Journal of Applied Ecology 2004
41, 238–251

A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales

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Summary

1. Visualizing the distribution of rare or threatened species is necessary for effective implementation of conservation initiatives. Generalized linear models and geographical information systems (GIS) are now powerful tools for conservation planning, but issues of data availability, scale and model extrapolation complicate some applications.

2. Mountain caribou are an endangered ecotype of woodland caribou *Rangifer tarandus caribou* that occurs across central and southern British Columbia, Canada. Currently, conservation professionals use coarse small-scale maps of important habitats to manage forest harvesting and human access across the northern extent of mountain caribou range. These maps were produced before the advent of readily available digital spatial information and are based on expert opinion and limited empirical data.

3. With the purpose of refining existing maps, we used survey results, radio-telemetry locations and GIS data to construct resource selection functions (RSF) that quantified the habitat affinities and predicted the relative probability of occurrence of mountain caribou at two spatial scales. At the scale of the patch, the most parsimonious RSF model consisted of covariates for vegetation and aptly predicted the occurrence of caribou across low- to mid-elevation habitats, but performed poorly across steep alpine terrain. At the landscape scale, a model containing Gaussian terms for elevation and slope was effective at predicting the broader distribution of caribou.

4. We produced a map consisting of the product of the relative probabilities of the patch and landscape RSF. The final map represented the relative probability of occurrence of caribou in vegetative patches weighted by the relative probability of occurrence across the larger study area. We found strong agreement between current definitions of important caribou habitats developed from expert opinion and RSF-based maps generated from empirical data.

5. *Synthesis and applications*. Both expert opinion and RSF-based approaches offer unique advantages for conservation mapping. Interpretability of results, documentation and repeatability of methods and data, estimates of precision and costs should all be considered when evaluating a technique. We argue that for some species and geographical locations, RSF is a superior technique, but expert opinion should play a role in model development and interpretation.

Key-words: expert opinion, GIS, logistic regression, *Rangifer tarandus*, resource selection function, woodland caribou

Journal of Applied Ecology (2004) **41**, 238–251

Introduction

Conservation planning for populations of rare or threatened species is an inherently spatial process (Abbitt, Scott & Wilcove 2000). Delineating the spatiotemporal extent of a threatened species' range is the first step in most conservation strategies. At finer scales, research, monitoring and planning efforts focus on identifying and protecting important habitat resources and reducing or mitigating limiting factors such as excessive sources of human-caused mortality (Loehle & Li 1996; Ceballos & Ehrlich 2002). The spatial representation of that information can serve as a powerful tool in the

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design and placement of ecological reserves, mitigating developments, directing remediation efforts and planning further research (Mladenoff, Sickley & Wydeven 1995; Flather, Knowles & Kendall 1998).

Various techniques are available to quantify and spatially represent species–environment relationships. Techniques range in sophistication from geographical information system (GIS) queries formulated from expert opinion to empirically derived statistical models (Guisan & Zimmerman 2000). The choice of technique is often guided by the availability of data, but consideration must also be given to project objectives and the ecology of the focal species (Austin 2002). Even when those criteria are considered, a number of issues, including inaccurate or unrepresentative data, poorly documented, complex or subjective methods, unclear interpretation of results and failures to evaluate the internal and external validity of predictions, can limit the usefulness of results and, in some cases, lead to incorrect conclusions when attempting to meet conservation objectives (Khagendra & Bossler 1992; Conroy & Noon 1996; Flather, Knowles & Kendall 1998).

Across central British Columbia, Canada, mountain caribou *Rangifer tarandus caribou* (Gmelin) are found at low densities (Heard & Vagt 1998). These animals inhabit mountain ranges during winter and primarily forage on arboreal lichens (*Bryoria* spp. and *Alectoria sarmentosa*), which are most abundant on old trees (Terry, McLellan & Watts 2000). During the past century, the distribution and abundance of mountain caribou has decreased considerably, leading to their being listed as endangered by provincial and federal conservation agencies. Proposed reasons for the decline and current threats include historical patterns of excessive hunting, loss of important habitats, reduction in connectivity of populations, increases in the distribution and abundance of predators, and displacement due to disturbance from industrial and recreation activities (Spalding 2000; Mountain Caribou Technical Advisory Team 2002).

Conservation of mountain caribou is facilitated through government-directed planning initiatives and legislation that recognizes and protects important habitats. Across the northern and central portion of mountain caribou range, these efforts are guided by small-scale maps that delineate areas as affording high, medium or low habitat values for caribou. The identification of boundaries and rankings was based on a number of sources including expert opinion, radio-telemetry and survey data, and continuous input from foresters and the public. However, data sources, map creation and evolution were poorly documented and habitat rankings are largely subjective.

We present a technique, resource selection functions (RSF), that combines GIS data and animal location information to generate spatially explicit predictive resource selection models. We used RSF to model and predict mountain caribou occurrence at two spatial scales: resources important within the vegetative patch; and topographic factors limiting the distribution of mountain caribou across multiple watersheds we term landscapes. We assumed patch occupancy was conditional on topography at the larger landscape scale and generated a single map predicting caribou occurrence across central British Columbia. Our principal objective was to develop and implement methods necessary to refine existing maps used by provincial land management agencies to identify and rank mountain caribou habitats. Secondarily, we evaluated and discussed the strengths and limitations of predictive RSF as a tool for conservation planning of rare and threatened species.

Methods

MODELLING APPROACH

The habitat requirements of large animals are often inferred through studies of use vs. availability of resources. These analyses require measurement of the use of resources relative to resource availability; a positive ratio suggests selection and a negative ratio suggests avoidance. When interpreting such results, it is often assumed that animals differentially select resources in direct accordance with the benefits that those resources afford. However, the link between fitness and selection is rarely tested.

All use vs. availability approaches for characterizing habitats are constrained by statistical and ecological limitations (Garshelis 2000). Of direct relevance to the mapping of species distribution is that most techniques do not allow the direct spatial extrapolation and presentation of results (Aebischer, Robertson & Kenward 1993). RSF, however, allow use of animal relocation data to estimate the strength of selection of resources and develop predictive equations that facilitate the extrapolation of those relationships across large areas. We used RSF to quantify the strength and precision of caribou–resource relationships and generate maps representative of the relative probability of occurrence of caribou across the study area.

Preliminary RSF models revealed that the distribution of mountain caribou was dictated by resource selection occurring at more than one spatial scale. At the finest scale of selection, we quantified the relationship between the observed distribution of individuals from one population of mountain caribou, the Yellowhead population (also referred to as the Hart Mountains and Northern Cariboo populations; Mountain Caribou Technical Advisory Team 2002), and vegetative resources that occur at the scale of patches. At a larger scale of selection, we modelled the distribution of observed mountain caribou (i.e. survey data) across the entire study area relative to topographic features that limit the suitability or availability of patches. For both scales of selection, we used the most parsimonious RSF models to generate maps of the relative probability of occurrence of caribou. As the final step in the mapping process, RSF models at the patch and landscape scales were combined to predict the total multiplicative effect of environmental variables from each

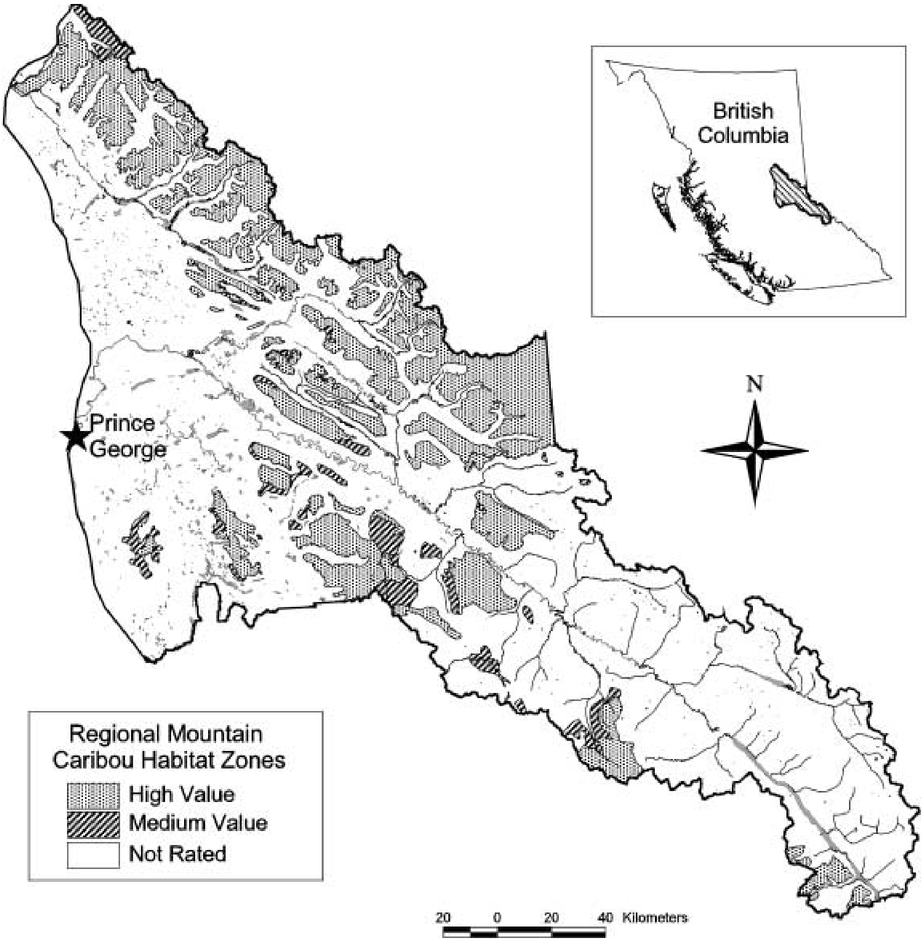


Fig. 1. Location and extent of study area across which resource selection functions were developed for mountain caribou of central British Columbia. Current rankings and boundaries for caribou management areas during winter are illustrated. Management areas were identified using expert opinion, census and radio-telemetry data.

scale of selection. We assumed a hierarchical selection strategy where selection of patches, as indicated by the Yellowhead caribou population, is consistent across the study area, but the availability of patches and resulting distribution of caribou is dictated by topographic factors. We assumed that predicted probability of occurrence was related to resource value and thus used that metric to rank habitats.

STUDY AREA

The study area encompassed 38 830 km^2 of forested and mountainous landscape centred at 121°2′ W 53°50′ N, 100 km east of Prince George, British Columbia, Canada (Fig. 1). Climate, topography and resulting vegetation associations vary considerably across that area (Meidinger & Pojar 1991). Elevation is most extreme in the south, where the Columbia and Rocky Mountain Ranges produce steep-walled valleys capped by open rocky alpine ecosystems and ice fields. Across the west-central portions of the study area the Rocky Mountain Trench opens to the relatively flat Interior Plateau, which is backed to the east by the northward continuation of the Rocky Mountains. The dominant low-elevation ecosystem occurs from valley bottoms to 1100–1300 m.a.s.l. and consists of coniferous forests of hybrid white spruce *Picea engelmannii* Parry ex Engelm. × *glauca* (Moench.) Voss, subalpine fir *Abies lasiocarpa* (Hook.) Nutt and, to a lesser extent, lodgepole pine *Pinus contorta* Dougl. ex Loud. on disturbed or dry sites. Wetlands are widely distributed and may include marshes, shrub fens and swamps with black *Picea mariana* (Mill.) Britton, Sterns & Pogg. and hybrid white spruce. A narrow wet belt is found at mid-elevations (400–1500 m.a.s.l.) across the central portion of the study area. Western redcedar *Thuja plicata* Donn ex D. Donn and western hemlock *Tsuga heterophylla* (Raf.) Sarg dominate mature forests, but white spruce, hybrid white spruce, Engelmann spruce *Picea engelmannii* Parry ex Engelm. and subalpine fir are common. The uppermost forested regions occur across steep rugged topography and are characterized by climax forests with canopies of Engelmann spruce and subalpine fir. Subalpine parkland is found at the forest–alpine ecotone and supports small stunted subalpine fir. Alpine tundra has the most severe climatic conditions, accommodating shrubs, herbs, bryophytes and lichens with sporadic trees occurring in krummholz form. Forest inventory data were inconsistent across a

Tree Farm Licence of approximately 1800 km^2; therefore, we did not generate RSF maps for that portion of the study area.

MODEL CONSTRUCTION: ANIMAL LOCATIONS AND ENVIRONMENTAL COVARIATES

Patch-scale selection

Across the study area, only the Yellowhead population had sufficient animal relocations to construct RSF at the patch scale. From 1988 to 1993, 29 female caribou were captured by net-gun fired from a helicopter and fitted with very-high frequency (VHF) radio-telemetry collars (Terry, McLellan & Watts 2000). Animals were relocated using fixed-wing aircraft at a median interval of 33 days during the winter, as defined by seasonal elevation changes in habitat occupancy (23 October–31 March; Stevenson *et al*. 1994). Given the relatively long relocation interval, we assumed independence between animal locations (Reynolds & Laundré 1990; Holzenbein & Marchinton 1992). The dependent variable for patch-scale RSF consisted of recorded animal locations and 10 random locations per animal location that served to quantify the availability of resources. We sampled each random location from within a circle that was centred on the preceding telemetry location, and had a radius equal to the distance between the preceding and next successive telemetry location. Independent predictor variables represented habitat and topographic features thought to influence selection of patches by mountain caribou (Table 1). Proxy variables for vegetation were represented by dominant canopy species taken from digital forest inventory data available at a scale of 1 : 20 000 (Ministry of Forests 1995). We used deviation coding to represent vegetation types as a single categorical variable. Deviation coding differs from indicator coding in that the effect of each variable in the set is contrasted against the overall mean effect of the independent variable, not an arbitrary reference class (Menard 1995). Stands of subalpine fir are rich in arboreal lichens, but range in productivity according to site conditions, stand age and topography (Goward 1998). We defined interaction terms of subalpine fir by stand age and forest site quality to incorporate lichen–stand relationships that may influence selection of habitats by caribou. We generated topographic variables of slope and elevation from a digital elevation model (DEM; cell size = 25 × 25 m). Linear and squared terms for elevation and slope were included as interaction terms with subalpine fir.

A number of statistical techniques are available to estimate RSF (Manly *et al*. 2002). We used conditional fixed-effects (CFE) logistic regression to model the selection affinities of caribou at the patch scale. The primary advantage of CFE logistic regression is that it allows representation of statistically fixed responses that may characterize clustered data (Pendergast *et al*. 1996; Hosmer & Lemeshow 2000). CFE regression differs from regular logistic regression in that data are grouped and the likelihood is calculated relative to each group (Collett 1991). In this case, we clustered the CFE regression on each animal location to control for changes in availability of resources across space and time.

Landscape-scale selection

At the scale of the landscape, we generated selection models that quantified the distribution of caribou relative to topographic factors that may limit the use of resources identified during the patch-scale RSF modelling. We assumed the distribution of mountain caribou conformed to a broad pattern of presence and absence and used survey and telemetry data to classify the study area accordingly. Between mid-February and late March of 2002 we surveyed areas of the study area

Table 1. Independent variables used to derive RSF models for mountain caribou found across central British Columbia during winter at patch (P) and landscape (L) scales. Variables were derived from British Columbia Ministry of Forests inventory data and a digital elevation model derived from Terrain Resource Inventory Mapping data

Variable	Scale	Description
Subalpine fir	P	Stands with > 80% subalpine fir
Mix subalpine fir	P	Mixed stands dominated by subalpine fir
Spruce	P	Mixed stands dominated by spruce
Mix pine	P	Mixed stands dominated by lodgepole pine
Cedar/hemlock	P	Mixed stands dominated by cedar or hemlock
Alpine forest	P	Low productivity, high elevation forest types typical of parkland or krummholz areas
Alpine	P	High elevation areas devoid of tree cover
Other	P	Vegetation types that occurred infrequently
Subalpine fir × stand age	P	Interaction term consisting of the age of subalpine fir stands
Subalpine fir × site product	P	Interaction term of site productivity and subalpine fir stands
Subalpine fir × elevation	P	Interaction term of elevation and subalpine fir stands
Subalpine fir × slope^2*	P	Interaction term of squared term for slope and subalpine fir stands
Elevation^2	L	Squared term for elevation above sea level
Slope^2	L	Squared term for slope (°)

*Where a squared term is included, the linear term is included as well.

identified as high-value caribou habitat (Fig. 1) located at or above the tree line. Where caribou tracks were noted, systematic searches were conducted until individual or groups of caribou were sited. Using a sample of marked animals, previous researchers reported that approximately 82% of mountain caribou are located during March surveys (Seip 1990).

We developed a protocol to delineate that portion of the study area that we assumed was occupied by caribou across the entire winter. We calculated the maximum-use radius for each individual or group of caribou sited during the 2002 survey as the median 24-h winter movement rate of caribou collared from the Yellowhead population multiplied by the winter period (169 m × 159 days = 26·87 km). For the range of the Yellowhead population, we used the distance between successive telemetry locations as the maximum-use radius. In total, the use radii for the survey and Yellowhead caribou delineated broad areas of the study area where we might expect presence or absence of mountain caribou. Within the presence or absence areas we used a stratified random sampling scheme to identify one geographical location per 5 km^2. Independent variables for the RSF included linear and non-linear terms for elevation and slope: topographic factors thought to dictate the use of vegetative patches and influence the distribution of caribou. In contrast to the patch selection models, we used conventional logistic regression to generate selection coefficients for caribou at the scale of the landscape.

MODEL SELECTION, FIT AND PREDICTIVE CAPACITY

We used Akaike's information criterion difference for small samples ($\mathrm{AIC_c}\,\Delta$), and Akaike weights (w) to evaluate and select the most parsimonious RSF model (i.e. the fewest variables to explain the greatest amount of variation). The model with the lowest $\mathrm{AIC_c}$ score is the most parsimonious and appropriate for explaining the observed data. Akaike weights provide a normalized comparative score for all specified models and are interpreted as the approximate probability that each model is the best model of the set of proposed models (Anderson, Burnham & Thompson 2000).

AIC provides evidence for selection of the most parsimonious model, but does not permit evaluation of discriminatory performance (Pearce & Ferrier 2000). We used k-fold cross-validation to evaluate predictive success of the most parsimonious patch and landscape models (Boyce *et al.* 2002). Using Huberty's (1994) training to testing ratio, the k-fold procedure was performed five times, withholding 20% of the data for each iteration. A Spearman rank correlation was used to assess the relationship between predicted probability of occurrence for withheld caribou locations and their frequency within 10 probability bins representing the range of predicted scores. A strongly predictive model will have a high correlation, indicating a greater number of locations in probability bins that approach 1.

For confirmatory purposes, we calculated log-likelihood χ^2 statistics for assessment of overall model fit. We used 95% confidence intervals to assess the strength of effect of each predictor covariate on the dependent variable. Poor power and inconclusive statistical inference is expected from covariates with confidence intervals that approach or overlap 0. We used the Pregibon (1981) $\Delta\beta$ and leverage (i.e. hat) statistics as well as the Hosmer & Lemeshow (2000) $\Delta\chi^2$ statistic to identify cases and clusters that had a large influence on the parameters of the model. We used tolerance scores to assess variables within each model for excessive collinearity (Menard 1995).

SPATIAL REPRESENTATION OF RSF MODELS

The logistic equation was convenient for calculating the coefficients for RSF, but scaled values from the log-linear model (equation 1) were used to estimate and project spatially a relative probability of use (w) for each 100 × 100-m cell across the study area:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_k x_k) \qquad \text{eqn 1}$$

We used a linear stretch to scale the predicted values (w) of the RSF between 0 and 1 (equation 2). The linear stretch is a common transformation for image enhancement and interpretation (Lillesand & Kiefer 1994) and takes the form:

$$\hat{w} = \left(\frac{w(x) - w_{\min}}{w_{\max} - w_{\min}}\right) \qquad \text{eqn 2}$$

where $w(x)$ is the product of equation 1 and $w_{\min}$ and $w_{\max}$ represent the smallest and largest RSF values, respectively. As scaled values ($\hat{w}$) approach 1, the spatial location is interpreted as having a relatively greater likelihood of being occupied or selected by caribou.

We generated maps of the relative probability of caribou occurrence for both patch- and landscape-scale models. The distribution of mountain caribou, however, is dictated by features of the environment (vegetation and topography) that operate at both scales of selection. The lack of telemetry data for all populations of caribou found across the study area prevented generation of a single RSF model. As a substitute for an inclusive model, we multiplied the relative probabilities from the maps of patch- and landscape-level occurrence. The landscape by patch map represents patch-scale selection, as demonstrated by caribou of the Yellowhead population, weighted by the relative probability of occurrence of mountain caribou across the study area.

For consistency with current provincial habitat maps and to ease interpretation, we rescaled the relative probabilities of occurrence for the patch by landscape map into broad classes of rare-, low-, moderate- and high-occurrence habitats. We used the mean relative probability of occurrence within ice fields as an ecological threshold value for rare occurrence of caribou. Ice-field

Table 2. Differences in Akaike's information criterion scores (AIC$_c$ Δ), AIC$_c$ weights (w) and number of model parameters (k) for candidate patch-scale winter RSF models developed for mountain caribou of the Yellowhead population of central British Columbia

Model	k	AIC$_c$ Δ	AIC$_c$ w
Veg {SA fir, mix SA fir, spruce, mix pine, ced/hemlock, alpine forest, alpine, other}	8	1·4	0·211
Veg + (SA fir × stand age)	9	3·5	0·074
Veg + (SA fir × site prod)	9	2·3	0·133
Veg + (SA fir × elev)	9	0·0	0·431
Veg + (SA fir × slope) + (SA fir × slope^2)	11	4·5	0·046
Veg + (SA fir × age) + (SA fir × site prod)	10	4·4	0·047
Veg + (SA fir × elev) + (SA fir × slope) + (SA fir × slope^2)	12	4·6	0·043
Veg + (SA fir × age) + (SA fir × site prod) + (SA fir × elev) + (SA fir × slope) + (SA fir × slope^2)	14	6·8	0·014

Veg, vegetation; SA, subalpine; ced, cedar; prod, productivity; elev, elevation.

boundaries were taken from 1 : 250 000 National Topographic Series digital planimetric data. We then used 33rd percentiles to stratify the remaining pixels of the study area as low-, medium- and high-occurrence habitats (Erickson, McDonald & Skinner 1998). We used a modal filter and a window of 500 × 500 m to generate contiguous patches of similar occurrence value more appropriate for large-scale conservation planning. The size of habitat patches can limit the scope of conservation initiatives (e.g. reserve design) and indicate the degree of fragmentation; therefore, we calculated the distribution of patch sizes for each of the occurrence classes.

Table 3. Coefficients and 95% confidence intervals of the most parsimonious RSF model for selection of vegetative patches during winter by mountain caribou of the Yellowhead population of central British Columbia

Variable	β coefficient	95% confidence interval
Subalpine fir	0·553	0·304, 0·803
Mix subalpine fir	–0·098	–0·398, 0·202
Spruce	–1·429	–1·788, –1·070
Mix pine	–0·858	–1·554, –0·162
Cedar/hemlock	–0·413	–1·136, 0·310
Alpine forest	1·543	1·243, 1·843
Alpine	1·104	0·820, 1·389
Other	–0·403	–0·820, 0·015

Results

PATCH-SCALE SELECTION

We used 429 locations from caribou of the Yellowhead population to construct eight ecologically plausible RSF models representative of patch-scale selection by mountain caribou (Table 2). The model consisting of variables for vegetation type and an interaction term of subalpine fir by elevation was the most parsimonious. The interaction term was highly collinear (tolerance = 0·023); therefore we chose the slightly less complex vegetation model as the final predictive RSF (Table 2). This model was statistically significant ($\chi^2(7) = 254{\cdot}94$, $P < 0{\cdot}001$) and explained 12% of the total deviance. A mean Spearman rank correlation of 0·902 ($P < 0{\cdot}001$) across five cross-validation samples indicated that the vegetation model had good predictive capacity. During winter, caribou of the Yellowhead population selected patches of alpine, alpine forest and subalpine fir and avoided patches of spruce and mixed pine (Table 3). Confidence intervals for those variables did not overlap 0, suggesting good precision and strong inference.

We had insufficient data to assess quantitatively prediction success of the patch-scale RSF to the larger study area. A qualitative review of the RSF map indicated that the vegetation model was a poor predictor of caribou habitat across steep high terrain found beyond the range of the Yellowhead population. Much of the southern portion of the study area is alpine; thus the model suggested a high relative probability of occurrence for caribou (Fig. 2c). In many areas, however, alpine consists of steep rocky terrain or ice fields and differs greatly in topography and ecology from alpine habitats used by Yellowhead caribou.

LANDSCAPE-SCALE SELECTION

We spent 40 h of flight time surveying high-elevation habitats for caribou. We sighted 135 discrete individuals, groups or confirmed tracks of caribou for a total of 633 animals. Randomly sampling the areas we assumed were occupied and unoccupied by caribou resulted in 4762 and 3085 locations, respectively, for the logistic regression analyses. AIC$_c$ weights provided convincing evidence that the distribution of mountain caribou was best modelled using quadratic terms for elevation and slope (Table 4). The most parsimonious model suggested that at large spatial scales caribou typically occupied vegetative patches at mid-elevations on moderate to steep slopes (Figs 2d and 3). Large sample sizes resulted in relatively precise estimates for these coefficients (Table 5). The landscape-scale RSF was statistically significant ($\chi^2(4) = 646{\cdot}31$, $P < 0{\cdot}001$), explained 6·2% of the total deviance and had excellent predictive performance ($\bar{X}\, r_s = 0{\cdot}995$).

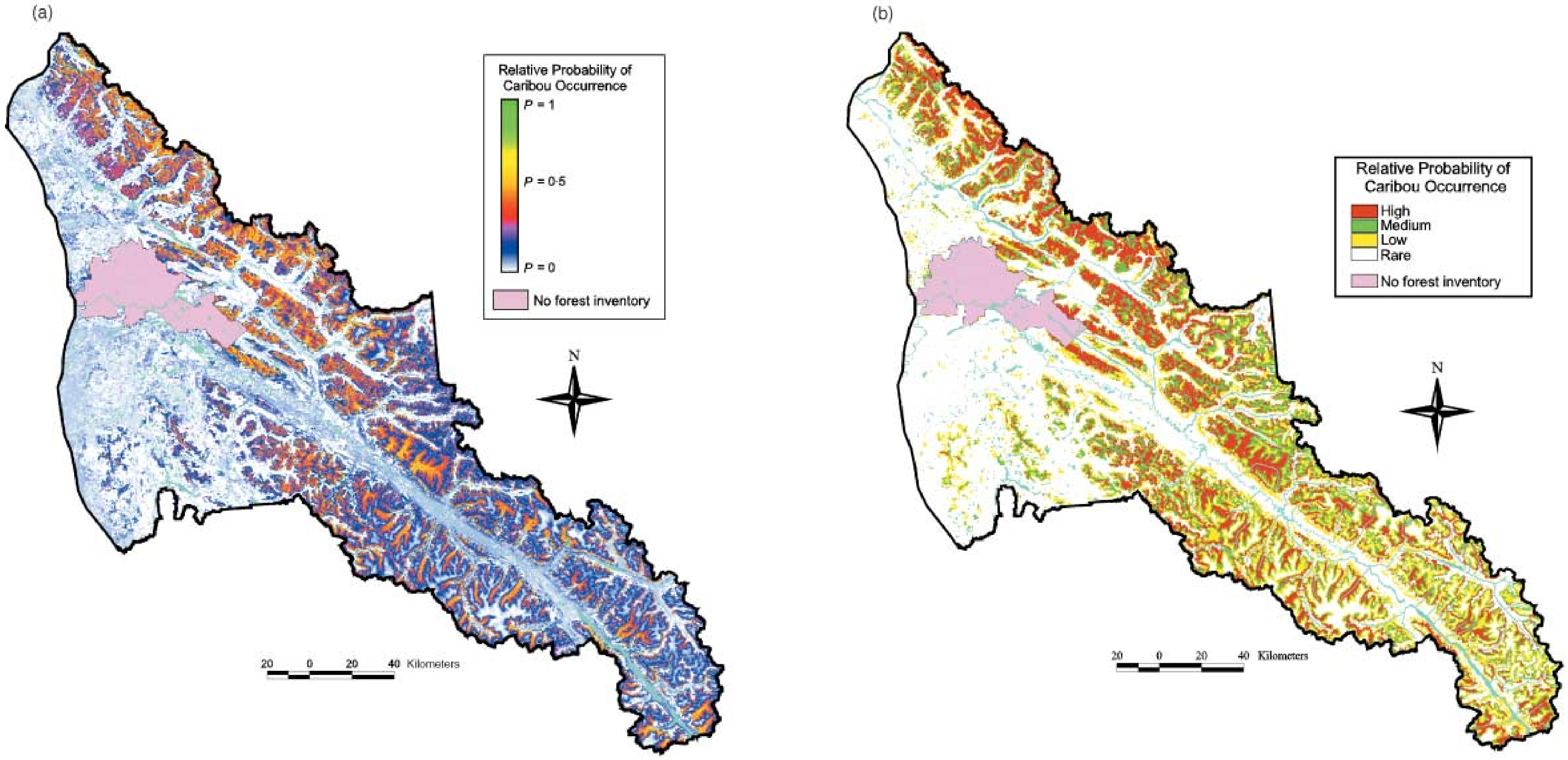
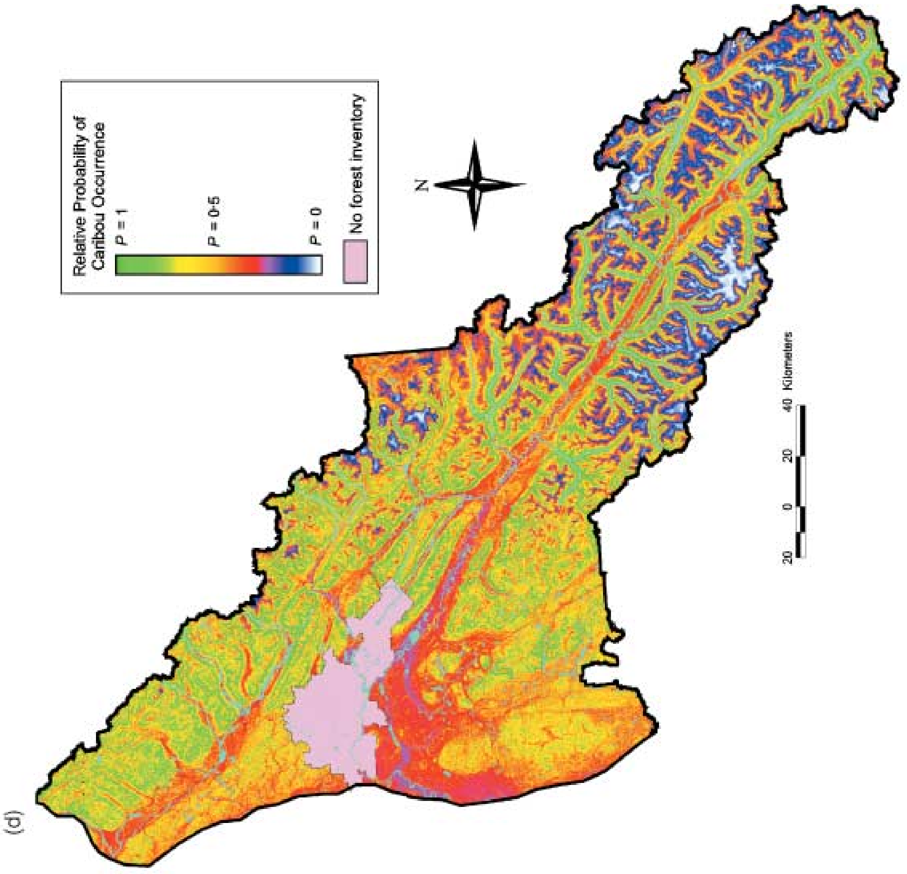


Fig. 2. Predicted (a) and categorized (b) probability of occurrence of mountain caribou across central British Columbia during winter. Maps represent the product of patch- (c) and landscape-scale resource selection functions (d).



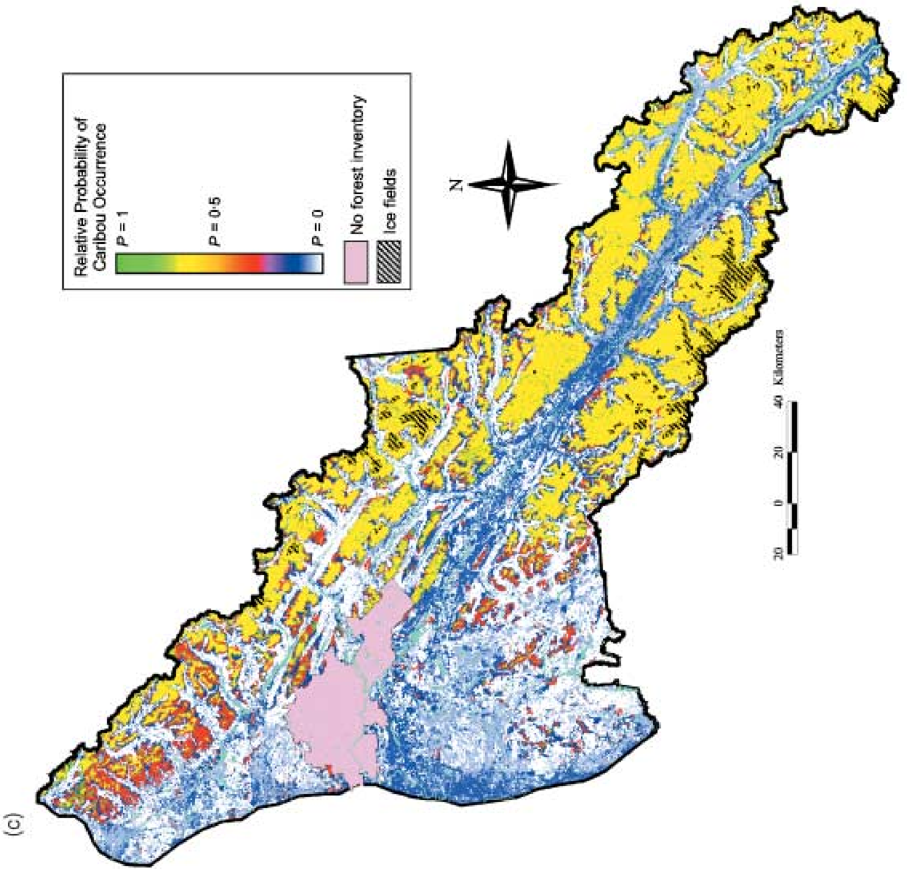


Fig. 2. *Continued*

Table 4. Differences in Akaike's information criterion scores (AIC$_c$ Δ), AIC$_c$ weights (w) and number of model parameters (k) for candidate landscape-scale RSF models developed for mountain caribou of central British Columbia

Model	k	AIC$_c$ Δ	AIC$_c$ w
Elevation (km)	3	491·6	< 0·001
Elevation^2*	4	73·4	< 0·001
Slope	3	638·4	< 0·001
Slope^2	4	561·7	< 0·001
Elevation + slope	4	367·1	< 0·001
Elevation^2 + slope^2	6	0·0	1·000

*Where a squared term is included, the linear term is included as well.

Table 5. Coefficients and 95% confidence intervals of the most parsimonious RSF models for selection of landscape features by mountain caribou of central British Columbia during winter

Variable	β coefficient	95% confidence interval
Elevation (km)	3·860	3·095, 4·624
Elevation^2*	−1·646	−1·912, −1·381
Slope	0·048	0·035, 0·062
Slope^2	−0·0007	−0·001, −0·0004

*Where a squared term is included, the linear term is included as well.

LANDSCAPE- × PATCH-SCALE SELECTION

The final product map, consisting of patch- and landscape-scale selection, suggested that during winter mountain caribou are most likely to be found in patches of alpine forest or alpine tundra distributed at mid-elevations on moderate slopes (Fig. 2a). Conditioning patch selection on the assumed distribution of caribou moderated the probability of occurrence across high, steep alpine terrain where we would expect to find few caribou. The mean relative probability of occurrence for caribou across areas identified as ice fields was 0·069 (SD = 0·067). Using that value as a threshold of occurrence, 22 610 km^2

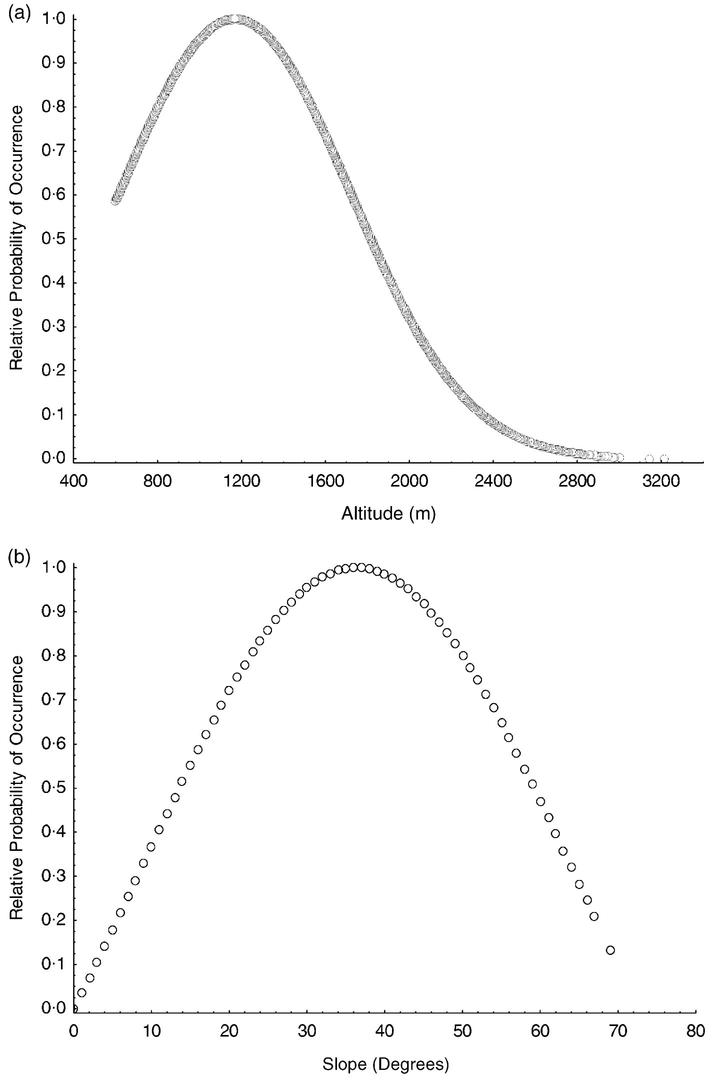


Fig. 3. Relationship between relative probability of occurrence of mountain caribou and elevation (a) and slope (b). Coefficients were taken from the most parsimonious RSF model describing distribution of caribou across central British Columbia (Table 5). The alternate variable was held constant at its mean.

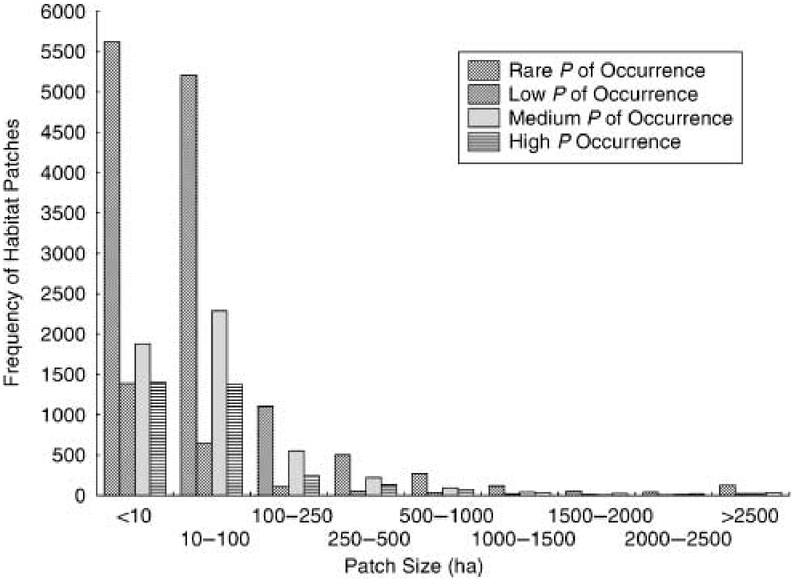


Fig. 4. Size distribution of patches of habitat across central British Columbia identified using resource selection functions (Fig. 2b) and classified according to the relative probability of occurrence of mountain caribou.

of the study area was classified as rare, and 4943, 5516 and 5767 km^2 were classified as having a low, medium and high relative probability of occurrence for caribou, respectively (Fig. 2B). After applying a modal filter, the majority of habitat patches of the latter three classes were less than 250 ha in size (Fig. 4). The mean patch sizes for the rare, low, medium and high habitat classes were 993 (SD = 40 634), 97 (SD = 377), 165 (SD = 1036) and 265 ha (SD = 1604), respectively. A qualitative comparison of the final map and that currently used by provincial land-use agencies suggested strong concordance in habitat classification across portions of the study area (Figs 1 and 2b).

Discussion

In general, the presented RSF coefficients agree with previous studies of habitat selection by the Yellowhead and other populations of mountain caribou found across British Columbia. During early winter, caribou of the Yellowhead population selected for mid-elevation forests on slopes of 16–30% that were dominated by subalpine fir (Terry, McLellan & Watts 2000). Finer-scale site investigations within those stands revealed that caribou selected foraging paths with more accessible biomass of the arboreal lichens *Alectoria sarmentosa* and *Bryoria* spp. During late winter, caribou selected higher elevation subalpine parkland habitats. Those authors used the same data as this study, but different analyses, scales of selection and habitat delineations. Pooling winter seasons, we found that Yellowhead caribou strongly selected for alpine forest, alpine and stands of subalpine fir. At the scale of multiple landscapes, mountain caribou demonstrated the highest relative probability of occurrence at elevations of approximately 1100 m and slopes of 35°. Those are steeper and lower areas than reported by Terry, McLellan & Watts (2000). The discrepancy results from our multivariate model and through sampling a wider variety of topography.

This is not the first application of RSF to issues of wildlife conservation. Among numerous examples, Apps *et al.* (2001) used logistic regression to model habitat selection of mountain caribou found across south-eastern British Columbia. Results were used to illuminate habitat selection patterns and generate maps of predicted caribou distribution. Both products allowed forest planners and wildlife biologists to designate important caribou habitats within regional land-use plans. Mladenoff, Sickley & Wydeven (1995) used logistic regression to estimate the amount and spatial distribution of potential habitat available for wolf *Canis lupus* L. recolonization across northern Minnesota, Wisconsin and upper Michigan, USA. Further observations confirmed that those models performed well at predicting the distribution of recolonizing wolf packs (Mladenoff, Sickley & Wydeven 1999). Mace *et al.* (1999) used RSF to model the cumulative effects of human activities on grizzly bear *Ursus arctos* L. habitat. RSF have a variety of other applications, including risk analysis for land-use change, habitat-based population viability analyses and population estimates (Boyce, Meyer & Irwin 1994; Boyce & McDonald 1999; McDonald & McDonald 2002).

Although the objectives were similar, the modelling approach employed here differed from past efforts. Conventional logistic regression has served as the statistical framework for the majority of previously published RSF studies. For the patch-scale analyses we used conditional fixed-effects logistic regression. The technique is widely employed in other fields of study, but only now is beginning to appear in the ecological literature (McCracken, Manly & Vander-Heyden 1998; Compton, Rhymer & McCollough 2002). CFE regression allowed us to control for variation in temporal and spatial factors between clusters defined by animal locations. The

CFE approach also permits a more precise estimate of availability, eliminating issues of selection, parameterization and validity of home-range analyses and relaxes the assumption of equal accessibility of all habitats across large home range areas (Arthur *et al.* 1996; Alldredge, Thomas & McDonald 1998; Arthur & Schwartz 1999).

We also presented an approach that relates habitat selection and animal distribution across spatial scales. Typically, researchers define scale according to the spatial extent of available habitats (Bradshaw *et al.* 1995; Poole, Heard & Mowat 2000). Although multiscale studies can reveal changes in patterns of selection it is difficult to determine the most appropriate scale for management or the most ecologically relevant scale to the species of interest (Apps *et al.* 2001). We defined two hierarchically related scales of selection that we assumed influenced the distribution of mountain caribou across the study area. Using logic founded in probability theory and simple image arithmetic we then calculated the joint relative probability of a caribou selecting patch A and topographic feature B [$P(\text{A and B}) = P(\text{A}) \times P(\text{B})$]. However, the RSF models do not represent independent events and we calculated scaled relative probabilities. It is more appropriate to consider the final map as the relative probability of occurrence of caribou in vegetative patches weighted by the relative probability of occurrence across the larger study area as opposed to a true joint probability.

Variation in spatial and temporal scales can be measurement or phenomenon based. Therefore, poor definitions of scale and associated concepts can lead to confusion when interpreting the objectives and results of multiscale studies (Dungan *et al.* 2002). For mountain caribou, resource selection probably occurs over a range of scales, from the feeding site to the annual range of each population to the wider distribution of the ecotype. RSF coefficients describing selection may change in a non-linear fashion according to the scale of measurement or the behavioural phenomenon of interest (Johnson *et al.* 2002). Considering the objectives of this study and the added complexity of interpreting results from modelling efforts at several arbitrary spatial scales, we chose to constrain observations and generalize inferences to two spatial scales. When interpreting the results, it is sufficient to consider selection functions as representative of the topographic conditions limiting the distribution of caribou across multiple watersheds and the behaviours caribou would demonstrate when moving within and between patches over a time span of approximately 7–33 days. We assumed that covariates in candidate models for the patch- and landscape-scale RSF represented resources or ecological factors important to caribou at those scales.

The primary objective of this project was the prediction of caribou distribution across the larger study area. Applying individual RSF models to the known range of a sample population is ecologically and statistically appropriate. Using those models to predict the distribution of caribou beyond the range of the populations from which samples were drawn can be problematic. It was imperative to develop models using a procedure that maintained the generalities of caribou–habitat relationships and that did not overfit sample data to the final predictive model (Olden & Jackson 2000). Automated statistical algorithms such as forward or backward stepwise procedures are commonly used to test a large number of combinations of independent variables iteratively and identify the model with the best statistical fit. These techniques lead to incorrect statistical inference and exploit random variations in sample data that result in models that fit well but generalize poorly to the larger population (Hurvich & Tsai 1990; Derksen & Keselman 1992; Menard 1995). We a priori defined a small set of ecologically plausible models and used AIC to select the most appropriate model from that set. When properly used, AIC guards against overfitting and provides a measure of best inference, given the data and the set of proposed models, which is not reliant on arbitrary levels of significance (Anderson, Burnham & Thomas 2000).

To maintain the external validity of the patch-scale model we applied vegetation covariates that had uniform definitions across the study area. Such a strategy probably sacrificed some capacity to model resource selection within the range of the Yellowhead population, but allowed us to apply those models to the wider distribution of mountain caribou. Extrapolation, however, was hindered by forest inventory types that were classified too coarsely to represent the variation in selection responses we might expect from mountain caribou across the larger study area. Most notably, the ecological characteristic of the alpine class varied considerably but was represented by a single code within the forest inventory (Johnson *et al.* 2003). This led to poor prediction of caribou occupancy across the steep and high portions of the study area, which was rectified using covariates for topography at the broader landscape scale. We had insufficient data to assess the predictive power of the patch-scale model beyond the range of the Yellowhead population. Therefore, caution should be exercised when interpreting and applying results.

Although the RSF models had good predictive power within the range of data used for construction, we did not parameterize all factors dictating mountain caribou distribution. Inclusion of only habitat covariates resulted in simplistic models and maps that represent the potential not the current distribution of mountain caribou. Predators, disturbance from industrial or recreation activities, size and connectivity of habitat patches, and historical declines in distribution and abundance, probably resulted in exaggerated estimates of occurrence. From a conservation perspective, however, we were interested in identifying potential habitats that may support caribou following the identification, understanding and remediation of limiting factors.

By definition RSF are proportional to the probability of use of a resource unit and allow prediction of relative probabilities of occurrence (Manly *et al.* 2002). The metric of interest for conservation and management is the relative probability of occurrence that does not necessarily correlate with habitat quality (VanHorne 1983; Hobbs & Hanley 1990). Where source–sink dynamics are present, RSF models may predict a high probability of occurrence, but those locations may negatively affect population productivity (Mattson & Merrill 2002). Thoughtless application and poor interpretation of RSF could result in the incorrect designation of habitat importance and ineffective or perhaps harmful conservation initiatives. We assumed that mountain caribou used resources out of proportion to their availability in direct accordance with survival and reproductive benefits. As with most long-lived low productivity species, the data necessary to evaluate natality and survival are lacking, making it difficult to test explicitly that assumption or build models that relate habitat to population processes (Johnson *et al*. 2005). In the case of mountain caribou, land-use managers and habitat biologists should consider the spatial adjacency of limiting factors such as human access and the distribution of predators when using relative probabilities of occurrence to assess habitat quality.

These results must also be considered in a temporal context. Vegetation communities are dynamic, leading to changes in habitat availability and the strength of selection for particular resources by caribou. Unlike other populations of mountain caribou, we saw no effect of stand age on selection (Apps *et al*. 2001). We attribute that result to the relatively homogeneous distribution of old subalpine fir stands across the range of the Yellowhead population. Increased natural or human disturbance would lead to younger stands with fewer arboreal lichens and presumably infrequent use of those stands by caribou during winter. Stand age may become an important predictor of occurrence following widespread disturbance.

We do not have a measure of truth by which to compare the absolute accuracy of the RSF or expert opinion maps, but it is clear that both approaches have distinct advantages and limitations. When solicited informally, the opinions of experts can be collected inexpensively and the GIS analyses necessary to represent that information spatially are relatively simple. In some cases, however, expert knowledge may be unreliable, variable or unavailable. Furthermore, it can be difficult to document and present the dialogue necessary to generate consensus on criteria used to designate habitat values. Rigorous methods are available for soliciting expert opinion, but they come with costs in time and financial resources (Alder & Ziglio 1996; Dixon 1997).

The greatest advantage of an RSF approach for conservation mapping is that methods, data and results are easily documented and relatively transparent. Geographic and temporal range of animal data can be evaluated for bias, precision of coefficient estimates are presented, and numerous methods are available to assess model fit and predictive capacity (Pearce & Ferrier 2000; Manel, Williams & Ormerod 2001; Boyce *et al*. 2002). Although caribou locations were available for these retrospective analyses, other geographical areas or species may require the initiation of expensive mark–relocation studies, which are typically conducted over periods of 2–4 years. RSF analyses also have limiting assumptions that may be restrictive for certain study designs, species or data sets (Alldredge, Thomas & McDonald 1998). Quantitative habitat use vs. availability approaches also have been criticized as being time, place and definition specific, with few links to mechanistic processes (Hobbs & Hanley 1990; Garshelis 2000). Most problematic to applications of conservation and management is the underlying assumption that probability of occurrence is related to habitat quality.

Ultimately, researchers should strive to incorporate expert opinion within RSF. Selection of appropriate scales of analysis and definition of ecologically plausible RSF models is best guided by current understanding of the study species. Past research and knowledge is also crucial for interpreting RSF models, which are often developed using GIS data that serve as proxies for the mechanistic responses of animals to resources or disturbance factors that occur at a range of spatial scales.

APPLICATION OF RSF MODELS TO MOUNTAIN CARIBOU CONSERVATION

The results of this work have a number of direct and indirect applications to the management of mountain caribou populations found across central British Columbia, but are not without limitations. RSF is a flexible and powerful tool for modelling habitat use, yet resulting coefficients describe only behaviours represented by the sample of radio-telemetry locations. Biases associated with collaring caribou or collecting location data will be reflected in coefficients describing the strength of selection for or avoidance of particular habitat types. Furthermore, reliability of predictive maps is dictated by the quality of the forest inventory data used to build and extrapolate RSF models across the study area.

Given those limitations, predictive maps, when applied appropriately, may serve to identify contiguous areas across central British Columbia with a high potential of being good caribou habitat. Identification of such areas will assist with large-scale land-use planning, forestry management and recovery efforts for threatened populations. However, the results of this work are likely to be inappropriate for stand-level habitat management. The resolution of the spatial data and the suspected response of caribou to finer-scale habitat attributes require that site inspections or more refined modelling efforts guide forest harvest prescriptions. RSF coefficients and predictive maps also can serve to generate hypothesis for future research and direct population inventories across areas where relatively little is known of the distribution of caribou.

We recommend that these models and maps, and results from similar applications, serve as a starting point within an adaptive framework for conservation. As demonstrated by Mladenoff, Sickley & Wydeven (1999), observations from further research and inventory efforts can be used in an iterative fashion to assess and update RSF and resulting maps. Such approaches to interpretation, application and ultimately revision are essential when generating out-of-sample predictions across large diverse geographical areas.

Acknowledgements

This work was supported by the Natural Sciences and Engineering Research Council of Canada and the British Columbia Crown Land Use Planning Enhancement Fund. We are grateful to E. Terry and G. Watts for collecting and allowing us to work with their hard-won caribou locations. D. Heard, C. Ritchie, G. Watts and H. Wittmer provided valuable comments on study design and earlier drafts of this work. We thank J. Pollard, S. Emmons and D. Janzen for assistance with compiling and preparing the spatial data.

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Received 14 March 2003; final copy received 12 December 2003