An evaluation of mapped species distribution models used for conservation planning

CHRIS J. JOHNSON* AND MICHAEL P. GILLINGHAM
Ecosystem Science and Management Program, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia, V2N 4Z9, Canada
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SUMMARY
The widespread use of spatial planning tools in conjunction with increases in the availability of geographic information systems and associated data has led to the rapid growth in the exploration and application of species distribution models. Conservation professionals can choose from a considerable number of modelling techniques, but there has been relatively little evaluation of predictive performance, data requirements, or type of inference of these models. Empirical data for woodland caribou Rangifer tarandus caribou was used to examine four species distribution models, namely a qualitative habitat suitability index and quantitative resource selection function, Mahalanobis distance and ecological niche models. Models for three sets of independent variables were developed and then a temporally independent set of caribou locations evaluated predictive performance. The similarity of species distribution maps among the four modelling approaches was also quantified. All of the quantitative species distribution models were good predictors of the validation data set, but the spatial distribution of mapped habitats differed considerably among models. These results suggest that choice of model and variable set could influence the identification of areas for conservation emphasis. Model choice may be limited by the type of species locations or desired inference. Conservation professionals should choose a model and variable set based on the question, the ecology of the species and the availability of requisite data.

Keywords: caribou, GARP, habitat suitability index, Mahalanobis distance, resource selection function

INTRODUCTION
Species distribution models are a powerful tool for achieving conservation objectives (Carroll et al. 2001; Raxworthy et al. 2003; Johnson et al. 2004a). When linked to geographic information systems (GIS), predictive models illustrate the distribution and infer the suitability and capability of habitats (Rivieccio et al. 2003; Gibson et al. 2004). Maps of habitats are an effective communication medium and serve to highlight areas where conservation professionals might focus efforts to mitigate human development and disturbance, or guide reserve placement, habitat remediation and species reintroduction (Abbitt et al. 2000; Treves et al. 2004). Some models can also serve as devices to explore ecological relationships. Although it is impossible to infer causation from correlation, strength of prediction, magnitude and sign of coefficients, and model selection uncertainty can reveal functional responses to components of the environment (Austin 2002). Examples of such relationships include selection of vegetation types, avoidance of habitats disturbed by humans, or responses to other risk factors such as predation (Compton et al. 2002; Johnson et al. 2002; Zabel et al. 2003).

The propagation of broad-scale spatial data in conjunction with the increased availability of GIS, statistical software and computing power have improved the ability and choices available, to model and map complex species-environment relationships (Rushton et al. 2004). Although increased choice enables us to tailor a model to a particular species or research question, selection of the most appropriate modelling technique can be daunting (Austin 2002). Following the selection of a technique, there are still numerous decisions about data sampling, model formulation, scales of analysis and validation. Review articles and texts (for example Buckland & Elston 1993; Guisan & Zimmermann 2000; Manly et al. 2002) provide some guidance as to the scope, strength and limitations of individual modelling approaches, but often differences can be subtle and relative performance is rarely compared (but see Loiselle et al. 2003; Brotons et al. 2004). Furthermore, even given advances in quantitative techniques, there is still a role for expert-based models for circumstances in which empirical data is absent or difficult to collect (Clevenger et al. 2002; Johnson & Gillingham 2004).

Recognizing the dearth of studies critically evaluating model performance, we performed a relative comparison of four species distribution models that can be applied in a GIS to rank and map habitats. We chose contemporary models commonly cited in the conservation and ecology literature that represent the range of data requirements. We acknowledge that conservation professionals may choose from a larger number of species distribution models (Guisan & Zimmermann 2000). When considering the range of options inherent to each modelling technique that choice set expands...
caribou are sensitive to habitat alteration and loss and are listed as a threatened species across much of Canada (Johnson et al. 2004b). Thus, this species is a good candidate for distribution models that can help direct conservation efforts. Across models, we measured differences in the distribution of ranked habitats, as well as the ability of each model to predict the occurrence of habitats that correlated with a set of independent caribou locations. We discuss the type and strength of inference inherent to each model and provide general recommendations for selection of the most appropriate model.

METHODS

Study animals

We developed species distribution models for a population of woodland caribou known as the Wolverine Herd (Heard & Vagt 1998). As part of another study, 16 individual female caribou were collared and monitored between March 1996 and March 1999 (Johnson et al. 2002). Caribou were located with differentially correctable global positioning system (GPS) collars (GPS 1000, Lotek Engineering, Newmarket, Ontario, Canada) scheduled to record one location every third or fourth hour.

We assessed model predictions with a temporally independent validation set of caribou locations. Between February 1991 and March 1996, 33 caribou from the Herd were captured and fitted with VHF radio-collars (Model LMRT-4, Lotek Engineering, Newmarket, Ontario, Canada). From April 1991 to March 1997, biologists used a Cessna 182 fixed-wing aircraft to locate collared caribou (Terry & Wood 1999; Wood & Terry 1999).

Study area

The Wolverine Herd is found approximately 250 km northwest of Prince George (British Columbia, Canada). The caribou’s altitudinal range varies from valley bottoms at c. 900 m to alpine summits at c. 2050 m and is characterized by numerous vegetation associations. Forest types below 1100 m altitude are dominated by lodgepole pine (Pinus contorta), white spruce (Picea glauca), hybrid white spruce (P. glauca × P. engelmannii) and subalpine fir (Abies lasiocarpa). Between 1100 and 1600 m altitude, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (P. engelmannii) and subalpine fir. Areas at altitudes > 1600 m are alpine tundra, distinguished by gentle to steep windswept slopes vegetated by shrubs, herbs, bryophytes and lichens, with occasional trees in krummholz form (Meidinger & Pojar 1991).

Modelling approaches

We selected species distribution models for comparison according to three criteria, namely contemporary and broad
prevalence in the literature, potential for application within a GIS to generate species distribution maps, and representation of the data types necessary to parameterize models. Models chosen for the comparison were dependent on both qualitative and quantitative data. We evaluated a HSI constructed from expert opinion, a logistic regression-based resource-selection function dependent on use and availability data, and Mahalanobis distance and ecological niche models that required presence-only data.

Habitat suitability index

A HSI was developed to rank and map seasonal woodland caribou habitats across the study area (Madrone Consultants 1999a). Information sources of caribou-habitat relationships included published literature, agency reports and expert opinion. Rankings were developed for mapped polygons that represented unique ecological associations (Resources Inventory Committee 1998a; Madrone Consultants 1999b). Some of the constituent attributes of those ecological associations served as variables in the HSI. Biologists ranked the suitability of polygons as foraging habitat according to slope, aspect, elevation, stand age, site disturbance history, soil, terrain type, vegetation composition of the understorey and the biomass of terrestrial lichen. Rankings conformed to a six-class scale (high, moderately high, moderate, low, very low, nil) that was bench-marked with the best woodland caribou habitat in British Columbia (Resources Inventory Committee 1999b).

Resource selection function

We used conditional fixed-effects logistic regression to estimate coefficients for the RSF model:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n)$$

where $\beta_1 \ldots \beta_n$ are coefficients generated from a logistic regression model and $w(x)$ represents the relative probability of species occurrence. Compared to conventional logistic regression, the fixed-effects approach performs a paired analysis. Thus, model coefficients were generated with matched use and available points allowing the technique to statistically control for temporal and spatial variation in resource availability (Pendergast et al. 1996; Hosmer & Lemeshow 2000). We paired each caribou location with five randomly selected sites that represented the availability of resource variables. We sampled these comparison sites from within a circle that was centred on the animal’s preceding location, and had a radius equal to the 95th percentile movement distance for that particular relocation interval (Arthur et al. 1996).

Mahalanobis distance

We calculated the Mahalanobis distance at each cell in our GIS using the formula:

$$D^2 = (x - m)^T C^{-1} (x - m)$$

where $D^2$ is the Mahalanobis distance, $x$ is a vector of habitat characteristics (i.e. variables) associated with each cell, $m$ is a mean vector of habitat characteristics recorded at cells of known animal or plant locations ($T$ indicates that the vector should be transposed), and $C^{-1}$ is the covariance matrix for the same vector of habitat characteristics. The distance statistic is simply the difference between mean habitat characteristics at cells where animals or plants were observed and not observed scaled by the variance and covariance of the descriptive variables.

When habitat variables are normally distributed, the Mahalanobis distance statistic follows a $\chi^2$ distribution and can be converted to probability values. In most cases, however, the assumption of normality is difficult to satisfy and the distance values are considered dimensionless (Knick & Rotenberry 1998). We assumed that monitored caribou selected the highest quality habitats. Therefore, increases in the distance statistic were interpreted as habitats of a progressively lower quality.

We used the ArcView (ESRI [Environmental Systems Research Institute] 2000) extension Mahalanobis Distances (http://www.jennessent.com/arcview/mahalanobis.htm) to calculate the mean vector and covariance matrix for habitat features recorded at caribou locations. Then, we used the raster GIS IDRISI (Clark Labs 2002) to perform the necessary matrix algebra and calculate the Mahalanobis distance surface of habitat quality for caribou.

Ecological niche

We adopted the Genetic Algorithm for Rule-Set Prediction (GARP) computational approach for modelling the fundamental niche of woodland caribou (for example Raxworthy et al. 2003; http://www.lifemapper.org/desktopgarp/). For our vegetation and caribou location data we allowed GARP to employ an iterative machine-learning process to develop rule sets that best identified the distribution of monitored caribou. We adopted the protocol of Anderson et al. (2003) when fitting unique GARP models to the caribou location data.

Model variables

Analysis of the HSI was retrospective; therefore, this defined model definition, area and time of year for the three quantitative approaches. For consistency, we adopted the ecosystem maps used for the HSI. Maps portrayed large-scale (1:20 000–1:50 000) ecological units developed within a hierarchical framework of climate, topography, vegetation and soil attributes (Resources Inventory Committee 1998a). Using past caribou research, the large number of ecological associations were combined into 11 land-cover types (Madrone Consultants 1999b; Johnson et al. 2003; Table 1). To provide variables in a metric suitable for calculation of the Mahalanobis distance, we quantified land-cover occurrence as the density of each type and the distance of each cell across the study area from each type. Patch density represented the variation in the availability of each land-cover type across the
study area at spatial scales larger than the patch. We used a moving window algorithm in the GIS to sum and calculate the density of pixels of each land-cover type. The size of the moving window was scale-dependent and varied according to the distribution and clumping of the patches (i.e. GIS pixels) of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type. We used the pattern analysis technique nine-term local quadrat variance to identify the scale of the land-cover type.

We parameterized the quantitative models using caribou locations that corresponded with the seasonal breaks defined for the HSI. Caribou of the Wolverine Herd are most abundant in the study area during the early winter (1 November to 30 December) and occur only infrequently during other periods (Madrone Consultants 1999a). Therefore, our models were developed and assessed only for the early winter season.

### Model construction and mapping

Species distribution maps were generated at a cell resolution of \(25 \times 25\) m. For consistency with the HSI maps, we adopted a six class ranking scheme, where we assumed that class 1 habitats were of the highest and class 6 were of the lowest quality. Resource selection function and Mahalanobis distance models produce continuous predictions. We used 16.7% quantiles to break the range of values into six classes that we assumed correlated with increasing quality of habitats for caribou (for example Knick & Dyer 1997; Erickson et al. 1998; Carroll et al. 2001; Johnson et al. 2004c). The genetic algorithm employed by GARP has a stochastic search method, potentially identifying different combinations of rules and environmental layers during each run of the model. Adopting the protocol of Anderson et al. (2003), we generated 30 models that met predefined criteria for omission and commission error. Maps for those models were summed and quantiles were used to define break points for six habitat classes. Areas of the study area that predicted presence of caribou for \(> 25\) models were considered as class 1 habitats and areas with \(\leq 5\) models were considered as class 6 habitats.

### Model evaluation and comparison

For the RSF, Mahalanobis distance and niche approaches, we developed three sets of models that included variables for patch density, patch distance, and both patch density and distance. Definition of the HSI was predetermined by past researchers. In total, we contrasted 10 species distribution models and maps. For each map, we overlaid the validation set of caribou locations and calculated the number of locations within each of the six habitat classes normalized by the area of that class. The standardization procedure effectively resulted in a measure of density of validation locations, controlled for variation in predicted area among classes of habitat quality. We used the Spearman rank and Pearson correlations to measure the relationship between the predicted habitat classes (i.e. 1–6) or the mid-point for each quantile, respectively, and the normalized frequency of caribou locations from the validation data set. We assumed that models with a greater predictive accuracy would have a greater number of validation locations within higher-quality habitats (i.e. class 1) and correspondingly a larger \(\hat{r}\) or \(r\). We employed both correlation

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### Table 1 Description and area of land-cover types found across the study area in north-central British Columbia, Canada, used to assess four species distribution models.

<table>
<thead>
<tr>
<th>Land-cover type</th>
<th>Area (ha)</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aspen/Cottonwood</td>
<td>384</td>
<td>Primarily stands of Populus tremuloides (97%), but also Populus balsamifera across flood plains</td>
</tr>
<tr>
<td>Mixed coniferous</td>
<td>48894</td>
<td>Mid-altitude stands composed of A. lasiocarpa, P. engelmannii, and P. contorta on moderate to steep slopes</td>
</tr>
<tr>
<td>Subalpine Fir</td>
<td>6532</td>
<td>Mid-altitude stands on moderate to steep slopes composed primarily of A. lasiocarpa</td>
</tr>
<tr>
<td>Krummholz</td>
<td>768</td>
<td>Stands dominated by P. contorta with secondary components of P. mariana or P. engelmannii × P. glauca in older stands</td>
</tr>
<tr>
<td>Pine</td>
<td>3752</td>
<td>Low-altitude sites dominated by P. contorta with abundant terrestrial lichen</td>
</tr>
<tr>
<td>Pine lichen</td>
<td>21043</td>
<td>Mixed stands of P. contorta and A. lasiocarpa found on moderate slopes</td>
</tr>
<tr>
<td>Pine/Fir</td>
<td>1974</td>
<td>Mixed low-altitude stands of P. contorta and P. engelmannii × P. glauca</td>
</tr>
<tr>
<td>Pine/Spruce</td>
<td>1996</td>
<td>Low-altitude sites dominated by P. engelmannii × P. glauca</td>
</tr>
<tr>
<td>Spruce</td>
<td>198</td>
<td>Low-altitude sites dominated by P. engelmannii × P. glauca</td>
</tr>
<tr>
<td>Water</td>
<td>823</td>
<td>Permanent and ephemeral rivers and lakes</td>
</tr>
<tr>
<td>Wetlands</td>
<td>8750</td>
<td>Shrub/sedge- and forb-dominated wetlands</td>
</tr>
<tr>
<td>Other</td>
<td>375</td>
<td>Miscellaneous land-cover types of a small area</td>
</tr>
</tbody>
</table>

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metrics because the Spearman rank is a less powerful test, only reporting differences in ranks between the six habitat classes. We used the Kappa index of agreement as a measure of spatial correlation between maps developed from the four modelling techniques (Monserud & Leemans 1992). Using the results of the correlation analysis for guidance, we compared only maps from the most predictive of the patch density, patch distance or model containing both patch density and distance covariates. We assumed that uncertainties in data, parameters and, ultimately, model predictions, were consistent across techniques. Therefore, we did not explore the impact of variation in predictions on our evaluations or comparisons.

RESULTS

We used 781 caribou locations to parameterize the three quantitative models. The HSI was developed following a review of published data for woodland caribou, informal discussions with experts in caribou biology, and completion of 60 full ecosystem plots and 223 ground inspection plots. Following application of each model to the corresponding GIS data, we used 126 independent caribou locations to evaluate the predictive performance of the 10 species distribution maps.

For each of the quantitative techniques, we developed models with patch density, patch distance and both density and distance variables. Spearman rank correlations calculated between the normalized frequency of independent caribou locations and the six classes of habitat quality were consistently large and very similar among models and variable sets (Table 2). Similarly we noted large Pearson correlations (i.e. \( r > 0.804, p < 0.054 \)) for the three combinations of land-cover variables (Table 2). No single variable set or quantitative model was a markedly better predictor of caribou occurrence. However, we did observe marginally better predictions for the Mahalanobis distance, RSF and niche models when using covariates descriptive of the distance of caribou locations from land-cover patches (\( r = 0.993, p < 0.001 \);

\[ r = 0.966, p = 0.002; \ r = 0.883, p = 0.020 \). When comparing quantitative to qualitative models, the map generated with the HSI had the weakest correlation (\( r = 0.511, p = 0.300 \)) with the independent caribou data and underperformed relative to the other techniques.

Across models and variable sets, we noted some variation in predictive success according to the class of habitat quality (Fig. 1). Mahalanobis distance was the most adept at predicting high-quality habitats (class 1), followed by the resource selection function and niche models, which performed similarly to each other. In contrast, the HSI was a poor predictor of high-quality habitats. All of the models accurately represented poor-quality habitats (classes 5 and 6); however, the Mahalanobis and niche models demonstrated a non-linearity in prediction for class 4, 5 and 6 habitats (Fig. 1).

Using the most predictive variable set for each modelling technique, we recorded considerable differences in the area and distribution of the various classes of habitat quality (Fig. 2). The niche model had the greatest area of high-quality habitat followed by the RSF, the Mahalanobis distance, and the HSI (Table 3). The Kappa index of agreement suggested poor spatial agreement between the predictions of the four models (Table 4). With a Kappa of 0.188, the maps generated from the RSF and Mahalanobis distance vegetation density models were most alike. Visual inspection of the maps, however, indicated that all of the techniques were good predictors of the distribution of caribou locations used to construct the quantitative models (Fig. 2). Discrepancies were most apparent in the south-western and southern portions of the study area, where habitat quality ranged from classes 1 to 6 depending on the model (Fig. 2).

DISCUSSION

This study is one of a number of recent works comparing the performance of species distribution models or assessing the sensitivity of model parameters and predictions to input data and design. As examples, Parra et al. (2004) evaluated

### Table 2

<table>
<thead>
<tr>
<th>Model/variable set</th>
<th>Spearman rank</th>
<th>Pearson</th>
</tr>
</thead>
<tbody>
<tr>
<td>HSI</td>
<td>0.657</td>
<td>0.156</td>
</tr>
<tr>
<td>RSF – distance/density</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>RSF – distance</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>RSF – density</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>Mahalanobis – distance/density</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>Mahalanobis – distance</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>Mahalanobis – density</td>
<td>0.886</td>
<td>0.019</td>
</tr>
<tr>
<td>Niche – distance/density</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>Niche – distance</td>
<td>0.943</td>
<td>0.005</td>
</tr>
<tr>
<td>Niche – density</td>
<td>0.943</td>
<td>0.005</td>
</tr>
</tbody>
</table>

Predictive accuracy of species distribution models

Parra et al. (2004) evaluated...
the performance of an ecological niche model parameterized with alternative environmental data sets; Loiselle et al. (2003) applied museum records for a variety of bird species to five species distribution models and assessed the effects of model choice on the identification of high-priority conservation areas; and Pearce and Ferrier (2000) focused exclusively on logistic regression and the variety of factors that might impact predictive accuracy. These studies and others (for example Stockwell & Peterson 2002; Farber & Kadmon 2003; Gu & Swihart 2004) are likely to be a response to the recent increase in the use of sophisticated species distribution models for investigating ecological relationships and guiding conservation planning (Rushton et al. 2004). We believe, however, that much work remains. The wide range of modelling techniques, sampling protocols and input data, in conjunction with increased reliance on species distribution maps (for example Carroll et al. 2001; Raxworthy et al. 2003; Johnson et al. 2004c), suggests that a full accounting of variability in predictions is required. In this paper, we have stressed the importance and measurement of prediction. Sensitivity and uncertainty analyses are a second level of investigation that can reveal the most sensitive model parameters, the range of possible predictions and guide the improvement of model performance (Elith et al. 2002; Johnson & Gillingham 2004).

In contrast to most previous work, we compared the predictive success of a larger number of techniques and considered the range of data, including expert opinion, use-availability and occurrence, typical for constructing species distribution models. When fit to one data set, our results suggest that RSFs, Mahalanobis distance and niche models are all effective approaches for developing species distribution maps. Our comparisons, however, were not exhaustive. We modelled distribution during a season when caribou are known to be highly selective for particular habitat features (Johnson et al. 2002). Given the expected response, we assumed a priori that all of the models would be good predictors of high-quality habitats (Hepinstall et al. 2002). Thus, deviations from that expectation should be strong evidence of poor model performance, at least for these data. Other factors that might impact model performance include sample size (Stockwell & Peterson 2002), different predictor data sets (Peterson & Cohen 1999; Parra et al. 2004), alternative algorithms for each of the models (Pearce & Ferrier 2000; Loiselle et al. 2003), and variation in the scale of input data and analysis (Karl et al. 2000).

Relative to the three quantitative models, the HSI was a poor predictor of caribou distribution during early winter. Specifically, the model was ineffective at identifying high-quality class 1 habitats (Fig. 1). We assume that the poor

Figure 1 Predictive accuracy of (a) habitat suitability index (HSI), (b) resource selection function (RSF), (c) Mahalanobis distance and (d) ecological niche model. Quantitative models were generated using variables representing the density (den) of land-cover patches, the distance (dis) of caribou locations from the nearest patch, and a combination of both variable sets.
Figure 2 Examples of species distribution maps for woodland caribou of the Wolverine herd during early winter. The habitat suitability index (a) was based on expert opinion and the (b) resource selection function, (c) Mahalanobis distance, and (d) ecological niche model were constructed using variables representing the distance of caribou locations from the nearest patch, the density of land-cover patches, and both variable sets, respectively. The inset map in (a) illustrates the location of the study area in north-central British Columbia, Canada.
correspondence with the validation data was a function of the benchmarking procedure designed to rank habitats across the study area in relation to the best woodland caribou habitat in British Columbia (Madrone Consultants 1999). Such an approach allows planners and managers to assess the value of habitats among individual mapping projects and geographic areas, but fails to recognize the relative significance of habitats within populations. In contrast, the quantitative approaches are specific to the data used to build the models. Past applications have shown that the quantitative models employed for this study may not be generally applicable to other populations, time periods or portions of a study area where animal locations are unavailable (Hobbs & Hanley 1990; Knick & Rotenberry 1998; Johnson et al. 2004).

Although the predictive success of the quantitative models was good, we found considerable variation in the spatial delineation of ranked habitats. There are similarities in the maps developed from the four techniques (Fig. 2), but the Kappa and area statistics suggest that the designation of important habitats (see Noss et al. 2002) or the approval of development proposals could be influenced by selection of a particular model or GIS data. A portion of intermap deviation was likely to be a result of differences in the variable set used to construct the models. Discrepancies also might be a product of the classification procedure we used to break the continuous distribution of predicted values into habitat classes.

Table 3 Area (ha) and number of validation locations (Locs) for six ranked habitat classes predicted for woodland caribou during the early winter using habitat suitability index (HSI), resource selection function (RSF), Mahalanobis distance, and ecological niche models.

<table>
<thead>
<tr>
<th>HSI</th>
<th>RSF</th>
<th>Mahalanobis distance</th>
<th>Niche</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>Locs</td>
<td>Area</td>
<td>Locs</td>
</tr>
<tr>
<td>1</td>
<td>991</td>
<td>1</td>
<td>15947</td>
</tr>
<tr>
<td>2</td>
<td>12590</td>
<td>42</td>
<td>15947</td>
</tr>
<tr>
<td>3</td>
<td>11220</td>
<td>31</td>
<td>15851</td>
</tr>
<tr>
<td>4</td>
<td>9734</td>
<td>10</td>
<td>15947</td>
</tr>
<tr>
<td>5</td>
<td>59657</td>
<td>42</td>
<td>15947</td>
</tr>
<tr>
<td>6</td>
<td>1297</td>
<td>0</td>
<td>15851</td>
</tr>
</tbody>
</table>

Table 4 Similarity in location for six habitat classes across four species distribution models measured using the Kappa index of agreement.

<table>
<thead>
<tr>
<th>Model</th>
<th>HSI</th>
<th>RSF</th>
<th>Mahalanobis</th>
<th>Niche</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area</td>
<td>Locs</td>
<td>Area</td>
<td>Locs</td>
<td>Area</td>
</tr>
<tr>
<td>HSI</td>
<td>1.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>RSF</td>
<td>0.049</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mahalanobis</td>
<td>0.034</td>
<td>0.188</td>
<td>1.0</td>
<td></td>
</tr>
<tr>
<td>Niche</td>
<td>0.013</td>
<td>0.153</td>
<td>0.174</td>
<td>1.0</td>
</tr>
</tbody>
</table>

evaluated, the types of ecological relationships captured by the independent variables are almost limitless. As we have demonstrated, those variables can be quantified using a variety of metrics (such as patch occupancy, patch density and patch distance) and at a number of spatial scales. Mahalanobis distance was the only model with restrictions on how independent variables were quantified. The calculation of mean habitat conditions required model variables that were measured on a continuous scale. Nominal or ordinal data, such as occupancy of different vegetation patches or ranked areas of road density, are incompatible with the calculation of the distance statistic. Generalized linear models, including resource selection functions derived from logistic regression, offer the greatest flexibility in model construction. Although we did not explore this flexibility, we could have modelled categorical variables, interactions or non-linear responses through the use of polynomial terms.

Selection of metric to represent independent variables can influence maps and the scale of inference. Distance, density and occupancy of patches measure different aspects of the spatial distribution and arrangement of vegetation and, through association, species-environment responses. Distance and density of patches represent not only patch composition, but also configuration. The spatial arrangements of environmental features can influence the distribution of some animal species (George & Zack 2001; Chamberlain et al. 2003). Such patch metrics, however, can alter or blur mapped polygon boundaries that may be important to conservation planning. As an example, the suitability index is based on ecological units identified for individual mapped polygons. Alternatively, patch density is a continuous function that might change over an area encompassing a number of discrete patch types. Maps generated using density or distance metrics will be more difficult to apply to fine-scale conservation decisions.

The type of location data often will dictate the choice of modelling approach. Data describing the presence and absence of a species are the most general and are applicable to all species distribution models. Presence-absence data offer a more descriptive picture of a species’ distribution possibly explaining the relative success of these models in other studies (Brotons et al. 2004). Care must be taken, however, when designing sampling protocols for the collection of this type of
location data (Diefenbach et al. 2003). We must guard against or model biases and misclassification of absence data (Tyre et al. 2003). Although similar in approach, the resource selection function models were not developed with true presence-absence data. The availability data may have contained some actual caribou locations and the sampling scheme prevented calculation of an absolute probability of occurrence.

The knowledge and computational tools necessary for model development range across the four techniques we assessed. Habitat suitability indices are heuristic models dependent on a body of knowledge describing species–habitat relationships. Indices can be formulated using simple spreadsheet tools, which are then applied to a GIS. Mahalanobis distance calculations involve covariance and correlation matrices and thus are more complex. As with habitat suitability indices, the approach has few assumptions or computational complexities aside from quality assurance for GIS and species location data. Development of logistic regression-based RSFs requires access to statistical software and a GIS, and a good understanding of sample design and the formulation, assumptions and limitations of generalized linear models (Hosmer & Lemeshow 2000). The GARP ecological niche model was the most complex of the four we evaluated. Some of the niche rules are simple and the user has control over fundamental parameters, but the process as a whole is difficult to visualize and evaluate, and can be considered more of a ‘black box’ approach to species distribution modelling.

We note, however, that the GARP software is free and easy to use and facilitates both calculation and mapping of models. A number of articles outline the workings of GARP and provide guidance on model construction (Stockwell & Peters 1999; Anderson et al. 2003).

Aside from maps depicting the distribution of a species, the type of inference varies with technique. Resource selection functions and habitat suitability indices produce coefficients that report the influence of individual variables on the distribution of a species. For resource selection functions, coefficients are accompanied by measures of precision and statistical significance. Typically, coefficients for suitability indices have no estimates of precision, although methods are available for calculating the variation around parameter estimates due to input data and differences in expert opinion (Bender et al. 1996; Burgman et al. 2001; Johnson & Gillingham 2004). Mahalanobis distance and the GARP niche models do not provide direct measures of variable influence. We can conceive of step-wise procedures where incremental changes in model prediction could be assessed against variable inclusion. Such approaches are relatively awkward and without simulation provide no estimate of precision.

Omnibus tests and assessment also vary among the models we evaluated. A number of statistical tests, information theoretic approaches and non-parametric techniques are available for evaluating resource selection functions and other logistic regression-based models (Fielding & Bell 1997; Anderson et al. 2000; Boyce et al. 2002). GARP models withhold and apply a portion of the location data to generate measures of model success including prediction accuracy and the probability of a non-random result as well as errors of omission and commission. The Mahalanobis distance and habitat suitability indices are not amenable to statistical tests or information theoretic approaches; however, as with the other two models, expert-generated maps or independent validation locations can serve as reference points to assess predictive capacity (Knick & Dyer 1997; Prosser & Brooks 1998; Loukmas & Halbrook 2001).

RECOMMENDATIONS FOR MODEL SELECTION

Given the wide-range of models and the potential for differences in predictive performance, the first consideration will be availability of data suitable for candidate species distribution models. Data requirements for each technique are straightforward and range from presence-absence to presence-only locations to qualitative expert opinion. If costs are prohibitive, expert opinion (from interview or published findings) might be the only source of information to construct a species-distribution model. Alternatively, Mahalanobis distance and niche models have greater predictive accuracy, but they are dependent on field collections describing the presence of a plant or animal. There is some evidence to suggest that presence-absence models outperform presence-only models, but this relationship is not fully explored (Hirzel et al. 2001; Brotons et al. 2004). Presence-absence or use-availability data (for example RSFs) are potentially more complex and expensive to collect and, for our case study, these models did not provide increased predictive accuracy.

Beyond data requirements, we note considerable differences in flexibility in model design, evaluation protocols and the types of inference. Of the techniques we evaluated, RSFs parameterize the greatest range of ecological relationships (for example polynomial terms and interactions) and provide widely accepted approaches (Anderson et al. 2000) for evaluating and choosing among competing models. Compared to the other quantitative techniques, RSFs have the added advantage of selection coefficients, which are easy to assess and interpret. The Mahalanobis distance and niche models do not provide metrics for assessing the strength of inference of individual variables and the coefficients associated with habitat suitability indices are difficult to evaluate for precision (Johnson & Gillingham 2004). As demonstrated here, predictions from all four techniques can be evaluated if an independent data set is available or cross-validation methods are employed (Boyce et al. 2002). However, a much fuller suite of evaluation techniques has been published for the niche and RSF models (Fielding & Bell 1997; Mangel et al. 2001).

Although we, and others, provide some empirical guidance for selecting a model based on predictive accuracy, it is unlikely that one type of model is best for all situations. The particular conservation issue and the ecology of the focal species should guide the selection of a technique, but often limitations of data
will severely restrict the choice set (Austin 2002). Practitioners must also ensure that the model and approach have ecological relevance and neither the data nor model violates statistical or ecological assumptions (Austin 2002). Where several models might be expected to perform equally, we recommend that practitioners consider issues such as flexibility in model design and type and assessment of inference or prediction. In our case, RSFs best meet those other criteria. We can provide no assurance, however, that under different circumstances (for example season, different range) the relative ranking, performance and applicability of these models will remain consistent.

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References


