediate nodes (e.g., describing attributes of caribou range) contain tables of conditional probabilities based on empirical studies and (or) expert judgment; and output nodes (caribou range values) are calculated as posterior probabilities. Some input nodes, which we refer to as "management levers," can represent environmental correlates that are dynamic either through unmanaged or managed disturbance. These levers can be adjusted based on scenario simulations to estimate management effects during BBN applications.

Our modeling methods generally followed guidelines for creating and updating BBNs presented by Marcot et al. (2006). This entailed developing simple influence diagrams, using the modeling shell Netica™ (version 2.17; Norsys Systems Corporation, Vancouver, British Columbia), to depict nodes and linkages; expanding these into initial alpha-level BBN models in which the node states and probabilities were parameterized mostly from expert judgment; and then refining those into beta- and higher-level BBN models from peer review and, where available, from empirical testing and updating from field data. Model changes were made by having experts qualitatively adjust parameters and (or) model structure to fit the new information if, and whenever, it became available.

The BBNs we created depict the likely state or condition of seasonal ranges for caribou given the observed states or conditions of the input environmental correlates. Our choices of seasonal range types to model, the environmental correlates, and the probabilistic relationships among correlates, were based on a series of consultative workshops with a modeling team of domain experts (McNay et al. 2002). These professionally facilitated workshops occurred over 2 years (2000–2002) during which five technicians explored and documented ecological relationships with six domain experts. The goal of the workshops was to translate available data (published and unpublished), anecdotal information, and professional judgment into each BBN structure. This involved using knowledge of the key ecological correlates and their interactions in creating the structure of the BBNs.

Once the structure of each BBN was created, then the essential aspects of the functional relationships between factors was translated into node states and conditional probabilities. If data were available regarding a functional relationship, they were used; if no data were available, then ecological principles and knowledge of functional relationships in other areas or related ecological situations was used. In either case, it was the expert's interpretation of the data that formed the basis for parameters in the BBNs. The goal was to reach consensus regarding the BBN structure and conditional probabilities, and this often required follow-up literature investigations or discussion with other domain experts. Consensus resulted in conditional probability estimates that experts agreed upon. Where consensus could not be easily reached, competing views were structured as explicit alternative hypotheses with supporting assumptions and explanation clearly stated in the product for follow-up review and discussion. Workshop minutes and model-refinement plans were recorded and circulated to the experts for review after each workshop. Comprehensive documentation of the workshop results has been presented by McNay et al. (2002).

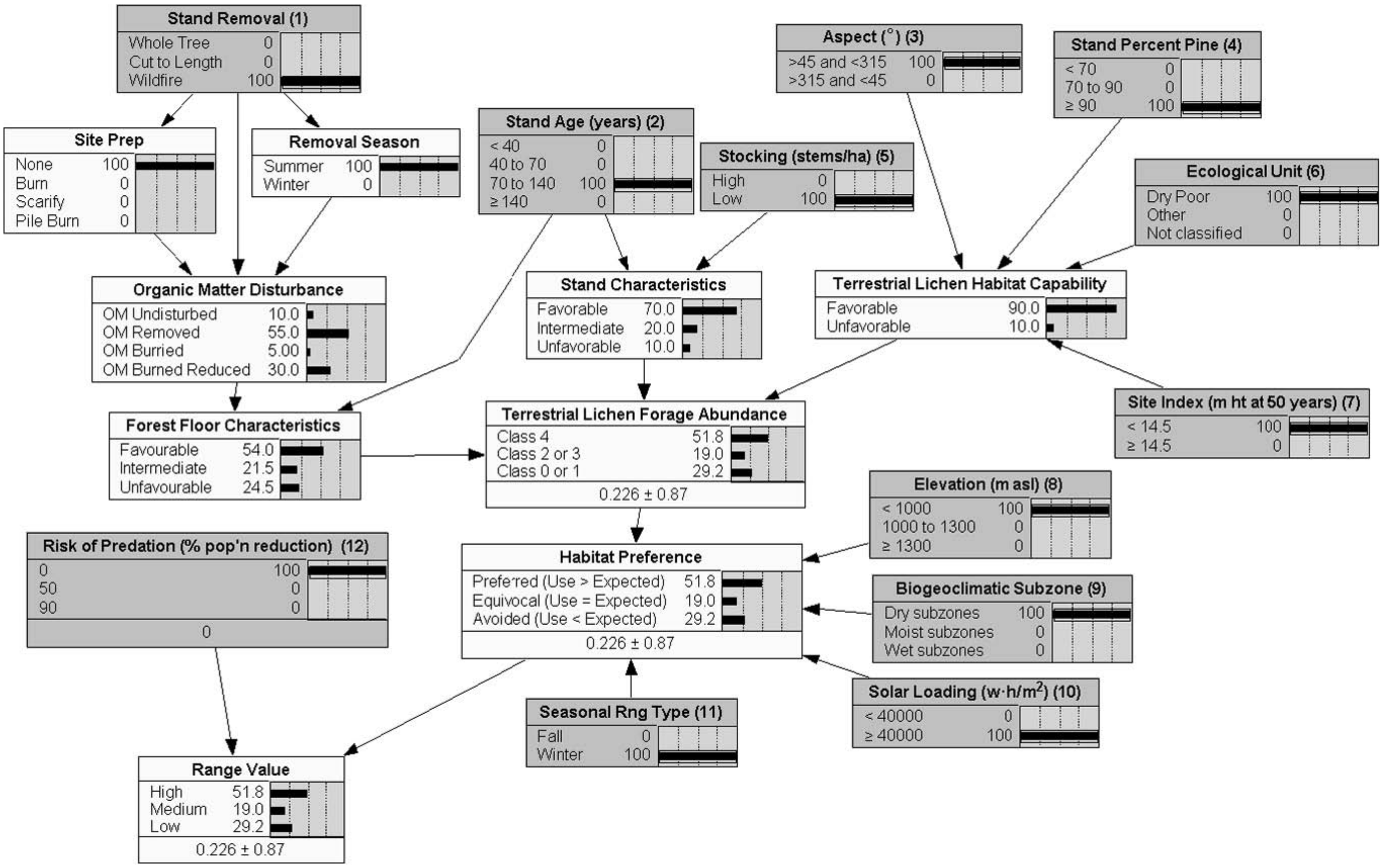
The final output from each seasonal range BBN (e.g., Fig. 2) was a caribou range value, intended to depict the relative quality of habitat and the posterior probabilities of the three discrete range states: high, medium, and low. The probabilities are calculated within the Netica™ modeling shell using standard Bayesian learning and are based on values and prior and conditional probabilities specified within the model. The specific conditional probabilities underlying the calculation of the range value node were set by best professional judgment and take the form of probabilities for each range value discrete state, which are dependent on the states of the two input nodes of risk of predation and habitat preference (Table 1). The state values were set to range from –1 (low range value), through 0 (medium), to +1 (high). We displayed resulting seasonal range values on maps as the expected value from the seasonal range node (i.e., the probability of a state multiplied by the state value, summed across all states) classified into the three outcomes of low, medium, or high based on equidistant intervals of the observed seasonal range values. Further, the Netica™ BBN models also displayed the standard deviation of the expected value, calculated under the plausible assumption of a Gaussian error distribution.

We used ArcView 3.2 (ESRI, Redlands, California) and Microsoft Access™ 2000 (Microsoft Corporation, Redmond, Washington) to construct and manage case files of environmental correlates taken from 1 ha cells in the study area (3 664 295 ha). The environmental correlates that we used came primarily from the British Columbia Forest Inventory Planning attribute database and the British Columbia Terrain Resource Information Management program (Table 2). Case files (i.e., one file for each BBN) were lists of records (i.e., one record for each cell in the study area) containing columns (i.e., one column for each input node) specifying the existing condition or state of the environmental correlates represented by input nodes. Our decision to map results at 1 ha resolution was based on our interests in focusing the management problem and did not imply accuracy of the input data nor any intent to resolve uncertainty or error resulting from input data resolution. We used Netica™ to determine probable caribou range states and then mapped those states and evaluated their geographic distribution. Beta-level models were applied to the recovery planning areas by first calculating the amount of potential range (i.e., a theoretical construct where all input nodes were constrained to their optimal state for caribou). We then evaluated current range conditions based on the current state of input nodes and finally, forecasted future range conditions based on simulated future landscape disturbances.

Forecasting future range values from simulated landscape disturbances

Landscape disturbance was simulated over 250 years in 10 year time steps from current conditions (year 2000) using the spatially explicit landscape event simulator (SELES; Fall and Fall 2001). SELES is a modeling shell that simulates vegetation or environmental conditions across a landscape over time, given initial conditions and disturbances to, or succession dynamics of, each condition. In SELES, the user allocates defined disturbances to a geographic area based on rule sets applied to spatial cells. In our application, we mimicked two different landscape disturbance scenarios described in detail by Fall (2003) and in general as follows: (*i*) a "conservation policy scenario," which represented the

Fig. 2. A Bayesian belief network used to predict the likely value (high, medium, or low) of ranges (postrut range or pine–lichen winter range) used by woodland caribou in north-central British Columbia. (All networks shown are beta-level models as described in the text. Input nodes are numbered for ease of reference.)



current forest management strategies for caribou range (BCMSRM 1999, 2000), and (*ii*) a “natural disturbance scenario,” which represented historic patterns (i.e., patch sizes and return intervals) of wildfire experienced within the study area (Delong 2002). The purpose of running the model under these two scenarios was to compare their relative outcomes, not to estimate absolute values of caribou ranges. We suggest that the most appropriate management for ensuring caribou range values, within the context of strategically managing for multiple resources, is to mimic natural disturbance regimes, that is, if and when model results under the conservation policy scenario match those under the natural disturbance scenario.

In both scenarios, we used variable density yield prediction (VDYP) growth curves (British Columbia Ministry of Forests (BCMF) 1999) to determine postdisturbance forest conditions where forest stands were always completely replaced (i.e., stand age set to zero) by disturbance. We defined ecological successional stages solely by forest age classes (i.e., regenerating forest stands were identical in species mix and composition to original predisturbance conditions). Disturbances occurred in multiples of adjacent 20 ha cells where the size of each disturbance varied according to its type and intensity.

For a cell to be available for logging in the conservation policy scenario, it was required to (*i*) be part of a predefined timber harvesting land base (BCMF 2001), (*ii*) be at least the minimum cutting age for the predominant tree species (BCMF 2001), (*iii*) be consistent with regulated patch size and seral distribution targets, and (*iv*) not contradict regulations for conservation of other resource values. To increase the reality of the simulation, we assigned available harvesting cells a probability of being selected based on proximity to predetermined locations of main haul roads. As SELES simulates forest harvest within cells, roads are added in the model using a “least-cost” approach based on the topographical and biogeographical features of the landscape within the cells. Roads were activated and deactivated according to their usefulness to the harvesting schedule as time progressed. The conservation policy scenario included constraints on harvest of trees in the pine–lichen winter range such that less than 50% of this range could be less than 70 years old, and patch sizes greater than 250 ha were favored. Contrary to current forest policy, we allowed natural disturbances to occur as part of the conservation policy scenario but only within parks.

In the absence of available models to predict unmanaged landscape conditions (especially if one contemplates impending climate change), we simulated a natural disturbance scenario strictly as a hypothetical base case of assumed landscape conditions. Natural disturbance conditions were assumed to be represented only once we ran this scenario over a 400 year cycle to eliminate any footprint (start-up bias) from current forest management. We ran multiple sim-

Table 1. Conditional probability table for the output node “range value” in the woodland caribou seasonal range Bayesian belief network models (Figs. 2–4).

		Habitat value		
Risk of predation	Habitat preference	High	Medium	Low
0	Preferred	100	0	0
50	Preferred	0	100	0
90	Preferred	0	0	100
0	Equivocal	0	100	0
50	Equivocal	0	0	100
90	Equivocal	0	0	100
0	Avoided	0	0	100
50	Avoided	0	0	100
90	Avoided	0	0	100

Note: Values for this node were parameterized based on collective best judgment by caribou experts. See text for explanation.

ulations in this manner and calculated a mean and standard deviation for the resulting seasonal range values. Because our number of simulations was low (n = 4; each simulation took 1 week for each planning area), the range of variation was necessarily smaller than otherwise, and comparisons of the conservation policy to natural disturbance were necessarily conservative; this is a justifiable position given that our problem concerns the future supply of threatened habitats.

Model assessment

Our approach to model assessment took three forms: (*i*) expert review; (*ii*) uncertainty and sensitivity analyses; and (*iii*) field verification.

Expert review

We began building beta-level models through a peer review process whereby seasonal range maps were presented in workshops to species experts, who were not involved in building the original alpha-level models, for their visual assessment and critique. The informal model assessment was typically focused on ensuring that our depiction of ecological relationships in the alpha-level models met with the expectation of experts and that calculated range values were generally consistent with their experience. We created the beta-level models by refining the alpha-level models based on recalibrating the conditional probability tables of the intermediate nodes, modifying the states represented within the nodes, and adding or deleting nodes as needed to respond to the reviewers’ critiques.

Uncertainty and sensitivity analyses

Sensitivity in the BBN calculations of expected caribou range value represented the degree to which the calculated expected values were sensitive to each input variable and was calculated in the Netica™ modeling shell using the standard Bayesian learning algorithm (see Marcot et al. 2006, for explanation of sensitivity analysis in BBN models). Uncertainty about model outcomes would be expected to result as a function of the spatial resolution of input data (i.e., uncertainty might differ and be lower in value, if levels of resolution coarser than 1 ha were to be used in the model); however, we had no control over this feature of our data inputs and could not readily assesses it’s affect as a component of BBN construction. Therefore, we addressed this uncertainty by assessing reliability of input data as a component of field verification.

Field verification

If our seasonal range BBNs were to be used for other than strategic purposes (e.g., winter range delineation), a final assessment phase was used which included the design and implementation of field-based procedures to verify predictions of range quality and its spatial location. These more operational aspects of BBN implementation go beyond the strategic-level decisions that we focus on, have been ongoing, and are not reported here.

Results

Modeling caribou seasonal ranges

Caribou pursue both migratory and sedentary strategies in their use of range and sometimes move relatively long distances (60–120 km). In mid-October through November, caribou congregate on postrut ranges at high elevations and by about late December, move to low-elevation pine–lichen winter ranges. Depending on snow conditions on these pine–lichen winter ranges, caribou may move back and forth between this range at low elevation and a high-elevation winter range (Johnson et al. 2004*b*). Although primarily differentiated by their relative elevation and snow conditions, these two winter ranges also differ in tree species composition and forage availability (Johnson et al. 2001). In April through mid-May, caribou travel from high-elevation winter ranges, through movement corridor ranges, to calving and summer ranges where they stay until the postrut congregation. Some caribou, in some years, remain relatively sedentary finding all seasonal resources within smaller areas. Generally, caribou choose to stay at higher elevations as long as possible as a way to avoid relatively higher risk of predation by wolves that typically exists at lower elevations (Bergerud and Page 1987; Seip 1992).

Pine–lichen winter range and postrut range

Pine–lichen winter range and postrut range were considered to be similar in ecological setting, differing only in elevation and snow accumulation. Hence, although caribou use the ranges differently, both ranges were described by the same influence diagram and BBN (Fig. 2). Capability for terrestrial lichens (*Cladina* spp.), the primary forage used by caribou during fall and winter (Johnson et al. 2001), was based on topographic aspect, ecological unit (i.e., a combination of soil moisture and nutrient regime), percentage of lodgepole pine in the overstory forest, and overall productivity of the site. We estimated productivity using an index of tree height at 50 years old. Generally, terrestrial lichens grow most successfully on south-facing sites having soils that are well drained with poor nutrient levels (Sulyma and Coxson 2001). Lodgepole pine also competes well on these sites and, therefore, was used as an indicator of terrestrial lichens (Sulyma 2001).

We used forest age, density of trees, and forest floor characteristics to determine current suitability of the sites for

Table 2. A list of data inputs contributing to case files used by Netica™ in processing Bayesian belief network models of seasonal range value for woodland caribou in north-central British Columbia.

Case file input	Description	Data source[a]	Model codes[b]
Stand removal	Method of harvest or natural disturbance	User defined	PLWR/PRR(1)
Stand age	Age stand a given time	FIP	PLWR/PRR(2), HEWR(5), MWR(1)
Aspect	Aspect of a slope in degrees	DEM	PLWR/PRR(3), HEWR(3)
Stand percent pine	Portion of a stand composed of pine	FIP	PLWR/PRR(4)
Stocking	Number of stems per hectare	User defined	PLWR/PRR(5)
Ecological unit	Plant community present at a given site	TEM	PLWR/PRR(6), HEWR(2), MWR(2)
Site index	Measure of tree height at age of 50 years	FIP	PLWR/PRR(7)
Elevation	Elevation in metres above sea level	DEM	PLWR/PRR(8), HEWR(7), MWR(5)
BGC subzone	Biogeoclimatic (BGC) subzone classification	BEC	PLWR/PRR(9)
Solar loading	Global radiation budget ($W \cdot h/m^2$)	DEM	PLWR/PRR(10)
Seasonal range	Lever for evaluating postrut or pine–lichen ranges	User defined	PLWR/PRR(11)
Predation risk	Risk of population reduction due to natural predation	MWR model, roads	PLWR/PRR(12), HEWR(9), CSR(4)
Curvature	Topographic curvature of landscape (concave or convex)	DEM	HEWR(1)
Stand percent fir	Portion of stand composed of subalpine fir	FIP	HEWR(4)
Tree height	Weighted mean height of (co)dominant tree species	FIP	HEWR(6)
Slope	Landscape slope in degrees	DEM	HEWR(8)
Ecological unit	Identifies vegetated high-elevation sites	FIP, BEC	CSR(1)
ITG	Tree species composition (inventory type group)	FIP	CSR(2)
Regulated hunt	Expression of moose harvest by regulated hunting	User defined	MWR(3)
Subsistence hunt	Expression of moose harvest by subsistence hunting	User defined	MWR(4)

[a] Data sources are as follows: user-defined, management lever nodes with states that can be toggled to alter environmental conditions of simulated planning scenarios; FIP, forest inventory planning attribute database (available from http://srmwww.gov.bc.ca/gis/Databases/); DEM, digital elevation model from the British Columbia Terrain Resource Information Management program (available from http://ilmbwww.gov.bc.ca/bmgs/trim/index.html#); TEM, terrestrial ecosystem mapping database available for selected areas in British Columbia (available from http://srmapps.gov.bc.ca); BEC, spatial coverage of the biogeoclimatic ecosystem classification system for British Columbia.

[b] Model codes are as follows: PLWR, pine–lichen winter range; PRR, postrut range; HEWR, high-elevation winter range; CSR, calving summer range; MWR, moose winter range. Values in parentheses identify the model-specific data input node in Figs. 2–5.

producing terrestrial lichens. The nature of site disturbance determined suitability of the soil substrate for growing lichens, with slightly exposed soil being best. As forest conditions change with age, stands exceeding 140 years old have higher and more developed canopies leading to subcanopy microclimates that are cool and moist where lichens do not grow as successfully as other vegetation (Sulyma and Coxson 2001). In early seral stages, terrestrial lichens communities tend to be dominated by *Cladonia* spp., a less preferred forage (Johnson et al. 2004*b*). Therefore, the modeling team determined that favorable conditions for terrestrial lichens used as forage, occurred on sites between 70 and 140 years old, and we expressed conditions at the response node in relative abundance classes.

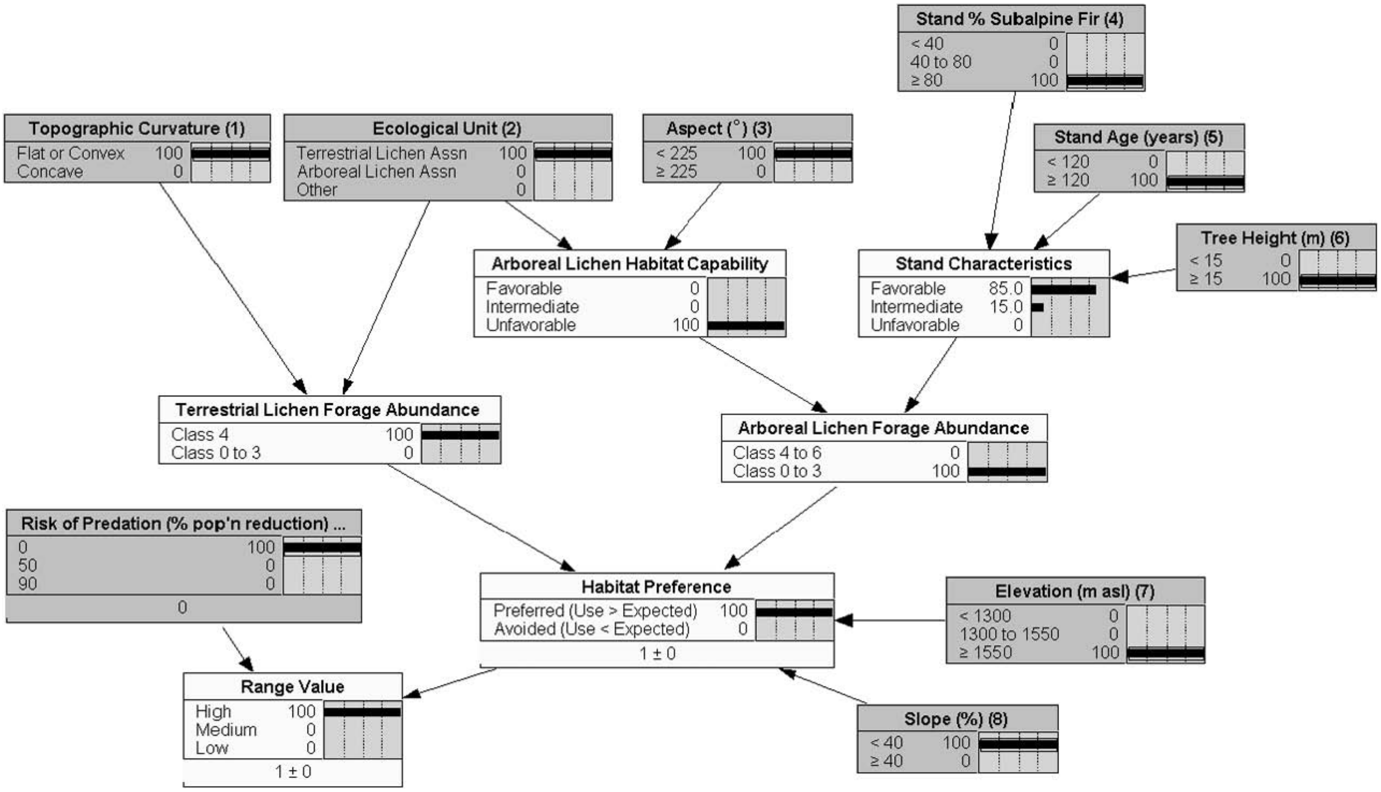
Use of winter ranges by caribou has been correlated with snow conditions (Fancy and White 1985), and some research indicates that caribou will not crater (dig) for terrestrial lichens if snow exceeds 90 cm depth (Johnson et al. 2004*b*; however, see Brown and Theberge 1990). We used elevation and modeled solar insolation (Solar Analyst version 1.0; Hu and Rich 2000) to index the modifying effect of ambient temperature on accumulation of snow during early winter. The modeling team determined that open sites between 1000 and 1300 m a.s.l., although unusable in winter due to deep winter snow, would still be useable early in the season (i.e., the postrut period) wherever relatively high amounts of solar insolation were received. Similar sites at lower elevation would generally have relatively less snow as winter progressed, and therefore, the modeling team classified these sites (lower elevation) as pine–lichen winter range. In some winters, snow depths may exceed those preferred by caribou even on pine–lichen winter ranges, forcing caribou to use high-elevation winter range (discussed in the following). The modeling team considered that caribou would prefer sites with abundant terrestrial forage lichens and little snow accumulation. Since calculation of preference indices is now widely available we chose to express the response conditions at this preference node in terms of Chesson's (1983) statistical test for preference.

Although risk of predation by wolves could alter caribou's selection of lichen sites, the modeling team agreed that caribou would continue to exhibit preference for sites and experience higher mortality rates if these sites were near abundant moose and wolves. Therefore, risk of predation was a probability of population reduction applied to the lichen site preference node to calculate a final value for seasonal range (Fig. 2).

High-elevation winter range

When snow depth at low elevations exceeds that in which caribou can crater for terrestrial lichens, the snow pack is usually consolidated sufficiently allowing caribou to walk on its surface and move to higher elevations (Seip 1992; Johnson et al. 2001). At these higher elevations caribou use 2–3 m deep snow packs to reach arboreal lichens (*Bryoria* spp., *Alectoria* spp.) in the lower crowns of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The modeling team determined that a site was favorable for supporting arboreal

Fig. 3. A Bayesian belief network used to predict the likely value (high, medium, or low) of high-elevation winter ranges used by woodland caribou in north-central British Columbia.



lichens if subalpine fir composed greater than 80% of the stand, was greater than 15 m in height, and was greater than 120 years old (Fig. 3).

At the highest elevations, in alpine tundra, caribou seek areas where persistent winds reduce snow to depths allowing them to crater for terrestrial lichens (Johnson et al. 2001, 2004*b*). Terrestrial lichen abundance in alpine tundra was determined to occur at most locations with the study area except for nonvegetated rock, glaciers, or hygric to subhydric soil moisture conditions (Fig. 3). We determined the potential for these areas to be windblown using a topographic curvature function to assess relative convexity of a digital elevation model in a 3 cell × 3 cell neighbourhood around the cell being assessed.

The modeling team determined that, if a site >1300 m a.s.l. met conditions for abundant forage lichens and was in relatively gentle terrain (i.e., slope less than 40%), then the site would be preferred by caribou (Chesson 1983). As in the previous range model, predation risk was a probability of population reduction applied against the preference node to calculate high-elevation winter range quality (Fig. 3).

Calving and summer range

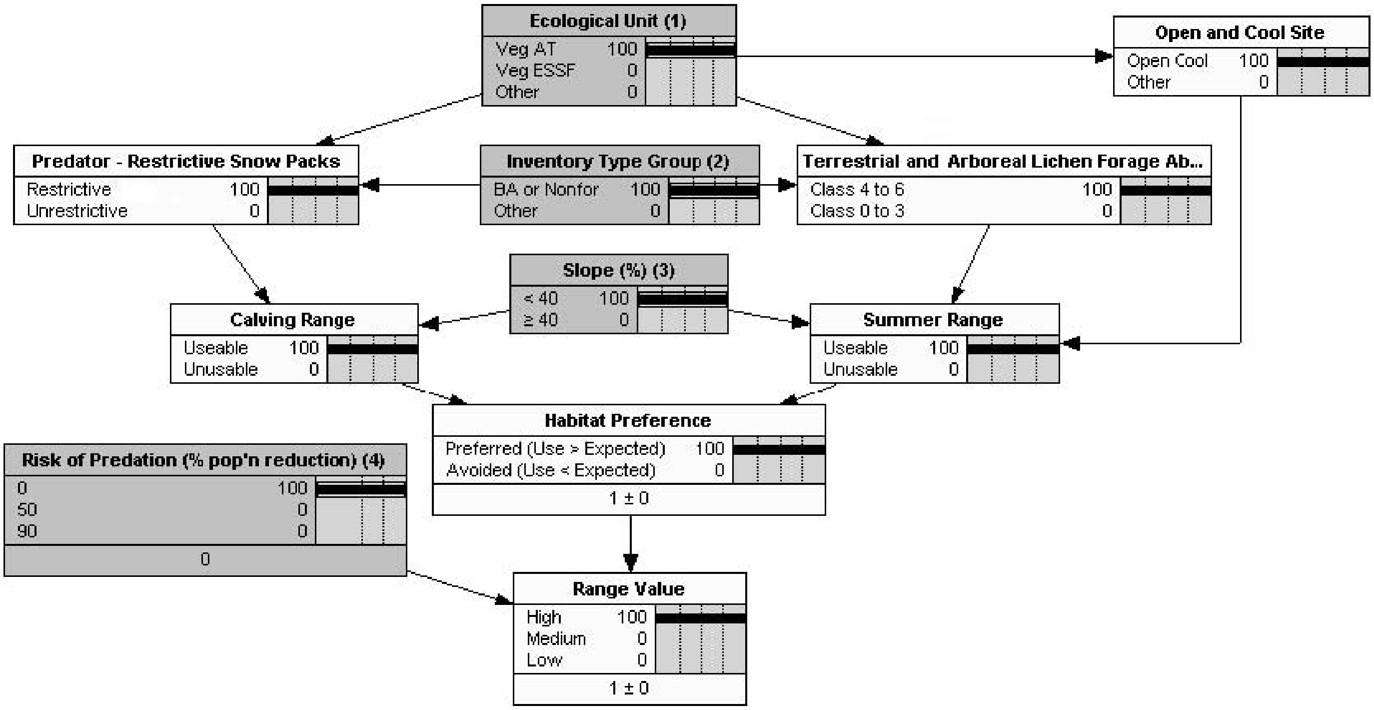
Caribou seek security from predators during calving (Bergerud and Page 1987; Seip 1992). This explains why genders separate their ranges, with females moving away from typical foraging sites to the security of islands or shorelines in lacustrine environments (Bergerud 1985; James et al. 2004) or areas with relatively deep and (or) soft snow in mountainous terrain (Seip 1992). We used alpine tundra and occurrence of subalpine fir adjacent to alpine tundra as indicators that deep snow would persist into the calving period of late May to early June (Fig. 4). Sites with deep snow and gentle slopes are used by caribou but less so by wolves (Seip 1992).

Caribou show little selection for specific conditions in summer. Rather, caribou herds disperse across large areas at this time to reduce encounters with predators (Seip 1992). Although forage is accessible at low elevations, caribou tend not to occur there, presumably due to the relatively higher risk of predation. Therefore, the modeling team described summer range using the same site conditions as those used for calving range (Fig. 4) but emphasized use of alpine areas by caribou where cool, windy conditions lessen harassment by flies (Ion and Kershaw 1989). Predation risk was again used as a probability of population reduction applied against the preference node to calculate calving and summer range quality.

Movement corridor range

The modeling team was unable to determine a set of predictive factors (ecological correlates) that would describe caribou selection of movement corridor range. However, Johnson et al. (2001) found that caribou traveled consistently within landscape features such as valley bottoms and lowlands with lakes and rivers. Based on this generalization, experts delineated general movement corridors on maps, which we buffered by a 1 km distance wherever slope was less than 40%. Within buffers, predation risk was a probability of population reduction applied against the corridor node to calculate movement corridor range quality.

Fig. 4. A Bayesian belief network used to predict the likely value (high, medium, or low) of calving and summer ranges used by woodland caribou in north-central British Columbia.



Predation risk

We modeled predation risk as a function of wolf density (Messier 1995). We also considered linear corridors, such as roads, to have high risk of predation. Although caribou are susceptible to many forms of mortality (Wittmer et al. 2005), experts agreed that wolves were the principle predator in our study area because grizzly bears (*Ursus arctos* Linnaeus, 1758) were at one of the lowest densities in British Columbia (Hamilton et al. 2004) and cougars (*Puma concolor couguar* (Kerr, 1792), another major predator of caribou, were rare to nonexistent. Experts concurred on representing predation risk for caribou using a 100 m buffer around linear features (mostly active roads) (James and Stuart-Smith 2000), and a 5 km buffer around areas where wolves would most likely be hunting moose, which was largely determined by moose density (Messier 1995). Other prey that might influence the distribution of wolves (e.g., *Odocoileus* spp.) was largely lacking in our study areas. Aside from moose and caribou, the most abundant ungulates are Stone's sheep (*Ovis dalli* Nelson, 1884) and mountain goats (*Oreamnos americanus* (de Blainville, 1816)), both of which experts agreed were not likely to influence the distribution of wolves. We estimated moose density with a BBN predicting range value for moose and proportional reduction in moose density through either regulated or subsistence hunting (Fig. 5). We defined winter moose range as elevations less than 1200 m and sites with abundant shrubby forage, the latter identified by nutrient-rich, subhygric to mesic sites less than 40 years old. Summer moose range was similar but not restricted by elevation.

Threats to the value of seasonal ranges

Strategic control of management levers (spatially and (or) temporally) could presumably mitigate threats to caribou and thereby aid recovery of threatened caribou populations. The management levers in our BBNs (Table 3) were primarily associated with forest harvesting, development of roads, and hunting regulations. Among all the levers, those affecting predation risk had the greatest influence on caribou seasonal range values (Table 3). Stand age as influenced by forest harvesting was the next most influential management lever, particularly because it affected pine–lichen winter range and postrut range. However, stand age affected all BBNs either directly as a determinant of forage or indirectly through the predation risk BBN, where the latter affected each caribou seasonal range spatially.

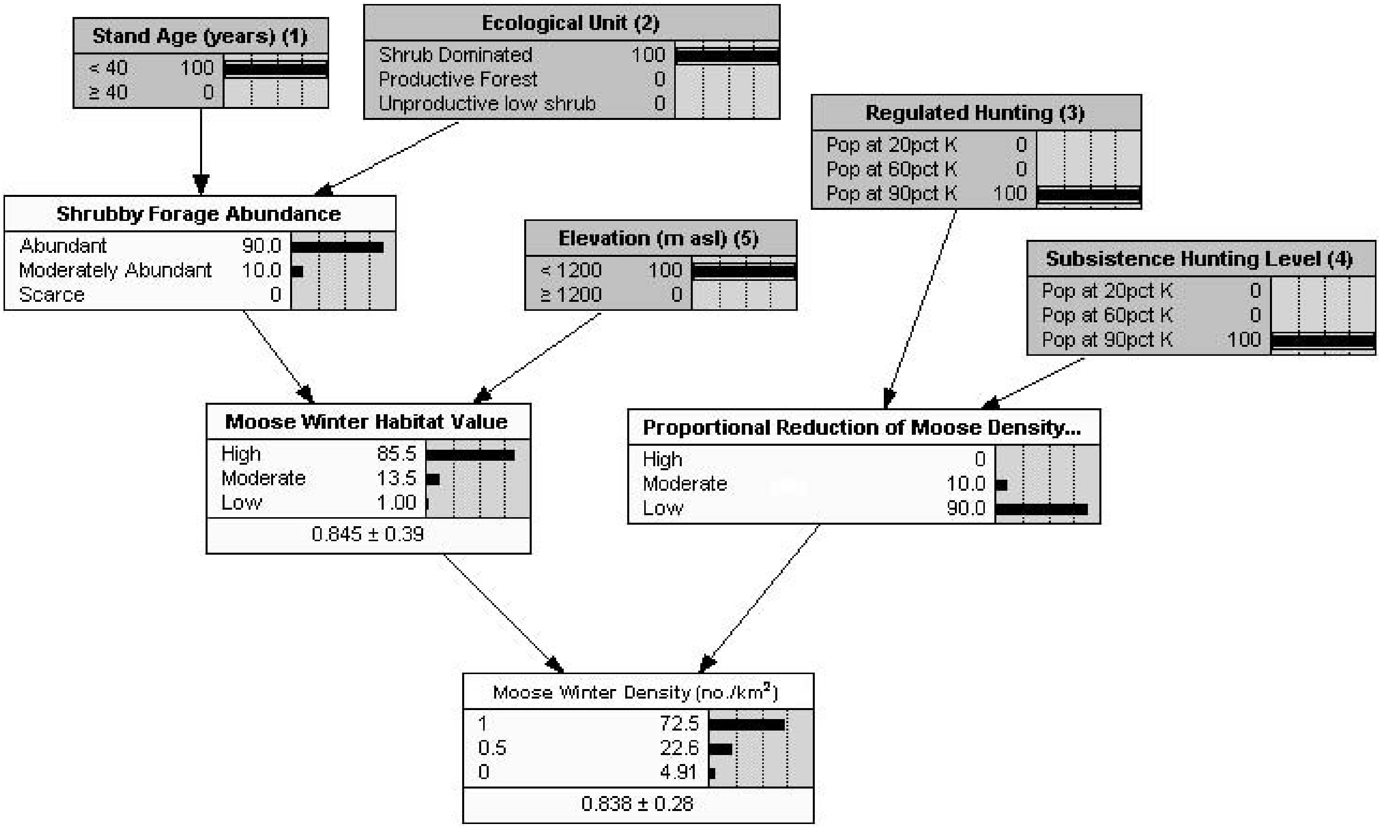
Assessment of seasonal range values

Potential range

As an example of BBN spatial output, we present maps of postrut range, calving and summer range, and moose density during winter within the Wolverine recovery planning area (Fig. 6). Generally, the location of potential seasonal ranges within planning areas indicated that caribou likely need to move among seasonal ranges and that calving and summer range is more generally dispersed around the recovery planning areas than are the other types of range. Experts agreed that this spatial difference in the location and dispersion among the types of ranges fit their experience with observed caribou movement patterns and correctly represented how caribou occur at low density during summer.

Across all recovery areas, the potential for calving and summer range far exceeded potential for any other range type, and there was relatively more of this potential range in the Chase and Wolverine recovery planning areas (Table 4). Potential for high-elevation winter range was the next most

Fig. 5. A Bayesian belief network used to predict the likely density of moose in winter in north-central British Columbia. Pct K, percent of carrying capacity.



abundant range across all areas, and again, this potential was best in the Chase and Wolverine recovery planning areas. The greatest potential area of postrut and pine–lichen winter ranges combined occurred within the Wolverine and Chase herd recovery planning areas (Table 4), although the Scott had the most potential area of pine–lichen winter range of all recovery planning areas. Generally across the study area, the Scott and Takla were distinct in their relative lack of potential area of any range as a percentage of the recovery planning area, particularly so for postrut range (<1%). The one exception was the apparent disproportionate amount of pine–lichen winter range in the Scott recovery planning area (Table 4). The Takla was distinct in that, as a percentage of the recovery planning area, almost all potential range was at high elevations.

Current range

For the most part, the current abundance of seasonal ranges across the study area was consistently much lower than potential (Table 4) with the exception that calving and summer range was almost equal to potential in all areas. Current high-elevation winter range was close to half the potential in the Scott and Takla but lower in the Chase and Wolverine recovery planning areas, 71% and 68% reduction from potential, respectively. Current abundance of both postrut and pine–lichen winter ranges was generally high in all areas. Because these two ranges reach optimal value if forest age is 70–140 years old, the area of current range would be half the area of potential range under a stable forest age-class distribution. The Scott recovery planning area was distinct in this respect, because it had a 70% difference between potential and current area of pine–lichen winter range. All other recovery planning areas had more pine–lichen winter range than would be expected under a stable age-class distribution, and all recovery planning areas had more postrut range than would be expected.

Regardless if increases in moose and wolves were due to a natural colonization of moose or if this was precipitated from past land use and management, our model predicts that predation risk now has a dramatic effect on seasonal range values for caribou in all recovery planning areas where reductions in abundance of seasonal ranges were usually from 21% to 100% (Table 4). Reductions in range value were highest on postrut ranges (83%–100%) for the Scott, Takla, and Wolverine recovery planning areas and on pine–lichen winter range (86%) for the Scott recovery planning area. Range value in the Chase area appeared to be affected the least by predation risk (Table 4) and had the lowest reduction of any seasonal range (21% on high-elevation winter range). By comparison, when predation risk is considered, the Scott and Takla areas were left with less than 1000 ha of postrut and pine–lichen winter ranges combined.

Forecasted range under conservation policy and natural disturbance scenarios

By way of an example where BBNs were used to assess discrete time steps of simulated landscape disturbance, we focus on the results of the conservation policy and natural

Table 3. Sensitivity (percent variance reduction) of predicted values of woodland caribou seasonal ranges to environmental correlates used as management levers in Bayesian belief network models.

	Seasonal range Bayesian belief network					
Environmental correlate	PLWR or PRR	HEWR	CSR	MC	MDS	MDW
Tree species	7.86	0.40				
Stand age	1.67	0.18			0.02	0.29
Stand preparation	0.66					
Stand removal method	0.04					
Stocking	0.00					
Subsistence hunting					1.95	1.07
Regulated hunting					1.95	1.07
Predation risk	9.80	21.90	42.9	100		

Note: Bayesian belief networks were constructed for pine–lichen winter range (PLWR), postrut range (PRR), high-elevation winter range (HEWR), calving and summer range (CSR), movement corridor range (MC), and for predation risk as a function of moose density in summer (MDS) and winter (MDW). Blank cells mean that the correlate was not used in that network model.

disturbance scenarios in the Wolverine recovery planning area for predicted values of pine–lichen winter range.[5] Under simulated conditions of forest harvest and, as evaluated by the BBNs, the conservation policy succeeded in sustaining the supply of pine–lichen winter range (Fig. 7A). The simulation began with the current "overstocked" condition of the range and, for the following five decades, showed a steep decline in forecasted supply of the range. In 2055, the amount of high- and medium-quality range under the conservation policy scenario was less than that expected under the natural disturbances as we projected them. Three decades later, however, the amount was more stable and remained greater than would be expected under natural disturbance for the rest of the simulation. The conservation policy was theoretically best at achieving an even supply of range because the sequence of cell disturbance was controlled as opposed to being based strictly on a probability of disturbance as it was in the natural disturbance scenario. However, gaining relative equilibrium in supply of pine–lichen winter range in this conservation scenario is only expected after a period of severe decline.

When risk of predation was considered, the decline of pine–lichen winter range was only exacerbated (Fig. 7B). Although the amount of high- and medium-quality pine–lichen winter range never dropped below that expected under the natural disturbance scenario, only about one-eighth of the range, less than 350 ha in 2075, was predicted as being free from relatively high predation risk. High-elevation winter range did not fare as poorly under assumed conditions prior to (Fig. 7C), or after (Fig. 7D), colonization by moose. Although the amount of high- and medium-quality high-elevation winter range was far below the landscape potential, it was always above the amount expected under the natural disturbance scenario. This result was expected from the conservation policy which biased disturbances from forest harvesting to lower elevations (easier access to higher volumes of wood fibre) and minimized fire-initiated disturbance at both high and low elevations. Risk of predation did not affect this range nearly as much as the lower elevation ranges because risk during winter was associated with moose habitat at lower elevations (Fig. 6C).

Model assessment

With respect to the use of our BBNs in strategic decisions, experts generally agreed that the modeling captured their current knowledge regarding use of habitat by caribou and spatially depicted the quality of habitats consistent with their understanding. Although only qualitative, the assessment provided a substantial basis toward a common understanding about the problem of caribou recovery among stakeholders.

Generally the BBN outcomes were most sensitive to variation in predation risk and the input factors that related to predation risk (Table 3, Fig. 5): stand age, subsistence hunt, and regulated hunt. The pine–lichen winter range BBN outcome was also sensitive to variation in tree species.

Discussion and conclusions

Use of BBNs in understanding the ecology of seasonal ranges

Although our research was similar to that reported by Weclaw and Hudson (2004) for caribou in Alberta, in contrast, we modeled expert judgment to forecast and map the spatial implications of conservation strategies in a probabilistic framework. In this application of BBNs to aid recovery planning for a threatened species, we chose Bayesian statistics over traditional "frequentist" statistics, because the former incorporates prior knowledge and explicitly represents probabilistic inference and knowledge uncertainty. For this reason, Bayesian approaches have been referred to as "problem solving" rather than "solution characterization" (Horvitz et al. 1988). Also, we note, as have others (e.g., Johnson and Gillingham 2004), that all models are sensitive to variation, some of which may be due to uncertainty. We assessed uncertainty in calculated values of caribou range, including sensitivity to management levers, and we used Netica™ to carry uncertainty in relationships through the BBNs to the calculated distributions of posterior probabilities in the resultant nodes. Although we mapped seasonal range values based on the expected probability of range quality, the uncertainty inherent in range quality can be considered explicitly in risk management and decision making. Decisions about conservation or recovery of caribou populations are

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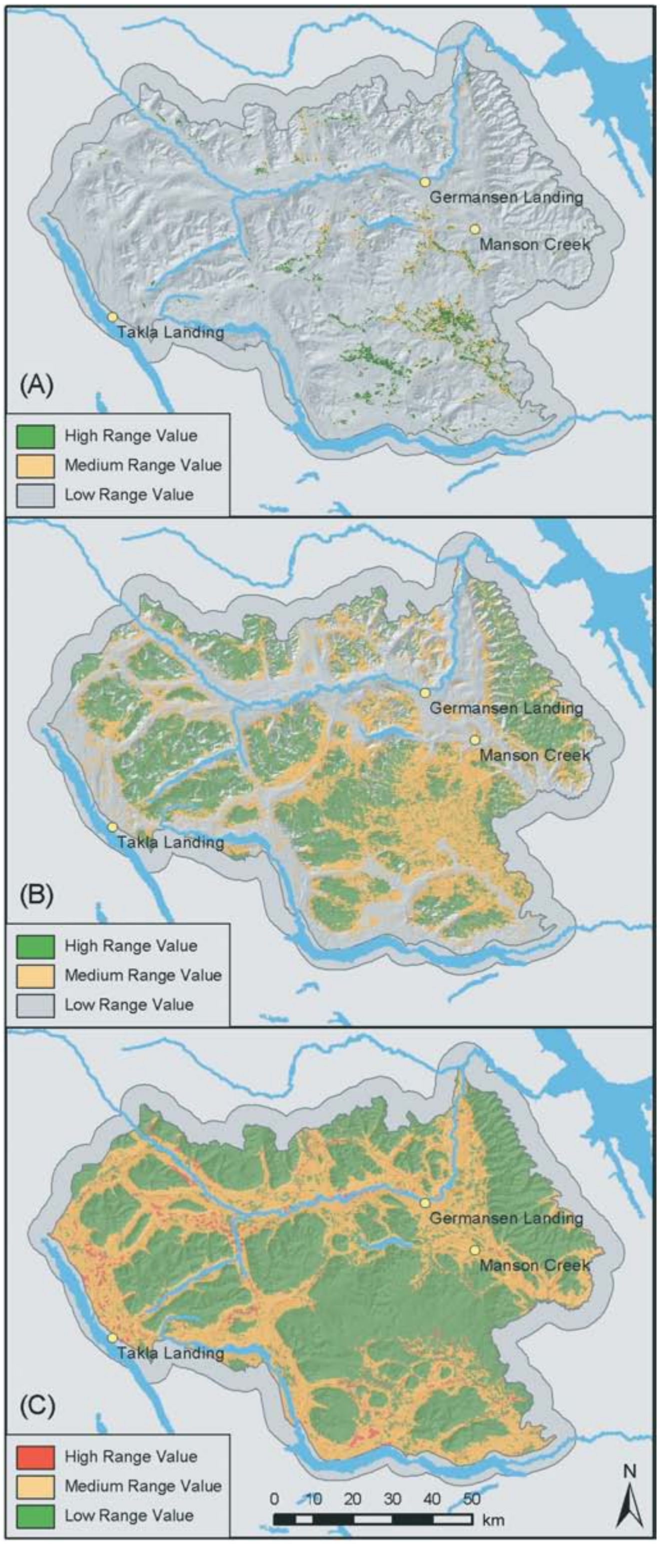
[5] Results of other seasonal ranges in the Wolverine recovery planning area and for all seasonal ranges in the remaining recovery planning areas were presented as part of the recovery planning process for these caribou herds.

Fig. 6. Spatial location of modeled, potential ranges for woodland caribou during (A) postrut, (B) calving and summer seasons, and (C) potential moose range during winter. The example range maps are for the Wolverine herd recovery planning area of north-central British Columbia.



made by managers even when faced with uncertainty, and therefore, decisions should be associated with a measure of risk of failure (i.e., used here as uncertainty factored by cost where cost could be any measure ranging from population change to actual financial cost of a management activity).

BBN models can be useful (McCann et al. 2006) and can complement other model forms (Nyberg et al. 2006). Apps et al. (2001) and Johnson et al. (2004*a*) have modeled caribou ranges using resource selection functions and logistic regression. These efforts described patterns of caribou selection for specific resource conditions but did not integrate such findings into a broader decision-aiding model to compare conservation actions with natural disturbance regimes as we did. We could have used resource selection functions or built our BBNs based only on empirical information but chose to form models based on characterization by experienced professionals, supported by available data, research, and observation, even though this approach has been scrutinized (Johnson and Gillingham 2004) and described as inferior (Pearce et al. 2001). If objectives for modeling only include characterizing observations of historic patterns, we concur that empirically driven approaches are likely best (Johnson et al. 2004*a*; Johnson and Gillingham 2005; Seoane et al. 2005). However, addressing objectives associated with recovery of threatened species cannot be restricted by incomplete or biased empirical information or bounded by spatial and temporal constraints typical of empirical information (Johnson et al. 2004*a*). Recovery decisions require use of prior knowledge, expert understanding, and comprehensive exploration of general alternatives, not necessarily attempts to repeat specific observations of historical patterns (Horvitz et al. 1988). We do not imply that decision-makers can disregard more general modeling assumptions and potential problems. Nelson (2003) presented “three sobering challenges” in the use of forest-level models, which we believe our BBNs can help address: data acquisition, model verification, and scientific credibility. Because our BBNs formally represent a summary of expert understanding about caribou ecology, based either on scientific investigation or new hypotheses, we can use this summary to technically identify, and to set priorities on, specific information needs associated with Nelson’s challenges. In this way, our BBNs are a pragmatic foundation for a holistic, simultaneous approach to management and research.

With respect to utility in research, our BBNs were constructed to explicitly express node states in measurable terms suitable for testing and inclusion of empirical data once available. Future data collection and model testing can be prioritized according to model sensitivity and uncertainty, which Turchin (1998) referred to as “model-motivated data collection.” For example, our understanding of seasonal range ecology could include tests of terrestrial and lichen forage abundance as a function of environmental correlates, migration as a function of snow depths, range preferences based on relocations of radio-collared caribou, and predation risk as a function of the spatial and temporal characteristics of caribou mortality, all of which most affected calculated range values.

With respect to utility in management, use of our BBNs in decision-making establishes a framework for adaptive man-

Table 4. High- and medium-quality woodland caribou seasonal ranges predicted using Bayesian belief network models applied to conditions in recovery planning areas in north-central British Columbia.

	Seasonal range type			
Recovery planning area	PRR	PLWR	HEWR	CSR
Chase				
Potential range (ha)	22 500	17 184	208 505	1 094 879
Percentage of total planning area	1	1	12	63
Current range (ha)	16 679	12 407	59 462	1 069 999
Percent reduction from potential range	26	28	71	2
Range with predation risk (ha)	7 343	4 587	47 078	579 012
Percent reduction from current range	56	63	21	47
Scott				
Potential range (ha)	2 319	21 883	26 069	204 831
Percentage of total planning area	<1	4	4	34
Current range (ha)	2 009	6 525	11 419	204 060
Percent reduction from potential range	13	70	56	0
Range with predation risk (ha)	0	929	5 354	90 172
Percent reduction from current range	100	86	53	56
Takla				
Potential range (ha)	492	835	22 420	186 322
Percentage of total planning area	<1	<1	4	38
Current range (ha)	477	812	10 529	186 122
Percent reduction from potential range	3	3	53	0
Range with predation risk (ha)	12	374	4 613	80,635
Percent reduction from current range	97	55	56	57
Wolverine				
Potential range (ha)	26 703	11 722	78 785	484 830
Percentage of total planning area	3	1	9	57
Current range (ha)	18 762	10 981	24 918	478 449
Percent reduction from potential range	30	6	68	1
Range with predation risk (ha)	3 101	4 545	15 430	249 703
Percent reduction from current range	83	59	38	48

Note: Potential range is the total amount of useable habitat when all range factors were set to the most optimal state for caribou, current range is the amount of useable habitat based on the current state of range factors, and range with predation risk is the amount of useable habitat when predation risk is considered as an influence on range quality. PRR, postrut range; PLWR, pine–lichen winter range; HEWR, high-elevation winter range; CSR, calving and summer range.

agement (Walters and Holling 1990; Nyberg et al. 2006), formalizes assumptions in the decision process, serves as a basis for monitoring, and stands as a record upon which to judge utility once a decision has been implemented. The BBNs presented here are one way to help facilitate such an analysis, while being explicit about uncertainty, and to provide a framework for incorporating new knowledge to revisit management decisions.

In summary, we found that BBNs and the use of expert knowledge to construct seasonal range models were useful in that the approach: (*i*) supported the development of common understanding across disciplines and among stakeholders (the corollary being that we learned where our understanding differed or was most lacking as well); (*ii*) allowed for consistent applications of general ecological understanding across variable situations; (*iii*) allowed for sources and implications of uncertainty to be transparent within a decision context; and (*iv*) allowed forecasts of alternative management scenarios prior to implementation, thereby providing decision-makers with relative assessments of risk and probabilities of success.

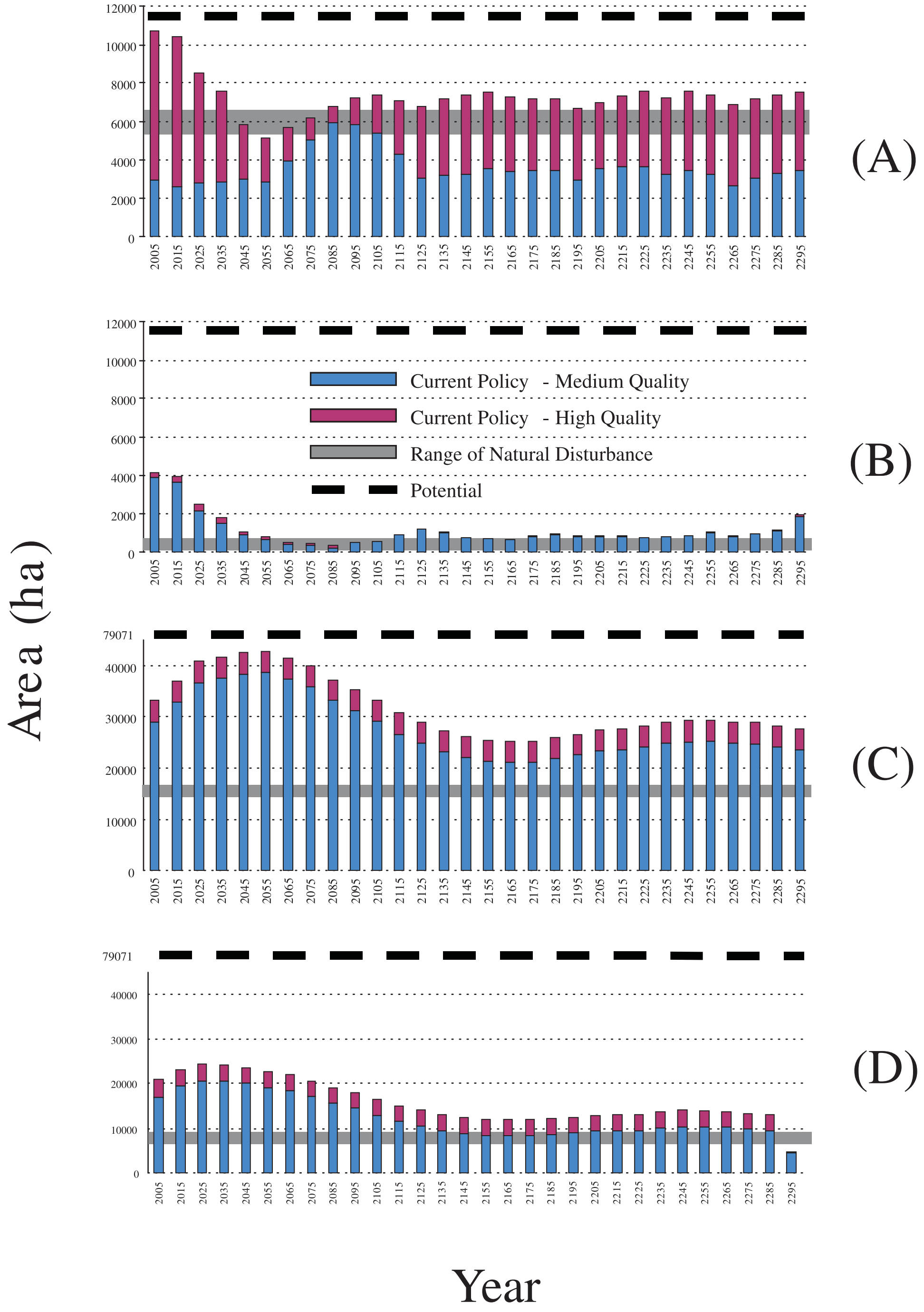
Future refinement of the models

The models presented here are largely structured to represent expert judgment about caribou use of ranges and the influence of environment conditions and to provide a decision tool for exploring potential effects on caribou populations from alternative management of caribou ranges. The model in toto has not been field validated, although parts of the model that likely should be tested are those factors that have the greatest influence on predicted outcomes. These are identifiable using sensitivity analysis (e.g., Table 3) and field evaluation of these factors is presently ongoing.

We also suggest several areas of potential future refinement:

(1) We demonstrated differences in the seasonal range composition of recovery planning areas but had no way to

Fig. 7. Forecasted supply of pine–lichen winter range (A and B) and high-elevation winter range (C and D) simulated for four alternative management scenarios (see text) under conditions prior to colonization by moose (Figs. 7A and 7C) and after colonization by moose (Figs. 7B and 7D) within the Wolverine caribou herd recovery planning area in north-central British Columbia.



infer the ecological implication of those differences. Understanding seasonal range limitations and use of habitat patches within seasonal ranges could be improved using a population modeling approach (Weclaw and Hudson 2004).

(2) Whereas use of the BBNs can be rationalized at a strategic level, operational use of the BBNs would require empirical estimates of the prior probabilities.

(3) We know there are other threats to caribou that could be explored in future modeling including effects of recreational and (or) commercial snowmobiling; heli-ski operations; and oil, gas, and mineral exploration.

(4) Recent large-scale disturbances in British Columbia, such as the mountain pine beetle epidemic, and the provincial management response should be inherent in any modeled conservation strategy.

(5) Although our use of a natural disturbance base case is hypothetical at best, further refinements to this scenario, including impending dynamics due to predicted climate change (Utzig 2002), could also be incorporated into future models.

Information from range evaluations: potential, current, and forecasted

Comparison of seasonal ranges within and among recovery planning areas enabled us to understand caribou habitat as a basis for population ecology (e.g., seasonal range limitations and excesses). This information about seasonal range area, in combination with an understanding of management threats, then provided us with a better understanding about potential risk to, and priority for, management of seasonal ranges. The BBNs allow for clear articulation of the threats to seasonal ranges; hence, the decisions to be made by recovery teams are focused, the analytical rationale for recovery options defendable, and the protocol for monitoring success and failures explicitly established.

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