Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou

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ABSTRACT

Models that predict distribution are now widely used to understand the patterns and processes of plant and animal occurrence as well as to guide conservation and management of rare or threatened species. Application of these methods has led to corresponding studies evaluating the sensitivity of model performance to requisite data and other factors that may lead to imprecise or false inferences. We expand upon these works by providing a relative measure of the sensitivity of model parameters and prediction to common sources of error, bias, and variability. We used a one-at-a-time sample design and GPS location data for woodland caribou (*Rangifer tarandus caribou*) to assess one common species-distribution model: a resource selection function. Our measures of sensitivity included change in coefficient values, prediction success, and the area of mapped habitats following the systematic introduction of geographic error and bias in occurrence data, thematic misclassification of resource maps, and variation in model design. Results suggested that error, bias and model variation have a large impact on the direct interpretation of coefficients. Prediction success and definition of important habitats were less responsive to the perturbations we introduced to the baseline model. Model coefficients, prediction success, and area of ranked habitats were most sensitive to positional error in species locations followed by sampling bias, misclassification of resources, and variation in model design. We recommend that researchers report, and practitioners consider, levels of error and bias introduced to predictive species-distribution models. Formal sensitivity and uncertainty analyses are the most effective means for evaluating and focusing improvements on input data and considering the range of values possible from imperfect models.

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1. Introduction

Species-distribution models are becoming an important tool for understanding ecological processes and patterns and for guiding the conservation and management of plants and animals (Raxworthy et al., 2003; Fortin et al., 2005). Once an effective model is identified, results provide a measure of the importance of ecological variables that correlate with species distribution and in some cases abundance (Boyce and McDonald, 1999). Also, model results can be applied to digital spatial data to produce maps representing the likelihood of species occurrence (Carroll et al., 2001). The absolute or rela-

tive likelihood of occurrence then serves as a metric to rank habitats for conservation initiatives such as habitat restoration, enhancement or protection (Johnson et al., 2004).

Numerous approaches are available for predicting and mapping species occurrence. Quantitative techniques range from the suite of generalized linear models to rule-based methods (Guisan and Zimmermann, 2000). Although there are many types of distribution models, most are dependent on two sources of data: an unbiased and precise sample of species locations and maps of environmental data that correlate with species distribution. Depending on the species, ecologically plausible variables could represent vegetation, soil parameters, topography, human disturbance, and interspecific interactions (Manly et al., 2002).

Arbitrary decisions during the modeling process, and error and bias in requisite data, can reduce predictive power or lead to incorrect inferences (Elith et al., 2002). A model that poorly reflects actual species–environment relationships will not enlighten our understanding of ecological processes and patterns and might result in misplaced resources or harmful conservation and management actions (Loiselle et al., 2003). Although modellers and practitioners often are aware of potential sources of error, bias, and variation during model construction and use, the impacts are seldom quantified and reported. This is despite the availability of formal methods for conducting sensitivity and uncertainty analyses (Crosetto and Tarantola, 2001). Where case-specific sensitivity and uncertainty analyses are impractical, much guidance can be gleaned from past research. For example, researchers have evaluated and discussed the predictive performance of a number of techniques (Pearce and Ferrier, 2000; Boyce et al., 2002; Loiselle et al., 2003); the sensitivity, uncertainty, and efficacy of expert-based approaches (Dettki et al., 2003; Johnson and Gillingham, 2004); and the lack of ecological theory to support these techniques and their applications (Austin, 2007). Although we have witnessed a recent surge in the use and evaluation of species-distribution models and requisite data, we are unaware of any work that provides a comparison of the relative sensitivity of model predictions to multiple sources of bias and error and variation in model design.

We performed a comprehensive sensitivity analysis for one type of species-distribution model, a resource selection function (RSF) formulated using logistic regression (Manly et al., 2002). Sensitivity analyses provide support for model predictions and highlight areas where assumptions need to be addressed and source data improved or augmented (Crosetto and Tarantola, 2001). With the objective of maintaining realistic ecological relationships we performed the analysis using previously published location data for woodland caribou (*Rangifer tarandus caribou*) and a map of vegetation generated from a classified Landsat Thematic Mapper image (Johnson et al., 2002a, 2003). We measured the sensitivity of model coefficients, prediction success, and maps of selected habitats to four factors: alternate model structures, various levels of bias and error in animal locations, and thematic misclassification of a vegetation map. Resource selection and resource selection probability functions are now ubiquitous in the conservation and ecological literature and, thus, are an excellent case to demonstrate methods for sensitivity analyses of species-distribution models (Arthur et al., 1996; Boyce

and McDonald, 1999; Compton et al., 2002; Boyce et al., 2003; Johnson et al., 2004; Fortin et al., 2005).

2. Methods

2.1. Study area

We developed and assessed RSF models for a population of woodland caribou known as the Wolverine herd located approximately 250 km northwest of Prince George, British Columbia, Canada (Fig. 1, Heard and Vagt, 1998). The study area varies in elevation from valley bottoms at ~900 m to alpine summits at ~2050 m and is characterized by numerous vegetation associations. Forest types below 1100 m elevation 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 elevation, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii*) and subalpine fir. Areas at elevations >1600 m are alpine tundra and are distinguished by gentle to steep windswept slopes vegetated by shrubs, herbs, bryophytes, and lichens, with occasional trees in krummholz form (Meidinger and Pojar, 1991).

2.2. Animal locations

For the sensitivity analyses, we used animal location data collected from 16 individual female caribou of the Wolverine herd monitored between March 1996 and March 1999. Caribou were located with differentially correctable Global Positioning System (GPS) collars scheduled to record one location every third or fourth hour (GPS 1000, Lotek Engineering, Newmarket, Ontario, Canada; Johnson et al., 2002b). For these analyses, we used only GPS locations collected during winter (December 1 to March 31). During this period, monitored caribou were known to demonstrate three coarse-scale selection strategies: foraging across forested habitats, foraging across alpine habitats, or foraging for some period of time within both forested and alpine habitats (Johnson et al., 2002a). Because we wanted to reduce model complexity due to behavioural variation, we restricted our analyses to only those monitored caribou that exclusively occurred across forested habitats. Following screening and the exclusion of out-of-season locations, we retained 2178 GPS fixes for the sensitivity analysis. All locations for the 16 caribou were pooled. We did not control for inconsistent sample sizes across animals; thus, model inference to the population is likely biased to caribou with the greatest relocation frequency.

2.3. Modelling approach

A RSF can take many mathematical forms, but is defined as any function that provides predictions of resource use that are proportional to the true probability of use (Manly et al., 2002). We used logistic regression to formulate RSFs that described the selection patterns and predicted the occurrence of female woodland caribou from the Wolverine herd. Logistic regression is commonly used to model species–environment
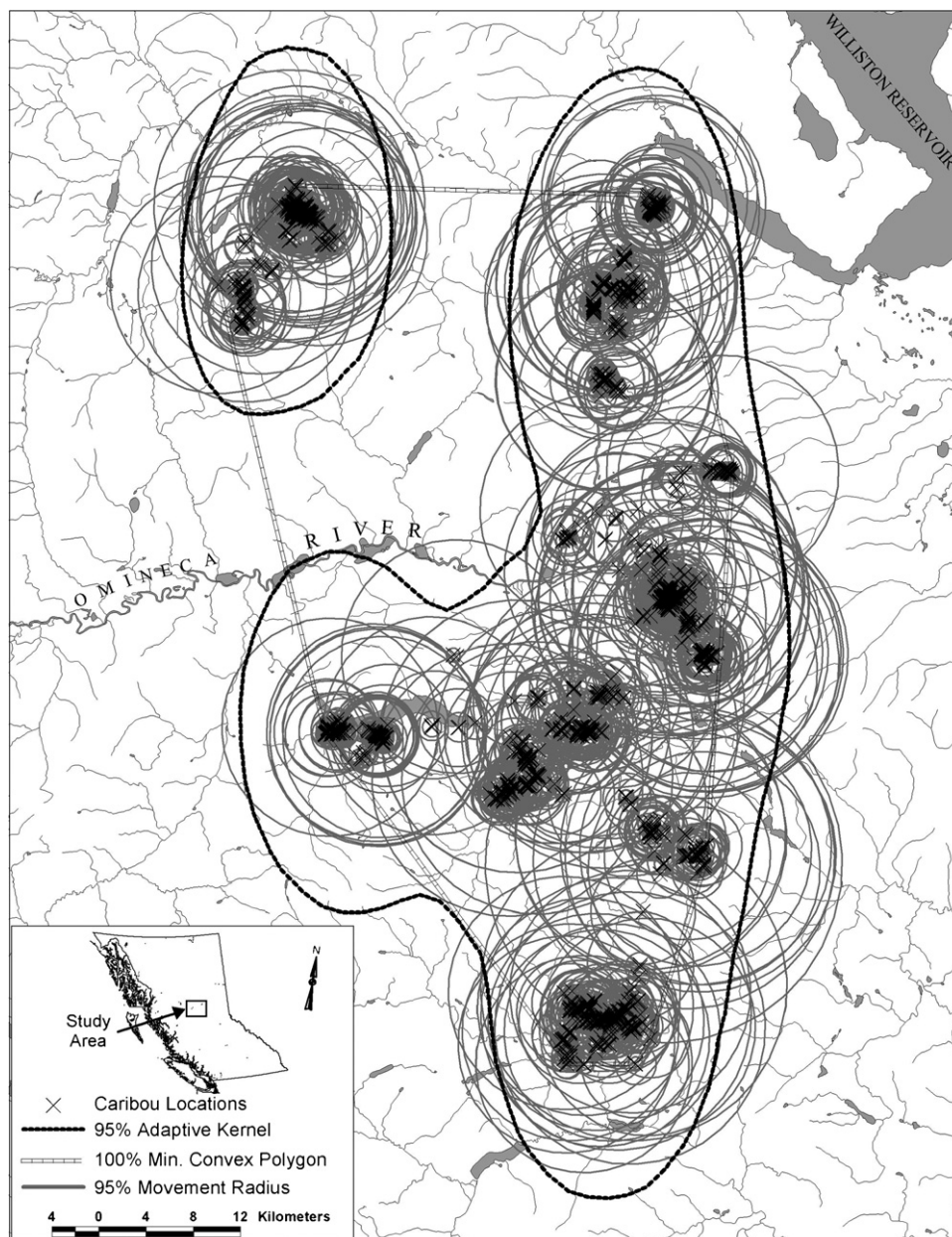
Fig. 1 – Woodland caribou locations (central British Columbia, Canada; Johnson et al., 2002a) and boundaries used to define the availability of habitats for sensitivity analyses of resource selection function species-distribution models.

relationships where the sampling scheme calls for a comparison of animal or plant locations with sites where the species is undetected or absent (Guisan and Zimmermann, 2000; Pearce and Ferrier, 2000). In the case of RSFs, one does not apply presence–absence data, but instead contrasts a sample of use locations with a series of random locations meant to represent resource availability. The extent and definition of available resources depends on the type of RSF model and the spatial and temporal scales of the behaviour of interest. Unlike logistic regression, however, a sample of resource availability does not accurately represent the proportion of sampled locations with animals absent and thus prevents the calculation of a true probability (see Manly et al., 2002; Keating and Cherry, 2004; Johnson et al., 2006).

An RSF constructed using conventional logistic regression takes the form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \tag{1}$$

where $\beta_1 \ldots \beta_n$ are coefficients generated from a logistic regression model, $x_1 \ldots x_n$ are covariates, typically environmental features sampled from GIS data, and $w(x)$ represents the predicted relative probability of species occurrence across any habitat patch within the study area (Manly et al., 2002).

RSFs can represent complex species–resource relationships. For the purposes of the sensitivity analyses we developed relatively simple models with one covariate representing variation in vegetation. We used categorical deviation

Table 1 – Description, area, patch size, and selection ratio of vegetation types found across the range of the Wolverine caribou herd and used to assess the sensitivity of resource selection functions to model design, error and bias of animal locations, and misclassification of resource inventories						
Vegetation type	Area (km^2)	Selection ratio	Patch size (ha)			Description
			$\overline{X}$	S.D.	Largest[a]	
Deciduous	384.4	0.566	0.88	9.12	819.8	Primarily stands of *Populus tremuloides* (97%), but also *P. balsamifera* across floodplains
Pine	498.0	0.648	0.62	6.23	814.9	Stands of *P. contorta* with secondary components of *Picea mariana* or *Picea engelmannii* × *P. glauca* in older stands
Spruce	463.6	0.397	0.88	9.43	624.9	Low-elevation sites dominated by *P. engelmannii* × *P. glauca*
Water	474.3	0.543	21.82	543.66	24993.4	Permanent and ephemeral rivers and lakes
Wetlands	347.3	1.118	0.56	4.24	558.6	Shrub/sedge- and forb-dominated wetlands
Krummholz	450.6	0.406	1.35	10.07	539.0	Stunted tree cover of *A. lasiocarpa* on gentle to moderate slopes at elevations of 1300–1600 m
Coniferous	2173.3	0.928	4.31	79.43	5905.2	Mid-elevation stands composed of *A. lasiocarpa*, *P. engelmannii*, and *P. contorta* on moderate to steep slopes
Pine/black spruce	634.7	1.188	0.94	14.41	1968.4	Mixed stands of *P. contorta* and *P. mariana* or pure stands of *P. mariana* found on level to moderate slopes
Pine/spruce	293.7	0.383	1.18	8.53	331.9	Mixed low-elevation stands of *P. contorta* and *P. engelmannii* × *P. glauca*
Pine/fir	212.6	0.729	0.74	4.40	197.1	Mixed mid- to high-elevation stands of *P. contorta* and *A. lasiocarpa*
Pine lichen	199.5	2.397	0.61	6.35	852.0	Low-productivity sites dominated by *P. contorta*
Other	1068.0	0.965	4.86	144.65	15510.1	Reference class for analysis consisting of shrub, lichen, or bryophyte dominated alpine vegetation types

The vegetation map was generated using a supervised classification of a Landsat Thematic Mapper satellite image (Johnson et al., 2003). The selection ratio was calculated as the percentage of animal locations versus the percentage of random locations within a vegetation type.

[a] All vegetation types had a minimum patch size equal to the grain of the GIS data (0.062 ha).

coding (Menard, 2001) to model selection by caribou during winter for 12 vegetation types (Table 1). Vegetation was mapped using a supervised classification of a Landsat Thematic Mapper image (30-m × 30-m pixel resolution; Johnson et al., 2003).

2.4. Introduced error, bias, and model variation

We used observed, not simulated, data to develop the sensitivity analyses. Application of empirical data to the sensitivity analyses allowed us to represent true animal–environment responses, but prevented us from controlling all sources of error and bias. Where possible, we described the error and bias inherent to the animal locations and the vegetation map. Also, given that we developed our analyses from one realisation of observed data these results should be construed as an example of sensitivity analyses, not an absolute finding with direct application to all resources selection studies.

We limited our analyses to what we considered common and controllable factors that influence model interpretation and predictions. These factors included (1) variation in model design; (2) geographic error in species locations; (3) bias in the frequency of sampled animal locations; and (4) thematic misclassification of resource (e.g., vegetation) data. Resource selection functions were developed using fixed-effects or conditional logistic regression, except when examining the effects of model design. Fixed-effects logistic regression requires a sampling approach that spatially relates or matches used to random locations (Compton et al., 2002).

2.4.1. RSF model design
Predictions from RSF species-distribution models can vary depending on how the availability of resources is defined (Boyce et al., 2003). Johnson's (1980) orders of selection often are reported as a rational for delineating resource availability. First-, second-, third-, and fourth-order selection represent the availability of habitats from within the geographic distribution of the species, boundaries of a population, home-range of an individual, and specific feeding patches or sites, respectively. For RSF designs, third-order selection often serves as the scale of interest. Thus, the definition of home-range boundary potentially could influence the area of available resources and selection coefficients. As an alternative to home-range dependent models, some authors have advocated the use

of matched fixed-effects logistic regression (Compton et al., 2002). Fixed-effects logistic regression, allows one to pair samples that are related according to some behavioural or other matching criterion. Here, the likelihood is premised on the difference between two or more paired samples of cases and controls or in this instance used and random locations. We matched used with available locations according to the movement distances of observed caribou. Matching controlled for variation in habitats and behaviour of caribou over time and space. Fixed-effects analyses can be conducted manually for 1-to-1 pairs using conventional logistic regression software, where the independent variable is the difference between the observed values for the case and the control of each pairing (see Hosmer and Lemeshow, 2000). For complex models of *n*-to-*n* relationships, more sophisticated methods are available; we used Stata's Clogit function (Stata Corporation, 2002).

To assess the sensitivity of RSFs to model design, we compared a fixed-effects logistic regression model with conventional logistic regression models developed at the third-order of selection using two commonly reported home-range algorithms (Johnson, 1980). For the matched analyses, each use location was paired with five random locations. Consistent with the approach presented by Arthur et al. (1996), the random locations were sampled from a circle centred on the preceding use location with a radius equal to the 95% movement distance for that GPS relocation interval (e.g., 4 h, 8 h, 12 h, etc.). The movement distance was the simple Euclidean distance between successive GPS collar locations; unique 95% movement distances were calculated for sets of animal locations with similar relocation intervals. For the home-range based RSFs, we calculated a 100% minimum convex polygon and a 95% adaptive kernel home-range with least-squares cross validation. We randomly plotted the same number of locations used for the matched fixed-effects design within each home-range boundary. These random locations quantified the availability of each vegetation type and in combination with the animal use locations served as the dependent variable for each logistic regression.

2.4.2. Positional error in locations
Many distribution models, including RSFs, relate the observed, assumed, or remotely collected locations of a species to a series of environmental features. Depending on the heterogeneity of the environment, location error could have implications for model performance. To assess the sensitivity of model results to positional error, we generated 20 datasets of simulated caribou locations with incrementally greater positional error. For each recorded animal location, we randomly selected *X*, *Y* coordinates from a bivariate normal distribution centred on the actual location, but with an error radius representing a 95% probability of occurrence. Error in the focal animal location was increased in 50-m increments from 50 to 1000 m. This approximates the range of error that one might experience using various monitoring technologies available for wildlife research.

2.4.3. Sampling bias
In addition to being imprecise, sampling of animal or plant locations might be biased. We define bias as a systematic reduction or increase in the frequency of recorded locations related to temporal or spatial constraints on observation. In the case of the monitored caribou, performance of GPS collars was negatively affected by vegetation and topography that blocked the receipt of satellite signals (Frair et al., 2004). Many factors will influence GPS collar performance, thus we could not directly quantify the bias associated with occupancy of particular vegetation types across the study area. To provide an approximate estimate of the sensitivity of model results to sampling bias, we systematically decreased the total number of locations available for analyses by 5% increments up to a 50% loss. The deletion of locations was in proportion to assumed bias associated with each vegetation type and percentage occurrence of caribou within the vegetation type as indicated by the sample data. Bias coefficients were largely subjective, but based on the canopy closure and stem diameter of dominant tree species as well as topography for each vegetation class as observed during field work (Johnson et al., 2001, C. Johnson unpublished data). As an example, the coniferous vegetation type was frequently used by caribou and was characterised by tall large-diameter trees; therefore, the largest proportion of biased location were removed from that type. The selection of each location for deletion within a vegetation class was random.

2.4.4. Misclassification of resources
Models predicting species distribution are often sampled from and extrapolated to digital data contained within a GIS. Thematic misclassification of vegetation, habitat or other resource maps could have implications for model results. To assess the sensitivity of RSF models to misclassification in vegetation maps we introduced systematic decreases in the accuracy of each vegetation type mapped across our study area. We used empirically defined errors of commission from an independent accuracy assessment of our resource map (Johnson et al., 2003) to reassign a percentage of locations to alternate vegetation types. Errors of commission or a decrease in "user's accuracy" occurs when a vegetation type is falsely classified and included within a second type. We randomly misclassified caribou and random locations in 5% increments until 50% of the total sample of locations found within each vegetation type were misclassified. The proportion of locations misclassified to a different type (e.g., pine to spruce) was based on the observed errors of commission for the study area. Introduced misclassification was in addition to existing inherent errors in the resource map (Johnson et al., 2003).

2.5. Assessment of model sensitivity

We assessed the relative sensitivity of model results in three ways. First, we plotted the coefficients and approximate 95% confidence intervals for each vegetation coefficient at their baseline unperturbed values and following the introduction of variation in model design, location bias, and error in animal position and resource mapping. We recognise that coefficients generated for an RSF design are correct, but standard errors might not truly represent sampling variation (Johnson et al., 2006). Thus, we generated bootstrapped confidence intervals using the normal approximation method and 1000 replicates of each perturbed model (Mooney and Duval, 1993).

We chose this method over the percentile or bias-corrected percentile methods because we wanted symmetrical confidence intervals and we noted low levels of bias (Efron, 1982) in the empirical distribution of bootstrapped coefficients. We reported "significant" effects when the perturbation in simulated data resulted in confidence interval bars that did not overlap with the confidence interval bars generated using the baseline model. In cases where the coefficient and confidence intervals changed sign we concluded that the model was extremely sensitive to a particular level of error, bias, or design. Simple interpretation of such coefficients would suggest selection for or avoidance of a resource when in fact coefficients from the baseline model supported the opposite conclusion.

Second, we used a k-fold cross validation procedure to evaluate the influence of the introduced perturbations on the predictive performance of the RSF models (Boyce et al., 2002). The k-fold procedure was performed five times randomly withholding 20% of the data for each iteration. We used a Spearman rank correlation to assess the relationship between predicted occurrence ($w(x)$; Eq. (1)) for withheld animal locations and their frequency within 10 incrementally larger bins of equal size, as defined by the range of predicted data. For example, if predicted occurrences ranged from 0 to 1.0, then the 10 frequency bins would span intervals of 0.1 (e.g., 0–0.1, ..., 0.9–1.0). A predictive model will have a strong mean rank correlation ($\bar{r}_s$) indicating a greater number of withheld locations in frequency bins with relatively larger values.

As a third measure of the sensitivity of model predictions, we calculated the change in area of selected habitats following the application of a different model or the introduction of error and bias. We used quantiles of the unperturbed RSF to rank predictions of caribou occurrence into one of four arbitrary categories that we assumed correlated with habitat quality (poor, low, good, high). Of the total range of predicted RSF values, the first 25% corresponded with poor-quality habitats and the largest 25% corresponded with high-quality habitats (e.g., Carroll et al., 2001). Change in the area of those habitat classes

served as an index of model sensitivity that could be related to conservation and management decisions.

We recognize that patch characteristics and the degree of selection for a vegetation type could potentially influence the magnitude of change in a coefficient. To place our results in the context of these confounding factors, we report a number of patch summary statistics and a simple univariate selection ratio determined as the percentage of use locations versus the percentage of available locations found within a particular vegetation type (Table 1). A ratio of 1 suggests that use of a vegetation type by caribou equals availability of that type across the study area and infers no selection.

3. Results

3.1. Sensitivity of coefficients

The 12 vegetation types found across the resource map varied considerably in their spatial extent and apparent selection by caribou (Table 1). Using the maximum absolute percentage change for each coefficient, median change was lowest for RSF model design (65.9%) followed by misclassification of resources (71.9%), sampling bias (76.7%), and positional error (121.8%) (Table 2). Following the introduction of positional error to animal locations six of the 11 vegetation types deviated from baseline coefficient values with an assumed location error of 0 m. We observed non-overlapping 95% confidence intervals after as little as 200 m of simulated error in the X, Y coordinates. Of greatest concern when interpreting such results, the coefficient for spruce changed sign, indicating selection by caribou versus avoidance, following the introduction of 1000 m of positional error (Table 2, Fig. 2).

Across all sensitivity analyses, the most strongly selected vegetation type, pine lichen, suffered the greatest influence of bias and error in data, and variation in model design. For example, pine lichen varied from the baseline model after only a 10% error in the classification of resources and a positional error of 200 m (Figs. 2 and 3). Across all vegetation

Table 2 – Sensitivity of RSF coefficients to variation in model design, positional error, sampling bias, and misclassification of vegetation types

Habitat	RSF model design		Positional error (m)		Sampling bias (%)		Misclassification of resources (%)	
	%β Change	Diff. β	%β change	Diff. β	%β change	Diff. β	%β change	Diff. β
Pine/fir	−65.9	No	−75.5	No	−76.7	No	−47.6	No
Pine	219.0	No	−155.2	No	−179.0	No	−133.3	No
Pine lichen	44.1	Yes	−69.9	200 m	29.5	No	−60.2	10%
Wetlands	−26.2	No	−76.1	250 m	−39.1	No	−71.9	35%
Coniferous	−118.6	No	−349.8	650 m	−4053.6	25%	−340.7	No
Spruce	−41.3	No	−129.2	350 m	142.2	45%	−49.5	No
Pine/spruce	−65.6	No	−121.8	250 m	24.1	No	−61.2	No
Krummholz	63.1	No	−64.5	No	−112.9	50%	−89.7	20%
Pine/black spruce	74.9	Yes	−43.0	No	17.8	No	−20.7	No
Deciduous	294.4	Yes	−122.6	No	−34.1	No	−157.8	No
Water	−163.8	No	−275.5	600 m	−282.3	No	−134.0	No

Percent β change represents the maximum change in coefficient (β) values for each vegetation type from the baseline unperturbed model; different (Diff.) β, indicates the level of error or bias at which coefficients and associated confidence intervals failed to overlap the baseline model.
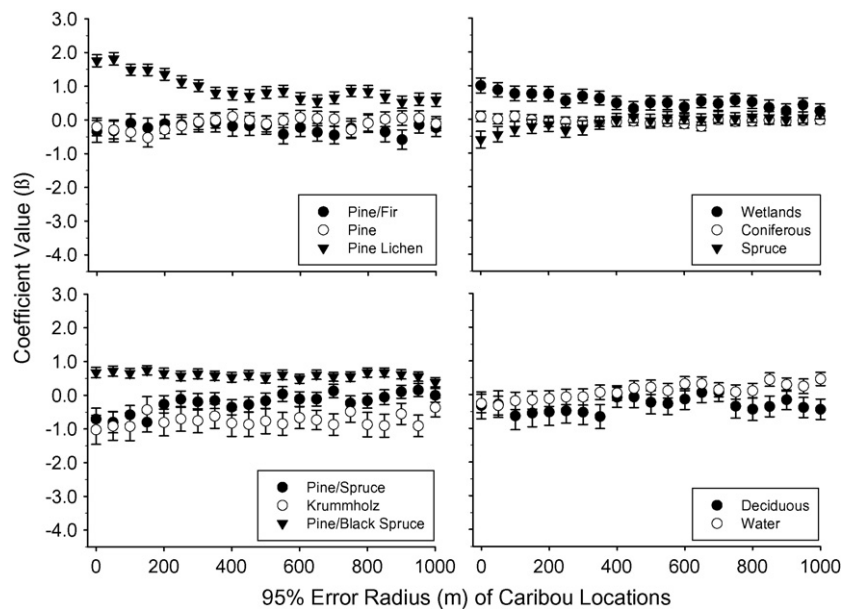
Fig. 2 – Change in β coefficients for 11 vegetation types generated from woodland caribou resource selection functions models following the systematic introduction of error in the X, Y coordinates of caribou locations. Error bars represent 95% confidence intervals.

types, the sensitivity analysis for positional error had the greatest number coefficients that deviated from the baseline values (Fig. 2). We observed only three coefficients with significant differences from baseline for each of the model design, sampling bias, and misclassification of resources scenarios (Figs. 3–5). Furthermore, systematic bias was apparent only for the resource misclassification scenario. In this case, increasing misclassification error caused most coefficients to trend toward a beta coefficient of 0 (i.e., no observable selection). Relative to sampling of resource availability, our

simulation suggested that the magnitude of effect was dependent on vegetation type. For example, depending on the vegetation type, the adaptive kernel home-range produced the largest or smallest coefficient of the three resource availability schemes.

3.2. Sensitivity of predictive accuracy

The unperturbed baseline RSF model had excellent predictive power ($\bar{r}_s = 0.933$, $P < 0.001$). Although 95% confidence inter-
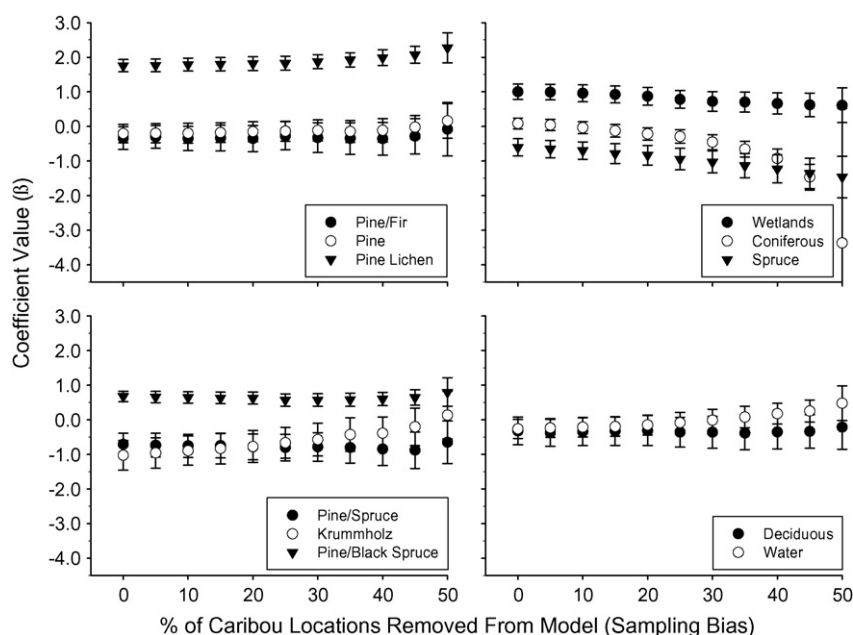

Fig. 3 – Change in β coefficients for 11 vegetation types generated from woodland caribou resource selection functions models following the systematic introduction of sampling bias to each type. Error bars represent 95% confidence intervals.
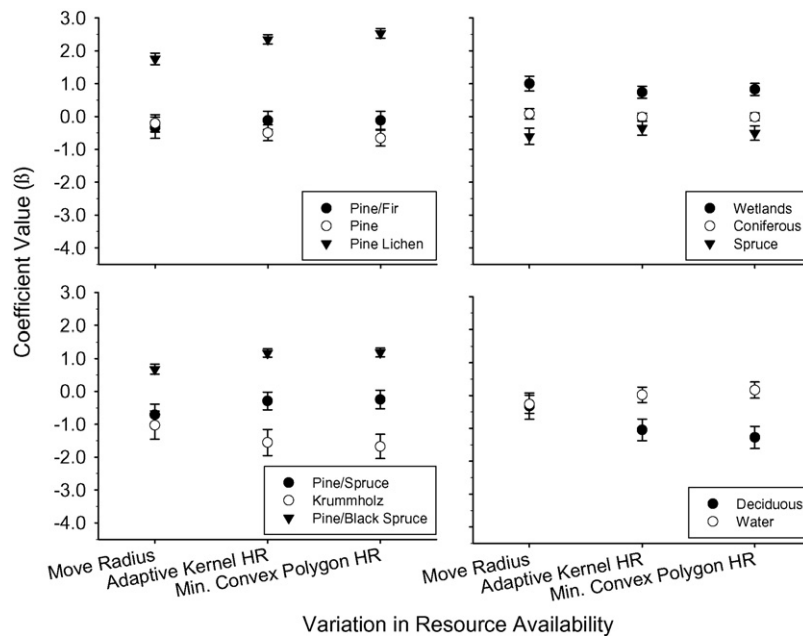
Fig. 4 – Change in β coefficients for 11 vegetation types generated from woodland caribou resource selection functions models using matched logistic regression and availability radii defined by the 95% movement radius for each location interval (see Fig. 1), and conventional logistic regression and availability defined by a 95% adaptive kernel or 100% minimum convex polygon home-range (HR; see Fig. 1). Error bars represent 95% confidence intervals.

vals generated from the five k-fold samples were large, mean Spearman correlation values suggested that positional error had the largest influence on the predictive performance of RSF models. For that sensitivity analysis, mean correlation values dropped below 0.8 following the introduction of 400 m of positional error (Fig. 6A). We recorded variation, but little

consistent drop in prediction success for home-range derived RSF models or models subject to location bias (Fig. 6B and C). The incorrect identification of resources appeared to be a factor for model prediction only following the misclassification of vegetation attributes recorded at >15% of caribou and random locations (Fig. 6D).
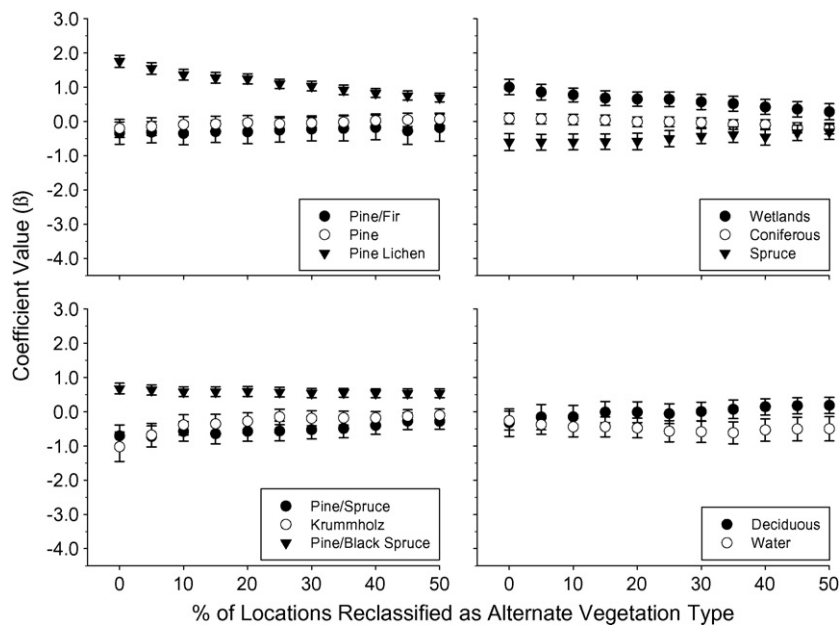

Fig. 5 – Change in β coefficients for 11 vegetation types generated from woodland caribou resource selection functions models following the systematic introduction of thematic misclassification to each vegetation type. Error bars represent 95% confidence intervals.
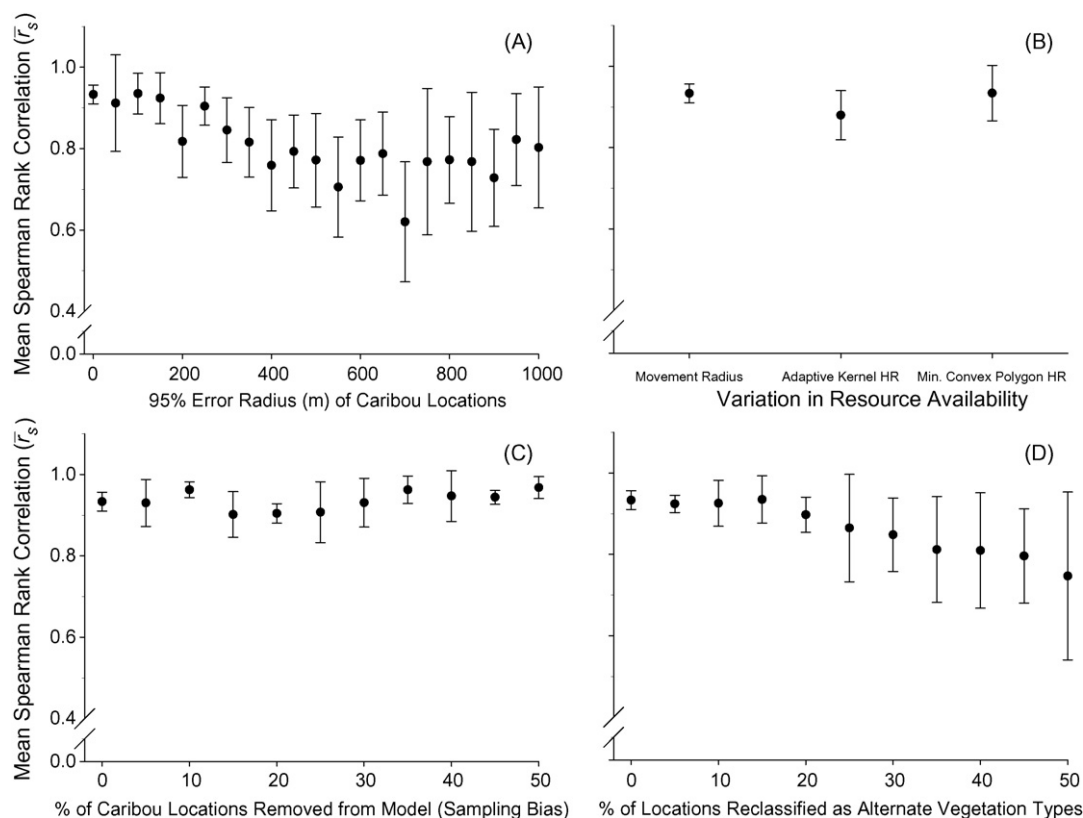
Fig. 6 – Change in the predictive success ($\bar{r}_s$) of resource selection function models for woodland caribou following the introduction of error in the X, Y coordinates at caribou locations (A), the redefinition of resource availability (B), the introduction of sampling bias to each vegetation type (C), and the introduction of thematic misclassification to each vegetation type (D). Error bars represent 95% confidence intervals generated from 5 k-fold replicates.

3.3. Sensitivity of selected habitats

Following the calculation of quartiles and extrapolation of model coefficients to GIS data, the high-quality habitat class was less sensitive than the other three habitat classes to the introduction of error and bias and variation in model design. For example, the area of high-quality habitat was consistent across the movement radius and home-range RSF models and converted to a less valued type after the introduction of 450 m of positional error or a 30% sampling bias for caribou locations (Fig. 7A–C). Misclassification of vegetation impacted the area of high-quality habitat across the range of introduced perturbation, but only up to a maximum of 304.6 km² (Fig. 7D). That sensitivity analysis was influenced not only by change in coefficient values, but also a modified distribution of vegetation types across the study area corresponding with the level of thematic misclassification. The largest and smallest changes in area across all habitat types occurred following the introduction of location bias and after varying RSF models, respectively (Fig. 7C and A). When considering location bias, the area of high-quality habitat nearly doubled after the selective removal of 30% of the caribou locations. A systematic decrease in the value of the coefficient with the largest distribution, coniferous, accounted for the dramatic change in the area of ranked habitats (Table 1).

4. Discussion

Our analyses revealed that coefficients and predictions of species-distribution RSF models are sensitive to bias and error in dependent and independent data and model design. Sensitivity, however, should be considered a relative construct specific to the question or prediction at hand. Model validity is only threatened by sensitive parameters when uncertainty eclipses the precision required for the decision making process. Given our results, when should practitioners question their data and modelling approach?

If the direct values of coefficients are an important component of model inference, then our analyses suggest that species-distribution RSF models are sensitive to some levels of the range of variation we simulated. Given the magnitude of change in coefficients we observed, one should be concerned about interpretations using metrics such as odds ratios (Menard, 2001). Change in coefficient values also invalidated simple conclusions such as statistically identifiable selection or avoidance of resources and in one case a coefficient changed sign suggesting an interpretation opposite from the true selection pattern. In general, increases in sampling bias and positional error led to coefficients that converged toward 0, decreasing our ability to statistically identify selection or avoidance of resources. That relationship, however, was nonlinear and inconsistent across vegetation types. Following
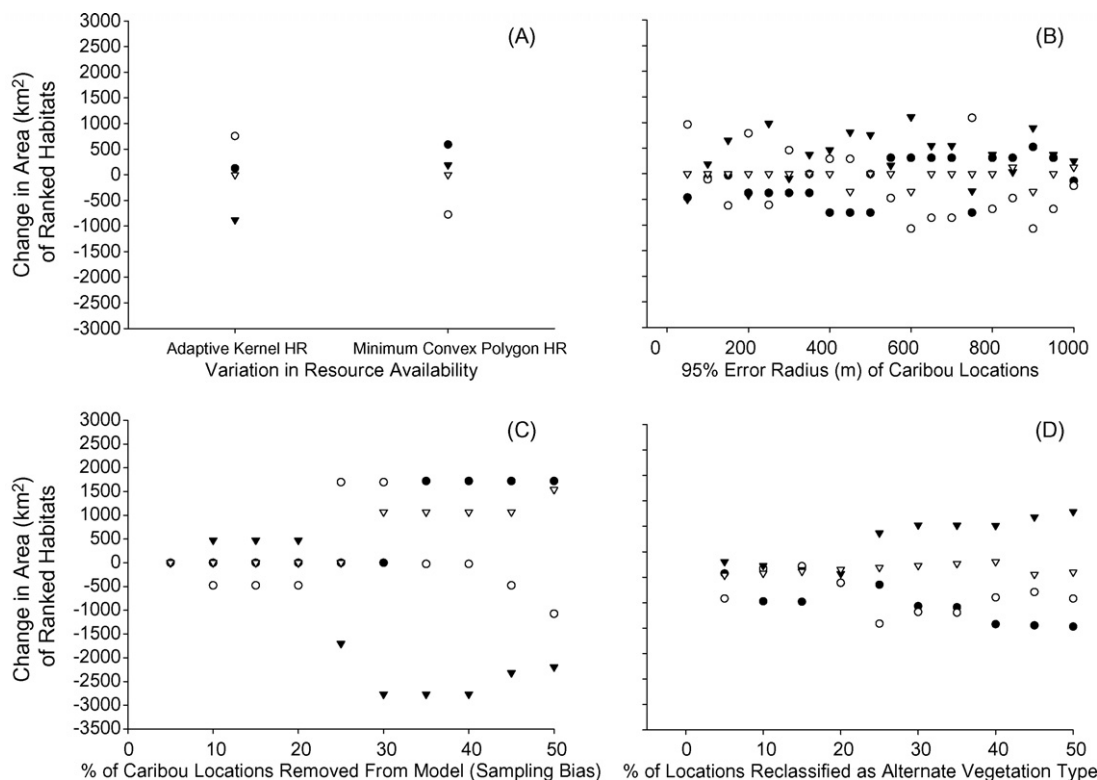
Fig. 7 – Change in the area (km²) of ranked habitats of woodland caribou with variation in resource selection models (A) and following the introduction of error (B) and sampling bias in caribou locations (C), and systematic misclassification of a vegetation map (D). A fixed-effects RSF served as the reference from which categorical breaks in habitat quality were defined and differences in habitat area were calculated. The fixed-effects RSF had 1207.9, 1071.3, 3739.4, and 1181.5 km² of poor- (●), low- (○), good- (▼), and high-quality (▽) habitats, respectively.

the introduction of location error, coefficients for some types appeared to increase or decrease sharply up to some level of error before maintaining a relatively consistent value. We suspect that such nonlinearities are a function of vegetation patch size (Table 1). When error exceeds mean patch size the influence of imprecision in species locations should stabilize (Rettie and McLoughlin, 1999). In general, practitioners should be most concerned about positional error when interpreting coefficients that are highly selected or avoided.

Inherent nonexperimental sources of bias and error limit our ability to make exact recommendations concerning model reliability. We can, however, perform a relative comparison of the four sensitivity analyses and assess model responses within the context of current expectations for data used in similar studies. Considering the three evaluation measures, RSF is least sensitive to the definition of resource availability. The fixed-effects and home-range-based models differed relatively little in predictive ability and the ranking of habitats. One could argue that fixed-effects models are a more precise method for studying resource selection as they allow control of temporal and spatial variation in resources and avoid issues of selecting and properly estimating home-range boundaries (Girard et al., 2002). Ultimately, however, if prediction of occurrence and important habitats are the primary products of a species-distribution model then logistic regression-based RSFs appear robust to such choices. This conclusion might not hold where availability radii are generated for markedly

different spatial scales than we represented, or where the interpretation of coefficient values is necessary (Boyce et al., 2003).

Model results and predictions were most sensitive to introduced error in the position of recorded animal locations. For our data, coefficients of highly selected or avoided vegetation types differed from the baseline model following ≥200 m of introduced positional error. Mean predictive success also declined at the 250-m mark; although, the area of ranked habitats varied within this error threshold. Fortunately, new technology has increased researchers' ability to collect precise location data for a range of species. Accuracy and precision of locations collected with GPS devices, collars, and tags should be well below the 250-m mark we identified. Other methods of location such as GPS assisted radiotelemetry, triangulation, map location, or Argos satellite collars may approach or surpass that error threshold (Keating et al., 1991; Leptich et al., 1994).

There is little a researcher can do to directly rectify positional error in species locations. Of a number of indirect solutions, one could amalgamate similar patch types with the goal of increasing the mean patch size. Such an approach would lower the error threshold of species locations occurring in some habitat types, but would sacrifice the resolution of inference. One also could generate error buffers around locations and include the percentage occurrence of a resource as a model covariate or sensor all point locations that might fall

within more than one habitat type (Zimmerman and Powell, 1995). Error buffers will decrease the ability to detect selection whereas censoring could potentially result in the elimination of a large number of locations for species that occupy ecotones or heterogeneous landscapes (Rettie and McLoughlin, 1999). A third approach is to subsample locations from within an error polygon to calculate the proportion and precision of used habitats (Samuel and Kenow, 1992; Kenow et al., 2001).

Although GPS devices provide unprecedented accuracy and precision, location acquisition success is correlated with habitat features and is therefore a potentially confounding factor for species-distribution models. A number of studies have attempted to measure and report the extent and sources of bias within different ecosystems (Edenius, 1996; Dussault et al., 1999; D'Eon et al., 2002). Although those efforts are noteworthy, we are aware of no work that has assessed the tradeoff in location accuracy for selection bias when employing GPS devices. Typically, researchers have looked at either the bias or accuracy issue and have reported that both can have significant influences on the results of resource selection and species-distribution studies (Johnson et al., 1998; Frair et al., 2004). For our study area, bias should be less of a concern than location quality.

For the majority of covariates in our models, bias was not important until confidence intervals failed to overlap following the selective loss of 25% or more locations. That value is larger than some fix acquisition rates reported for GPS collars in forested environments and levels of false negatives for visual or audible presence–absence surveys (Moen et al., 1996; Edenius, 1996; Dussault et al., 1999; Johnson et al., 2002b; Diefenbach et al., 2003; Gu and Swihart, 2004; but see Tyre et al., 2003). We reiterate that our bias factors are only scaled approximations of how GPS collars performed across our study area relative to canopy closure and topography. Based on field experience and the results of other studies, relative differences among vegetation types are likely realistic, but absolute differences cannot be determined.

Field and controlled research has demonstrated that fix acquisition rates are not exclusively a product of vegetative and topographic elements of habitats (D'Eon et al., 2002; Heard et al., In Press). Thus, it is difficult for researchers to conclusively determine the level of bias in data collected from collars deployed on free-ranging animals. Based on experimental studies, we should expect a reduced number of locations from GPS collars in vegetation types with large-diameter, dense stands of trees with closed canopy conditions (Moen et al., 1996). Detection rates may be easier to establish for studies where presence is determined through visual or audible cues (Diefenbach et al., 2003). Regardless of the approach, where bias is thought to be an issue, sample weighting, iterative simulation, appropriate statistical models, and buffers around locations or movement vectors might be suitable solutions (Rettie and McLoughlin, 1999; Kenow et al., 2001; Johnson et al., 2002a; Tyre et al., 2003; Frair et al., 2004). As with location error, some corrective efforts come at a cost including decreased location accuracy and reduced ability to detect resource selection.

For the levels and types of thematic misclassification we introduced, most coefficients did not significantly differ from the baseline model, although pine lichen and krummholz types demonstrated change after as little as a 10 and 20% misclassification rate, respectively. Mean predictive accuracy, as assessed with the k-fold cross validation procedure, declined following the introduction of a 20–25% misclassification rate and the area of the four habitat classes began to vary markedly with a 25% misclassification rate. Most reported accuracy assessments for vegetation or habitat maps fall close to or below this threshold. As examples, the map used for this work had an overall accuracy of 77% (Johnson et al., 2003), Franklin et al. (2001) reported an accuracy of 75% for vegetated grizzly bear habitat classes mapped using satellite imagery, and Morrison (1997) achieved an average accuracy of 90% when using satellite imagery to map shorebird habitats.

With the exception of radiometric error across a small portion of pixels, misclassification of resource maps should be considered a source of bias not error. A map will have a finite number of resources, habitats, or vegetation types and typically misclassification from one type to another is not a random process. Using remotely sensed spectral data, misclassification rates will covary for types with similar reflectance patterns (Franklin et al., 2001; Johnson et al., 2003). Errors of commission could lead to changes in coefficient values that falsely suggest selection or avoidance or errors could offset for no net change in apparent selection, as we observed for the pine/black spruce type. These relationships could be difficult to determine for resource maps consisting of many different types.

5. Recommendations and conclusions

Our results suggest that the interpretation of RSF species-distribution models can be confounded by error and bias in the dependent and independent variables and differences in model design. Conclusions are most sensitive to the strict interpretation of coefficients when compared to prediction success and categorical maps of habitat quality. Species location error appeared to be the greatest contributing factor to reduced accuracy in selection coefficients. Uncertainty inherent to model selection, non-representative sampling of study subjects, and positional error in resource maps are other factors that could further threaten the precision and accuracy of predictions.

We must caution that the results of our simulations may be specific to the study species or area we modelled. We expect some parallels with other ungulate species and data types, but interactions between coefficient values, resource types, patch size, and the distribution of the organism will confound indices of model sensitivity. We have, however, provided a framework for practitioners to conduct study-specific sensitivity analyses. Although we believe such follow-up analyses are important we could find few examples of species-distribution studies reporting the sensitivity of model data and uncertainty around predictions (but, see Buckland and Elston, 1993; Loiselle et al., 2003). Although less onerous, most researchers also fail to evaluate and report anticipated or measured error and bias in species locations and maps or the implications of model choice. Our results confirm the recommendations of others: researchers should evaluate and report the data from which models are constructed, rectify the most sensitive

sources, and conclude with an uncertainty analysis to determine the range of potential results (Burgman et al., 2001; Elith et al., 2002; Regan et al., 2002). Sensitivity and uncertainty analyses are essential if models are to enlighten our understanding of ecological processes and patterns or to provide useful guidance for management and conservation decision making.

Acknowledgments

REFERENCES

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., 2007. Species distribution models and ecological theory: a critical assessment and some possible approaches. Ecol. Modell. 200, 1–19.

Boyce, M.S., McDonald, L.L., 1999. Relating populations to habitats using resource selection functions. Trends Ecol. Evol. 14, 268–272.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K.A., 2002. Evaluating resource selection functions. Ecol. Modell. 157, 281–300.

Boyce, M.S., Mao, J.S., Merrill, E.H., Fortin, D., Turner, M.G., Fryxell, J., Turchin, P., 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10, 421–431.

Buckland, S.T., Elston, D.A., 1993. Empirical models for the spatial distribution of wildlife. J. Appl. Ecol. 30, 478–495.

Burgman, M.A., Breininger, D.R., Duncan, B.W., Ferson, S., 2001. Setting reliability bounds on habitat suitability indices. Ecol. Appl. 11, 70–78.

Carroll, C., Noss, R.F., Paquet, P.C., 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecol. Appl. 11, 961–980.

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.

Crosetto, M., Tarantola, S., 2001. Uncertainty and sensitivity analysis: tools for GIS-based model implementation. Int. J. Geogr. Inf. Sci. 15, 415–437.

D'Eon, R.G., Serrouya, R., Smith, G., Kochanny, C.O., 2002. GPS radiotelemetry error and bias in mountainous terrain. Wildl. Soc. Bull. 30, 430–439.

Dettki, H., Lofstrand, R., Edenius, L., 2003. Modelling habitat suitability for moose in coastal northern Sweden: empirical vs process oriented approaches. Ambio 32, 549–556.

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.

Dussault, C., Courtois, R., Ouellet, J.-P., Huot, J., 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. Wildl. Soc. Bull. 27, 965–972.

Edenius, L., 1996. Field test of a GPS location system for moose Alces alces under Scandinavian boreal conditions. Wildl. Biol. 3, 39–43.

Efron, B., 1982. The Jacknife, the Bootstrap, and Other Resampling Plans. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.

Elith, J., Burgman, M.A., Regan, H.M., 2002. Mapping epistemic uncertainties and vague concepts in predictions of species distribution. Ecol. Modell. 157, 313–329.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., Mao, J.S., 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86, 1320–1330.

Frair, J.L., Nielson, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B., Beyer, H.L., 2004. Approaches for removing GPS-collar bias in habitat-selection studies. J. Appl. Ecol. 41, 201–212.

Franklin, S.E., Stenhouse, G.B., Hansen, M.J., Popplewell, C.C., Dechka, J.A., Peddle, D.R., 2001. An integrated decision tree approach IDTA. to mapping landcover using satellite remote sensing in support of grizzly bear habitat analysis in the Alberta Yellowhead Ecosystem. Can. J. Remote Sens. 27, 579–592.

Girard, I., Ouellet, J.-P., Courtois, R., Dussault, C., Breton, L., 2002. Effects of sampling effort based on GPS telemetry on home range size estimations. J. Wildl. Manage. 66, 1290–1300.

Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. Biol. Conserv. 116, 195–203.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186.

Heard, D.C., Vagt, K.L., 1998. Caribou in British Columbia: a 1996 status report. Rangifer 10, 117–123.

Heard, D.C., Ciarniello, L.M., Seip, D.R., In Press. Grizzly bear behavior and GPS collar fix rates. J. Wild. Manage.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. John Wiley and Sons, New York, New York, USA.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71.

Johnson, C.J., Gillingham, M.P., 2004. Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. J. Appl. Ecol. 41, 1032–1041.

Johnson, B.K., Ager, A.A., Findholt, S.L., Wisdom, M.J., Marx, D.B., Kern, J.W., Bryant, L.D., 1998. Mitigating spatial differences in observation rate of automated telemetry systems. J. Wildl. Manage. 62, 958–967.

Johnson, C.J., Parker, K.L., Heard, D.C., 2001. Foraging across a variable landscape: behavioural decisions made by woodland caribou at multiple spatial scales. Oecologia 127, 590–602.

Johnson, C.J., Parker, K.L., Heard, D.C., Gillingham, M.P., 2002a. A multiscale behavioral approach to understanding the movements of woodland caribou. Ecol. Appl. 12, 1840–1860.

Johnson, C.J., Heard, D.C., Parker, K.L., 2002b. Expectations and realities of GPS animal location collars: results of three years in the field. Wildl. Biol. 8, 153–159.

Johnson, C.J., Alexander, N.D., Wheate, R.D., Parker, K.L., 2003. Characterizing woodland caribou habitat in sub-boreal and boreal forests. Forest Ecol. Manage. 180, 241–248.

Johnson, C.J., Seip, D.R., Boyce, M.S., 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J. Appl. Ecol. 41, 238–251.

Johnson, C.J., Nielsen, S.E., Merrill, E.H., McDonald, T.L., Boyce, M.S., 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. J. Wildl. Manage. 70, 347–357.

Keating, K.A., Cherry, S., 2004. Use and interpretation of logistic regression in habitat-selection studies. J. Wildl. Manage. 68, 774–789.

Keating, K.A., Brewster, W.G., Key, C.H., 1991. Satellite telemetry: performance of animal-tracking systems. J. Wildl. Manage. 55, 160–171.

Kenow, K.P., Wright, R.G., Samuel, M.D., Rasmussen, P.W., 2001. Integrating SAS and GIS software to improve habitat-use estimates from radiotelemetry data. Wildl. Soc. Bull. 29, 1006–1009.

Leptich, D.J., Beck, D.G., Beaver, D.E., 1994. Aircraft-based Loran-C and GPS accuracy for wildlife research on inland study sites. Wildl. Soc. Bull. 22, 561–565.

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. Conserv. Biol. 17, 1591–1600.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002. Resource Selection by Animals, second ed. Kluwer Academic Publishers, Dordrecht, The Netherlands.

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

Menard, S., 2001. Applied logistic regression, second ed. Sage University Paper Series on Quantitative Applications in the Social Sciences, series no. 07–106, Thousand Oaks, California, USA.

Moen, R., Pastor, J., Cohen, Y., Schwartz, C.C., 1996. Effects of moose movement and habitat use on GPS collar performance. J. Wildl. Manage. 60, 659–668.

Mooney, C.Z., Duval, R.D. 1993. Bootstrapping a nonparametric approach to statistical inference. Sage University Paper Series on Quantitative Applications in the Social Sciences, series no. 07-095, Thousand Oaks, California, USA.

Morrison, R.I.G., 1997. The use of remote sensing to evaluate shorebird habitats and populations on Prince Charles Island, Foxe Basin. Canada Arctic. 50, 55–75.

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecol. Modell. 133, 225–245.

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

Regan, H.M., Colyvan, M., Burgman, M.A., 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. Ecol. Appl. 12, 618–628.

Rettie, W.J., McLoughlin, P.D., 1999. Overcoming radiotelemetry bias in habitat-selection studies. Can. J. Zoolog. 77, 1175–1185.

Samuel, M.D., Kenow, K.P., 1992. Evaluating habitat selection with radio-telemetry triangulation error. J. Wildl. Manage. 56, 725–734.

Stata Corporation, 2002. Stata Statistical Software: Release 7.0. College Station, Texas, USA.

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K., Possingham, H.P., 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecol. Appl. 13, 1790–1801.

Zimmerman, J.W., Powell, R.A., 1995. Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Can. J. Zoolog. 73, 1123–1133.