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An evaluation of mapped species distribution models used for conservation planning

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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.* 2004*c*). 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

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considerably (see Loiselle *et al.* 2003). We leave the questions specific to uncertainty and sensitivity of each technique to other researchers (for example Pearce & Ferrier 2001; Parra *et al.* 2004; Johnson & Gillingham 2004).

We compared the predictions generated from four species distribution models commonly reported in the conservation literature: a habitat suitability index, logistic regression-based resource selection function, Mahalanobis distance and an ecological niche model. As a brief review of those approaches, habitat suitability indices (HSI) formalize the application of expert knowledge and meta-analyses to the identification and ranking of wildlife-habitat relationships (United States Fish and Wildlife Service 1981). Typically, a HSI is an equation of an additive, multiplicative or logical form, with coefficients ranging from 0 to 1 representing the relative value of environmental features (such as forest type, shrub cover, availability of water). In conjunction with a GIS, a HSI can generate maps of ranked habitat units (Li *et al.* 2002; Larson *et al.* 2003; Store & Jokimaki 2003). Researchers have developed hundreds of indices, typically for situations where quantitative data documenting the distribution of a species do not exist or are difficult to collect (for example Schroeder & Vangilder 1997; Oldham *et al.* 2000; Storch 2002; Larson *et al.* 2003).

A resource selection function (RSF) is any mathematical function that provides predictions of resource or habitat use that are proportional to the true probability of use (Manly *et al.* 2002). The model is premised on the theory of habitat selection; where use of a habitat exceeds availability, selection is inferred and where use is less than availability, we conclude that habitats are avoided. Resource selection functions can take many mathematical forms (Manly *et al.* 2002).

Mahalanobis distance is a multivariate dissimilarity statistic. When applied as a species distribution model, the mean conditions of a set of habitat variables are typically contrasted, as described by a number of plant or animal locations, with locations found across the broader landscape (Clark *et al.* 1993; Knick & Dyer 1997). Larger values of the statistic indicate a relatively greater distance from the mean habitat conditions described by the reference locations.

Ecological niche models are conceptually similar to the other approaches presented here, but niche models are explicitly linked to niche theory and typically address distribution across broad regional scales (Anderson *et al.* 2002). The set of environmental factors that dictate where a species can and cannot maintain a population are based on evolutionary constructs and, depending on that set, reveal the fundamental or realized niche (Peterson & Vieglais 2001). Niche theory has a long history in ecology and has spurred the development of numerous approaches to quantify and map species' niche dimensions (for example Austin *et al.* 1990; Rutherford *et al.* 1995, Hirzel *et al.* 2002).

We used three sets of vegetation variables and a HSI, a RSF, Mahalanobis distance and an ecological niche model to predict the distribution of habitats for a population of woodland caribou *Rangifer tarandus caribou*. Woodland caribou are sensitive to habitat alteration and loss and are listed as a threatened species across much of Canada (Johnson *et al.* 2004*b*). 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 north-west 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 1999*a*). 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 1998*a*; Madrone Consultants 1999*b*). 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 1998*b*).

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 χ^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 1998*a*). Using past caribou research, the large number of ecological associations were combined into 11 land-cover types (Madrone Consultants 1999*b*; 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

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.

Land-cover type	*Area (ha)*	*Description*
Aspen/Cottonwood	384	Primarily stands of *Populus tremuloides* (97%), but also *Populus balsamifera* across flood plains
Mixed coniferous	48894	Mid-altitude stands composed of *A. lasiocarpa*, *P. engelmannii*, and *P. contorta* on moderate to steep slopes
Subalpine Fir	6532	Mid-altitude stands on moderate to steep slopes composed primarily of *A. lasiocarpa*
Krummholz	768	Stunted tree cover of *A. lasiocarpa* on gentle to moderate slopes at 1300–1600 m altitude
Pine	3752	Stands dominated by *P. contorta* with secondary components of *P. mariana* or *P. engelmannii* × *P. glauca* in older stands
Pine lichen	21043	Low-altitude sites dominated by *P. contorta* with abundant terrestrial lichen
Pine/Fir	1974	Mixed stands of *P. contorta* and *A. lasiocarpa* found on moderate slopes
Pine/Spruce	1996	Mixed low-altitude stands of *P. contorta* and *P. engelmannii* × *P. glauca*
Spruce	198	Low-altitude sites dominated by *P. engelmannii* × *P. glauca*
Water	823	Permanent and ephemeral rivers and lakes
Wetlands	8750	Shrub/sedge- and forb-dominated wetlands
Other	375	Miscellaneous land-cover types of a small area

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 distribution of each land-cover type and correspondingly the size of the moving window (Johnson *et al.* 2004*a*). Distance from patches was a simple measure of adjacency that also captured occupancy of patch types (i.e. distance of 0 m). RSFs accommodate polynomial and interaction terms, whereas the HSI, Mahalanobis distance and the niche model do not accommodate non-linear ecological relationships. To maintain consist comparisons among the techniques we used only linear terms for each vegetation variable.

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 1999*a*). 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 × 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.* 2004*c*). 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 ≤ 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 $\bar{r}_s$ or r. We employed both correlation 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 Spearman rank and Pearson correlations describing the strength of the relationship between the predicted habitat classes (i.e. 1–6) or the model-specific values used to define each class, respectively, and the normalized frequency of independent validation locations for a habitat suitability index (HSI), resource selection function (RSF), Mahalanobis distance, and ecological niche models. Data models were generated with locations collected from GPS-collared woodland caribou monitored from November 1996 to March 2000.

Model/variable set	*Spearman rank*		*Pearson*	
	$\bar{r}_s$	p	r	p
HSI	0.657	0.156	0.511	0.300
RSF – distance/density	0.943	0.005	0.907	0.013
RSF – distance	0.943	0.005	0.966	0.002
RSF – density	0.943	0.005	0.915	0.011
Mahalanobis – distance/density	0.943	0.005	0.977	<0.001
Mahalanobis – distance	0.943	0.005	0.993	<0.001
Mahalanobis – density	0.886	0.019	0.947	0.004
Niche – distance/density	0.943	0.005	0.878	0.023
Niche – distance	0.943	0.005	0.883	0.020
Niche –density	0.943	0.005	0.804	0.054

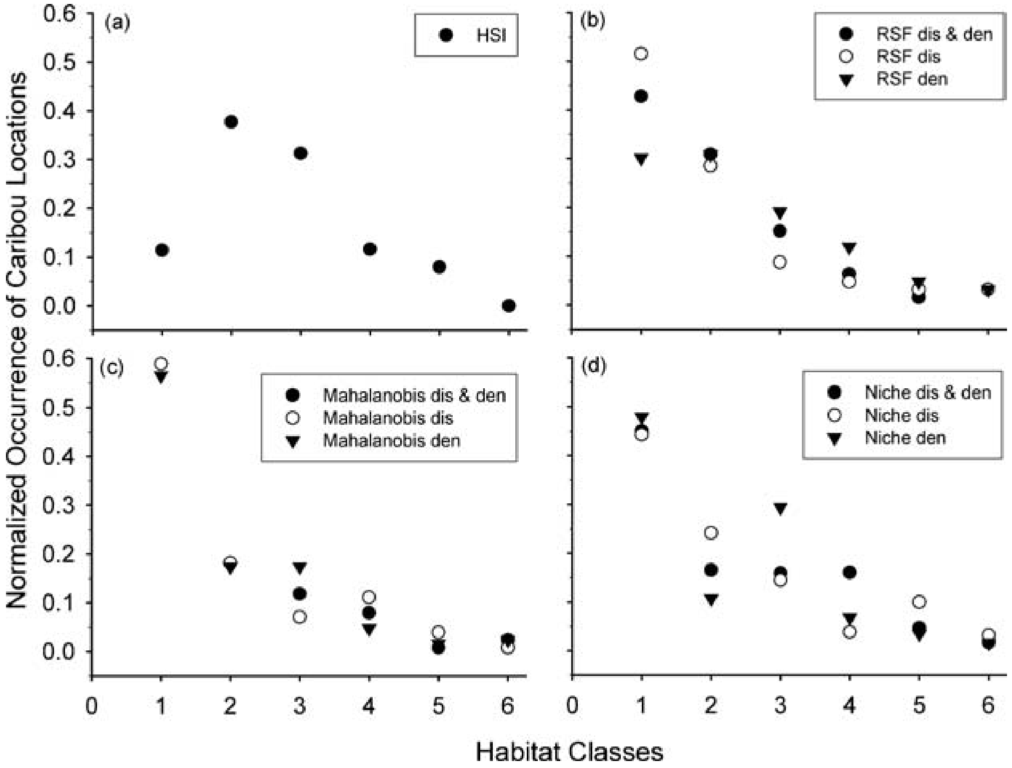

Figure 1 Predictive accuracy of (*a*) habitat suitability index (HSI), (*b*) resource selection function (RSF), (*c*) Mahalanobis distance and (*d*) ecological niche model. Quantitative models were generated using variables representing the density (den) of land-cover patches, the distance (dis) of caribou locations from the nearest patch, and a combination of both variable sets.

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.* 2004*c*), 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 & Cohoon 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

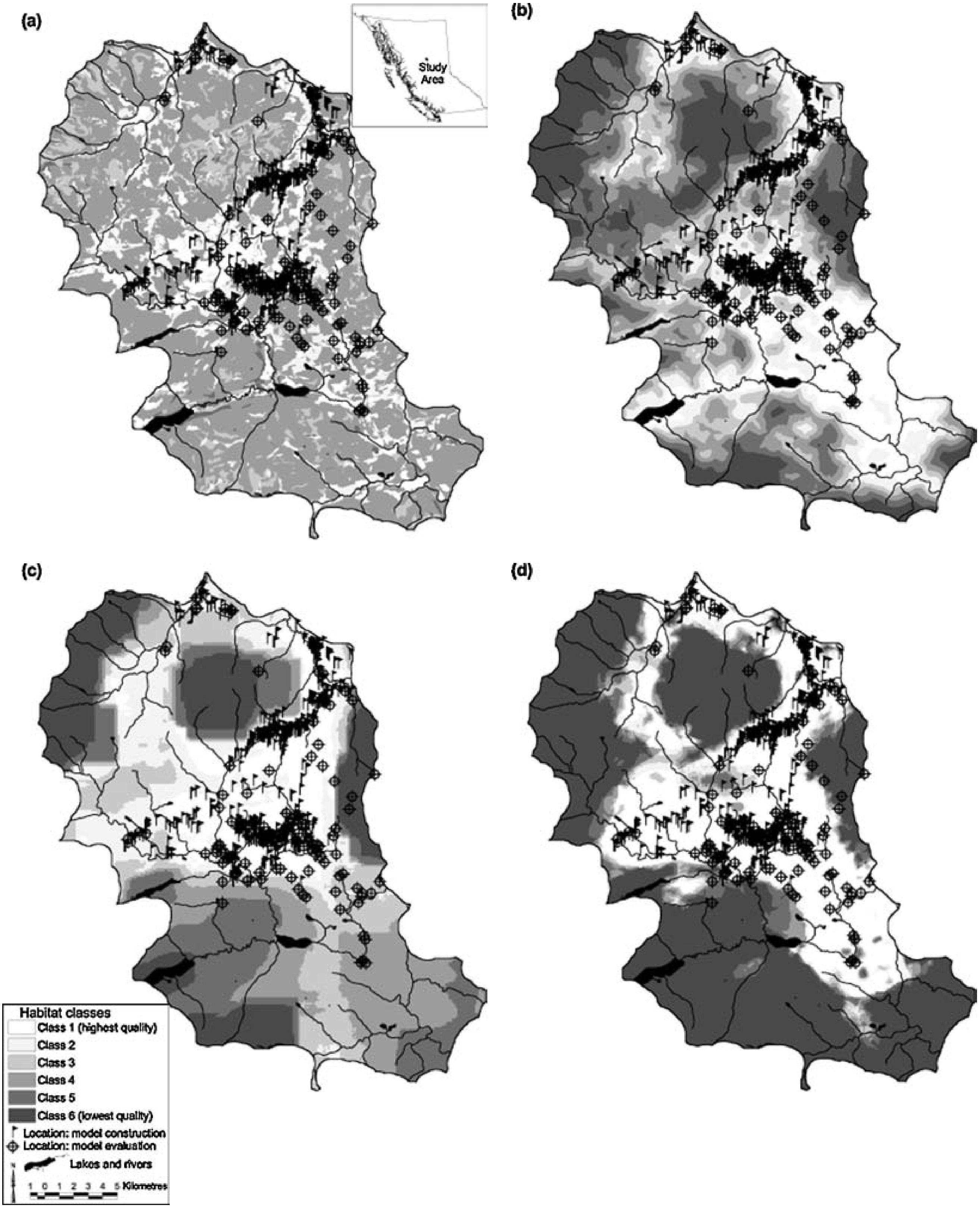

Figure 2 Examples of species distribution maps for woodland caribou of the Wolverine herd during early winter. The habitat suitability index (*a*) was based on expert opinion and the (*b*) resource selection function, (*c*) Mahalanobis distance, and (*d*) ecological niche model were constructed using 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.

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.

Habitat	*Model*							
	HSI		*RSF*		*Mahalanobis distance*		*Niche*	
	Area	*Locs*	*Area*	*Locs*	*Area*	*Locs*	*Area*	*Locs*
1	991	1	15947	65	15851	74	22801	91
2	12590	42	15947	36	15946	23	4596	10
3	11220	31	15851	11	15947	9	3072	4
4	9734	10	15947	6	15851	14	2901	1
5	59657	42	15947	4	15947	5	3333	3
6	1297	0	15851	4	15947	1	58787	17

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

	Model			
	HSI	*RSF*	*Mahalanobis*	*Niche*
HSI	1.0			
RSF	0.049	1.0		
Mahalanobis	0.034	0.188	1.0	
Niche	0.013	0.153	0.174	1.0

correspondence with the validation data was a function of the bench-marking procedure designed to rank habitats across the study area in relation to the best woodland caribou habitat in British Columbia (Madrone Consultants 1999*a*). 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*c*).

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.

Modellers and practitioners should expect considerable variation in data requirements, required expertise and knowledge, and inference when building and interpreting alternative species distribution models. For the models we 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; Manel *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

Abbitt, R.J.F., Scott, J.M. & Wilcove, D.S. (2000) The geography of vulnerability: incorporating species geography and human development patterns in conservation planning. *Biological Conservation* **96**: 169–175.

Anderson, D.R., Burnham, K.P. & Thompson, W.L. (2000) Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**: 912–923.

Anderson, R.P., Lew, D. & Peterson, A.T. (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling* **162**: 211–232.

Anderson, R.P., Gómez-Laverde, M. & Peterson, A.T. (2002) Geographical distributions of spiny pocket mice in South America: insights from predictive models. *Global Ecology and Biogeography* **11**: 131–141.

Arthur, S.M., Manly, B.F.J., McDonald, L.L. & Garner, G.W. (1996) Assessing habitat selection when availability changes. *Ecology* **77**: 215–227.

Austin, M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**: 101–118.

Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990) Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecological Monographs* **60**: 161–177.

Bender, L.C., Roloff, G.J. & Haufer, J.B. (1996) Evaluating confidence intervals for habitat suitability models. *Wildlife Society Bulletin* **24**: 347–352.

Boyce, M.S., Vernier, P.R., Nielson, S.E. & Schmiegelow, F.K.A. (2002) Evaluating resource selection functions. *Ecological Modelling* **157**: 281–300.

Brotons, L., Thuiller, W., Araujo, M.B. & Hirzel, A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. *Ecography* **27**: 437–448.

Buckland, S.T. & Elston, D.A. (1993) Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* **30**: 478–495.

Burgman, M.A., Breininger, D.R., Duncan, B.W. & Ferson, S. (2001) Setting reliability bounds on habitat suitability indices. *Ecological Applications* **11**: 70–78.

Carroll, C., Noss, R.F. & Paquet, P.C. (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* **11**: 961–980.

Chamberlain, M.J., Conner, L.M., Leopold, B.D. & Hodges, K.M. (2003) Space use and multi-scale habitat selection of adult racoons in central Mississippi. *Journal of Wildlife Management* **67**: 334–340.

Clark, J.D., Dunn, J.E. & Smith, K.G. (1993) A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* **57**: 519–526.

Clark Labs (2002) IDRISI32. Version I32.22. Clark Labs, The Idrisi Project, Worcester, Massachusetts, USA.

Clevenger, A.P., Wierzchowski, J., Chruszcz, B. & Gunson, K. (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* **16**: 503–514.

Compton, B.W., Rhymer, J.M. & McCollough, M. (2002) Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* **83**: 833–843.

Diefenbach, D.R., Brauning, D.W. & Mattice, J.A. (2003) Variability in grassland bird counts related to observer differences and species detection rates. *Auk* **120**: 168–1179.

Elith, J., Burgman, M.A. & Regan, H.M. (2002) Mapping epistemic uncertainties and vague concepts in predictions of species distribution. *Ecological Modelling* **157**: 313–329.

Erickson, W.P., McDonald, T.L. & Skinner, R. (1998) Habitat selection using GIS: a case study. *Journal of Agricultural, Biological and Environmental Studies* **3**: 296–310.

ESRI (2000) ARCVIEW. Version 3.2. Environmental Systems Research Institute, Inc., Redlands, California, USA.

Farber, O. & Kadmon, R. (2003) Assessment of alternative approaches for bioclimatic modeling with special emphasis on the Mahalanobis distance. *Ecological Modelling* **160**: 115–130.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction error in conservation presence/absence models. *Environmental Conservation* **24**: 38–49.

George, T.L. & Zack, S. (2001) Spatial and temporal considerations in restoring habitat for wildlife. *Restoration Ecology* **9**: 272–279.

Gibson, L.A., Wilson, B.A., Cahill, D.M. & Hill, J. (2004) Modelling habitat suitability of the swamp antechinus (*Antechinus minimus maritimus*) in the coastal headlands of southern Victoria, Australia. *Biological Conservation* **117**: 143–150.

Gu, W. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation* **116**: 195–203.

Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling* **135**: 147–186.

Heard, D.C. & Vagt, K.L. (1998) Caribou in British Columbia: a 1996 status report. *Rangifer Special Issue* **10**: 117–123.

Hepinstall, J.A., Krohn, W.B., & Sader, S.A. (2002) Effects of niche width on the performance and agreement of avian habitat models. In: *Predicting Species Occurrences: Issues of Accuracy and Scale*, ed. M.S. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson, pp. 593–606. Washington, DC, USA: Island Press.

Hirzel, A.H., Helfer, V. & Métral, F. (2001) Assessing habitat-suitability models with a virtual species. *Ecological Modelling* **145**: 111–121.

Hirzel, A.H., Hausser, J. & Perrin, N. (2002) Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology* **83**: 2027–2036.

Hobbs, N.T. & Hanley, T.A. (1990) Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management* **54**: 515–522.

Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*, Second edition. New York, USA: John Wiley & Sons.

Johnson, C.J. & Gillingham, M.P. (2004) Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. *Journal of Applied Ecology* **41**: 1032–1041.

Johnson, C.J., Alexander, N.D., Wheate, R.D. & Parker, K.L. (2003) Characterizing woodland caribou habitat in sub-boreal and boreal forests. *Forest Ecology and Management* **180**: 241–248.

Johnson, C.J., Boyce, M.S., Mulders, R., Gunn, A., Gau, R.J., Cluff, H.D. & Case, R.L. (2004*a*) Quantifying patch distribution at multiple spatial scales: applications to wildlife-habitat models. *Landscape Ecology* **19**: 869–882.

Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002) A multiscale behavioral approach to understanding the movements of woodland caribou. *Ecological Applications* **12**: 1840–1860.

Johnson, C.J., Parker, K.L., Heard, D.C. & Seip, D.R. (2004*b*) Movements, foraging habits, and habitat use strategies of northern woodland caribou: implications for forest practices. *British Columbia Journal of Ecosystems and Management* **5**: 22–35.

Johnson, C.J., Seip, D.R. & Boyce, M.S. (2004*c*) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. *Journal of Applied Ecology* **41**: 238–251.

Karl, J.W., Heglund, P.J., Garton, E.O., Scott, J.M., Wright, N.M. & Hutto, R.L. (2000) Sensitivity of species habitat-relationship model performance to factors of scale. *Ecological Applications* **10**: 1690–1705.

Knick, S.T. & Dyer, D.L. (1997) Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* **61**: 75–85.

Knick, S.T. & Rotenberry, J.T. (1998) Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. *Journal of Agricultural, Biological, and Environmental Statistics* **3**: 311–322.

Larson, M.A., Dijak, W.D., Thompson, F.R. & Millspaugh, J.J. (2003) Landscape-level habitat suitability models for twelve wildlife species in southern Missouri. United States Department of Agriculture, Forest Service General Technical Report NC-233, St. Paul, Minnesota, USA.

Li, X.H., Li, D.M., Li, Y.M., Ma Z.J. & Zhai, T.Q. (2002) Habitat evaluation for crested ibis: a GIS-based approach. *Ecological Research* **17**: 565–573.

Loiselle, B.A., Howell, C.A., Graham, C.H., Goerck, J.M., Brooks, T., Smith, K.G. & Williams, P.H. (2003) Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology* **17**: 1591–1600.

Loukmas, J.J. & Halbrook, R.S. (2001) A test of the mink habitat suitability index model for riverine systems. *Wildlife Society Bulletin* **29**: 821–826.

Madrone Consultants (1999*a*) Wildlife interpretations for the Klawli Management Unit North-central BC. Unpublished report, Slocan Group, Mackenzie, British Columbia, Canada.

Madrone Consultants (1999*b*) Terrestrial ecosystem mapping of the Klawli study area. Unpublished report, Slocan Group, Mackenzie, British Columbia, Canada.

Manel, S., Williams, H.C. & Ormerod, S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* **38**: 921–931.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals*, Second edition. Dordrecht, the Netherlands: Kluwer Academic Publishers.

Meidinger, D. & Pojar, J. (1991) Ecosystems of British Columbia. Special Report Series No. 6, British Columbia Ministry of Forests, Victoria, British Columbia, Canada.

Monserud, R. & Leemans, R. (1992) Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling* **62**: 275–293.

Noss, R.F., Carroll, C., Vance-Borland, K. & Wuerthner, G. (2002) A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology* **16**: 895–908.

Oldham, R.S., Keeble, J., Swan, M.J.S. & Jeffcote M. (2000) Evaluating the suitability of habitat for the great crested newt (*Triturus cristatus*). *Herpetological Journal* **10**: 143–155.

Parra, J.L., Graham, C.C. & Freile, J.F. (2004) Evaluating alternative data sets for ecological niche models of birds in the Andes. *Ecography* **27**: 350–360.

Pearce, J.L. & Ferrier, S. (2000) An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling* **128**: 127–147.

Pearce, J.L. & Ferrier, S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation* **98**: 33–43.

Pendergast, J.F., Gange, S.J., Newton, M.A., Lindstrom, M.J., Palta, M. & Fisher, M.R. (1996) A survey of methods for analyzing clustered binary response data. *International Statistical Review* **64**: 89–118.

Peterson, A.T. & Cohoon, K.P. (1999) Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling* **117**: 159–164.

Peterson, A.T. & Vieglais, D.A. (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *BioScience* **51**: 363– 371.

Prosser, D.J. & Brooks, J.P. (1998) A verified habitat suitability index for the Louisiana waterthrush. *Journal of Field Ornithology* **69**: 288–298.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A. & Peterson, T.A. (2003) Predicting distributions of known and unknown reptile species in Madagascar. *Nature* **426**: 837–841.

Resources Inventory Committee (1998*a*) Standards for terrestrial ecosystems mapping in British Columbia. Unpublished document, Ecosystems Working Group, Terrestrial Ecosystems Task Force, Resources Inventory Committee, Victoria, British Columbia, Canada.

Resources Inventory Committee (1998*b*) British Columbia wildlife habitat rating standards. Unpublished document, Wildlife Interpretations Subcommittee, Wildlife Branch, Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

Rivieccio, M., Thompson, B.C., Gould, W.R. & Boykin, K.G. (2003) Habitat features and predictive habitat modeling for the Colorado chipmunk in southern New Mexico. *Western North American Naturalist* **63**: 479–488.

Rushton, S.P., Ormerod, S.J. & Kerby, G. (2004) New paradigms for modelling species distributions? *Journal of Applied Ecology* **41**: 193–200.

Rutherford, M.C., Callaghan, M.O., Hurford, J.L., Powrie, L.W. & Schulze, R.E. (1995) Realized niche spaces and functional types: a framework for prediction of compositional change. *Journal of Biogeography* **22**: 523–531.

Stockwell, D.R.B. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographic Science* **13**: 143–158.

Stockwell, D.R.B. & Peterson, A.T. (2002) Effects of sample size on accuracy of species distribution models. *Ecological Modelling* **148**: 1–13.

Storch, I. (2002) On spatial resolution in habitat models: Can small-scale forest structure explain Capercaillie numbers? *Conservation Ecology* **6** [www document]. URL http://www.consecol.org/vol6/iss1/art6

Store, R. & Jokimaki, J. (2003) A GIS-based multi-scale approach to habitat suitability modeling. *Ecological Modelling* **169**: 1–15.

Terry, E.L. & Wood, M.D. (1999) Seasonal movements and habitat selection by woodland caribou in the wolverine herd, North-central BC. Phase 2: 1994–1997. Peace/Williston Fish and Wildlife Compensation Program Report No. 204, Prince George, British Columbia, Canada.

Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley T.A. & Wydeven, A.P. (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* **18**: 114–125.

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, F., Parris, K. & Possingham, H.P. (2003) Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* **13**: 1790–1801.

United States Fish and Wildlife Service (1981) *Standards for the Development of Habitat Suitability Index Models*. United States Fish and Wildlife Service, ESM 103, Department of the Interior, Washington, DC, USA.

Wood, M.D. & Terry, E.L. (1999) Seasonal movements and habitat selection by woodland caribou in the Omineca Mountains, North-central BC. Phase 1: The chase and wolverine herds (1991–1994). Peace/Williston Fish and Wildlife Compensation Program Report No. 201, Prince George, British Columbia, Canada.

Zabel, C.J., Dunk, J.R., Stauffer, H.B., Roberts, L.M., Mulder, B.S. & Wright, A. (2003) Northern spotted owl habitat models for research and management application in California (USA). *Ecological Applications* **13**: 1027–1040.