

American black bear habitat selection in northern Lower Peninsula, Michigan, USA, using discrete-choice modeling

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Abstract: Since 1990, increases in American black bear (*Ursus americanus*) population and distribution in the Lower Peninsula of Michigan, USA, have led to positive trends in black bear harvests, sightings, and nuisance reports. Policy makers and wildlife managers can prepare for the difficult task of managing future bear–human interactions by using resource selection models to assess bear habitat selection and predict future bear range expansion. We modeled habitat selection by black bears in the northern Lower Peninsula of Michigan using 6 environmental variables based on radiotelemetry locations from 1991–2000 for 20 males and 35 females. We developed Bayesian random effects discrete-choice models for males and females separately to estimate probability of bear selection of grid cells at 3 spatial resolutions (1 km², 4 km², 9 km²). These models weight individual bears and their relocations, allowing inference about both individual and population-level selection characteristics. We assessed goodness-of-fit of individual models using a Bayesian *P* value that estimated deviance between a simulated dataset and the observed dataset. Models for males at the 9-km² resolution and for females at 4-km² resolution fit our data better than others; both indicated that locations of bears were negatively associated with water, small and medium roads, mean patch size, patch size coefficient of variation, edge density, developed land-use, and non-forested wetlands, and positively associated with Shannon's diversity index, aspen (*Populus* spp.), and forested wetlands. Furthermore, the variability in selection by individual female bears for non-forested wetland and individual male bears for agriculture was large relative to the variability in selection of other land-use or land-cover types. Male bears had more heterogeneity with respect to selection of land-use or land-cover types than female bears. There were significant correlations between male bear age and their respective selection parameter estimates for small roads, medium roads, and developed land-use. Running Bayesian random effects discrete-choice models at multiple resolutions accounted for variability due to unequal sample sizes and bear behavior, and demonstrate the utility of the Bayesian framework for bear management purposes.

Key words: American black bear, Bayesian, discrete-choice, habitat modeling, habitat selection, Michigan, northern Lower Peninsula, random effects, *Ursus americanus*

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Trend information since 1990, as indicated by American black bear (*Ursus americanus*, hereafter, bear) harvest reports, sightings, and nuisance reports, demonstrates that bear numbers have been increasing and expanding their range in Michigan's Lower Peninsula. Analysis of bear distribution

through time supports the conclusion that the bear population in Michigan will likely expand from the northern Lower Peninsula (NLP) to the southern Lower Peninsula in the future (Etter 2002). A larger population of bears throughout the state presents several unique opportunities for state and federal wildlife management agencies, including the potential to increase recreational wildlife viewing and

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sport hunting, both of which are significant industries in Michigan's economy (US Department of the Interior 2006).

However, an increase and southward expansion of Michigan's bear population will present difficult challenges for wildlife agencies as well. If current patterns of human land-use changes continue, forest acreage in Michigan could decrease 2 to 7% and developed areas could increase by 178% by 2040 (Public Service Consultants 2001). The expansion of human land uses coupled with bear population growth will likely increase bear–human conflicts, a trend occurring in several places in the eastern United States (Carr and Burgess 2001, Ternent 2005). Such conflicts, although rarely involving human injury or death, often have economic impacts. Thus, modeling bear habitat selection may provide useful information on the distribution and dynamics of bear populations, enabling wildlife management agencies to plan for bear–human interactions accordingly.

Discrete-choice models are well suited to modeling the aggregate statistical properties of a bear population over large spatial extents. The underlying theory of discrete-choice is derived from economic theory that suggests consumers choose some product over others to maximize their satisfaction (Cooper and Millspaugh 1999). McCracken et al. (1998), Cooper and Millspaugh (1999), and Manly et al. (2002) modified and extended the application of discrete-choice models to wildlife studies of resource selection, which have since been used to model the likelihood of habitat use by spotted owls (*Strix occidentalis*; McDonald et al. 2006) and caribou calves (*Rangifer tarandus*; Thomas et al. 2006), as well as the tendency of female black bears to stay in the same habitat type (Ramsey and Usner 2003). In discrete-choice modeling, the probability that an individual bear will select a patch of land (not confined to a specific habitat type) relative to all other available patches is modeled as a discrete-choice from a choice set. Discrete-choice models allow each patch of the choice set to be characterized by both categorical and continuous variables (McCracken et al. 1998, Thomas et al. 2006).

Habitat selection analyses typically do not incorporate individual heterogeneity in resource selection adequately when determining population-level selection criteria. For instance, some studies average individual parameters to estimate population-level selection (Glenn et al. 2004). If the animals under

study have differing numbers of relocations (e.g., telemetry locations), such averaging would lead to incorrect calculation of error terms. Other studies use equal-sized subsets of animal relocation data to estimate population-level selection (Miller et al. 2000), which wastes relocation data that are informative, hard to collect, and may have otherwise improved selection parameter estimation. A model with random effects can weight individual bears based on the number of relocations, and in doing so, account for individual heterogeneity when estimating population-level selection (Gillies et al. 2006). As a result, inferences including valid error terms can be made about individual and population-level selection characteristics (Thomas et al. 2006). Measuring individual animal habitat selection, in addition to population-level selection, enables wildlife researchers and managers to explore the ecological relationships among landscape features and specific animal characteristics. This is particularly useful in evaluating wildlife–habitat relationships with respect to life-history stage, which in turn can help predict the demographic response of an animal population to a set of landscape features. Random effects have been employed in wildlife studies, including models of demographic change in spotted owls (Clark 2003), population trends of harbor seals (*Phoca vitulina*; Ver Hoef and Frost 2003), and habitat selection by cerulean warblers (*Dendroica cerulea*) across multiple spatial scales (Link and Sauer 2002).

Bayesian analysis is well suited for models with random effects because all parameters are treated as random variables with probability distributions (Ellison 1996, Link et al. 2002). Ecologists are increasingly using Bayesian statistical inference to estimate habitat selection parameters (Ellison 2004). However, in a Bayesian framework, the complexity and high dimensionality of models with random effects make direct computation of selection parameter estimates unfeasible. Recently, software packages like WinBUGS (<http://www.mrc-bsu.cam.ac.uk/bugs>) have employed a Bayesian framework and used Markov Chain Monte Carlo (MCMC) simulations to estimate parameter distributions (Lunn et al. 2000).

The primary objective of this research was to create and apply a model that quantified how various environmental attributes influence bear (at individual and population-level) habitat selection at a landscape scale. We then use this model to estimate and map the likelihood of habitat selection

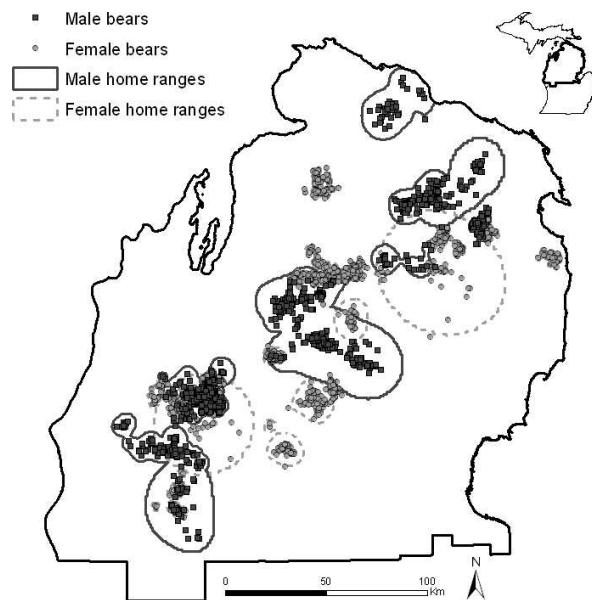


Fig. 1. Aggregate home range calculated separately for male and female American black bears by combining 95% kernel home ranges of individual bears. Kernel home ranges calculated from radiotelemetry locations collected 1991–2000 in the northern Lower Peninsula of Michigan, USA.

throughout the NLP. We also use the model results to explore how habitat selection varies with respect to individual animal age and sex.

Bear radiotelemetry location data were collected throughout the NLP by the Michigan Department of Natural Resources, 1991–2000. In addition, data on environmental and habitat attributes in Michigan that may be important to bear populations were collected or, in some cases, derived. Bayesian random effects discrete choice models were used to model bear selection of grid cells at 3 spatial resolutions: 1 km², 4 km², and 9 km². Different resolutions were used to evaluate model results for sensitivity to scale. The GIS model predictions also indicated spatial relationships (proximity and dispersion) between preferable habitats across the landscape.

Study area

Bears were trapped and radiocollared in the NLP of Michigan, which encompassed 47,120 km² and included 33 counties (Fig. 1). The NLP is in the Northern Lacustrine-Influenced Region of Lower Michigan and is distinguished from the southern

Lower Peninsula by having cooler temperatures throughout the year and a shorter and more variable growing season. Precipitation is more uniform across the state than temperature (Barnes and Wagner 2004).

Approximately 12,981 km² (27.5%) of the NLP is publicly owned (national forests, state parks, wildlife refuges). The land use and land cover of the NLP comprised 15% agriculture, 16% upland non-forested (low density trees, upland shrub, and herbaceous open land), 17% northern hardwood and mixed hardwood (upland deciduous, mixed upland deciduous, upland mixed forest), 9% oak (dominated by *Quercus* spp.), 10% aspen (dominated by *Populus* spp.), 9% pine (dominated *Pinus* spp.), 11% forested wetland (lowland deciduous forest, lowland coniferous forest, lowland mixed forest), 6% non-forested wetland (lowland shrub, emergent wetland, floating aquatic), and 7% other. The land use and land cover of the region has changed considerably since the middle of the 19th century because of intensive logging for white pine (*Pinus* spp.), hemlock (*Tsuga* spp.), and northern hardwoods. Following this intensive logging were catastrophic fires that additionally altered the land cover. For this reason, early successional forest types including aspen and birch (*Betula* spp.) forests were more prevalent during the study than they were in the middle of the 19th century (Barnes and Wagner 2004).

Methods

Radiotelemetry and home range estimation

During 1991–2000, the Michigan Department of Natural Resources (MDNR) captured bears throughout the NLP in barrel traps or in winter dens (Etter 2002). Bears were fitted with radiocollars equipped with a time-delayed mortality switch. MDNR field staff attempted to collect a location for each bear no less than once/2 weeks during the non-denning season (Apr–Nov). Bears were located during daylight hours at intervals of at least several days. Bears were located to the nearest 16 ha using a GPS unit from a fixed-winged aircraft or triangulated from the ground using a hand-held yagi antenna. Triangulated locations were determined using a minimum of 2 radiotelemetry bearings with the maximum likelihood estimator in LOCATE II (Nams 1990). Locations with error polygons >16 ha were removed from analysis, as were bears <2 years old because they were likely correlated with locations

of their mothers. Using these criteria, 2,670 radio-telemetry locations from 35 females and 1,408 locations from 20 males (Etter 2002:Fig 1) qualified for inclusion in our models. The MDNR estimated the ages for all females and for 19 of 20 males using a cross section of a pre-molar tooth collected at capture (Willey 1974). We calculated the mean age of each bear across the years contributing radiotelemetry data.

We estimated home range size for each bear using the kernel density estimator tool from HawthsTools extension within ESRI's ArcGIS software program (ESRI 2002). We mapped 95% home range areas using a fixed kernel with a least-squares cross-validation smoothing parameter. For home range estimation, we included only bears with at least 30 locations because that sample size is required for dependable fixed kernel estimates of home range size (Seaman et al. 1999). Although sample size should be >30 for accurate home range estimation, small samples do not disqualify application of the discrete choice model itself, which can use any number of observations. We used the union of home ranges among males and females to represent available habitat to all bears of each sex. We used separate models for males and females because of their different habitat requirements and behavior (Clark et al. 1993).

Model resolution and data preparation

Model resolution. We chose grids with cell resolutions of 1 km², 4 km², and 9 km² to correspond approximately with ranges of daily bear movements (1, 2, 3 km) identified from previous black bear studies (Amstrup and Beecham 1976, Alt et al. 1980). We overlaid these grids on home range coverages of male and female bears using ArcGIS (ESRI 2002). For female bears we used 2,856 (1 km²), 1,467 (4 km²), and 990 (9 km²) grid cells, and for males we used 2,040 (1 km²), 1,290 (4 km²), and 1,088 (9 km²) grid cells. We used 6 broad environmental characteristics in the model, subdivided into 9 categorical and 13 continuous covariates (Table 1). Results from the models at all 3 resolutions were compared to provide additional information on bear selection criteria and model limitations.

Land use and land cover (LULC). LULC is a crucial determinant of bear presence because of its association with food abundance and den selection (Rogers and Allen 1987, Clark et al. 1993, van Manen and Pelton 1997). We obtained a Lower

Peninsula land-cover dataset with 30 m resolution for the year 2001 developed by the Forest, Mineral, and Fire Management Division of the MDNR as part of the Integrated Forest Monitoring, Assessment, and Prescription (IFMAP) project. We reclassified the original 32 cover classes into 9 cover classes relevant to bear biology: agriculture, upland non-forested, northern hardwood and mixed hardwood, oak, aspen, pine, forested wetlands, non-forested wetlands, and developed land. LULC proportions were summarized for each of the model grid cells at all 3 resolutions. We assigned each grid cell a categorical value associated with the majority LULC (e.g., aspen, agriculture, etc.).

Hydrological features. Bears frequently use water bodies for drinking and cooling down (Rogers and Allen 1987). We created a raster dataset with a resolution of 30 m (consistent with LULC image resolution) that combined lake and stream data throughout the NLP. We reclassified this raster layer so that each raster cell represented either presence or absence of water. We tabulated the area of water for each of the model grid cells at all 3 target resolutions.

Roads. Bears sometimes use logging, service, and unpaved roads as travel routes or as food sources (soft mast and green vegetation along roadside; Manville 1983). Frequently traveled roads, however, result in high numbers of vehicle-related bear deaths (Rogers and Allen 1987). We used a vector dataset (Michigan Department of Information Technology 2002) divided into 3 categories (large, medium, and small) based on approximate size and traffic volume. We converted the reclassified road layer into a 5-m resolution raster dataset and calculated total road length for each road category for each of the model grid cells at all target resolutions.

Topography. We assumed that bear energy expenditure increases as the variability in terrain slope increases. We hypothesized that bears avoid areas with greater slope variability to minimize energy expenditure. We derived slope data from a 30-m digital elevation model for the State of Michigan using ArcGIS (ESRI 2002). We calculated the standard deviation of slope (30-m resolution) for each of the model grid cells at all target resolutions.

Human population. Census block population estimates are very coarse and not the optimal method of depicting human population densities relative to bear presence. For instance, some areas within a census block are populated while others are not (Wright 1936). We reclassified the LULC raster

Table 1. Covariates, variable type, and calculation used to parameterize male and female American black bear habitat selection models based on data from 1991–2000. Covariates were measured across the northern Lower Peninsula of Michigan at grid resolutions of 1 km², 4 km², and 9 km².

Variable Covariate	Covariate type	Calculation per grid cell
Hydrological features		
Water area	Continuous	Sum, m
Topography		
Slope deviation	Continuous	Slope standard deviation, degrees
Road length		
Large volume road	Continuous	Sum, m
Medium volume road	Continuous	Sum, m
Small volume road	Continuous	Sum, m
Human population		
Human density	Continuous	Sum of density from 30 m raster cells
Landscape metric		
Number of patches	Continuous	Number of land cover patches
Mean patch size	Continuous	Mean land cover patch size
Patch size coefficient of variation	Continuous	Standard deviation of mean patch size
Edge density	Continuous	Total patch edge/total land area per cell
Area-weighted mean shape index	Continuous	1 when all patches are circular; increases with increasing patch shape irregularity 0 when there is only one patch in the landscape; increases as number of patch types increases 0 when patches are clumped; approaches 1 when evenly distributed
Shannon's diversity index	Continuous	
Shannon's evenness Index	Continuous	
Land cover		Majority land cover type
Human development	Categorical	
Agriculture	Categorical	
Upland non-forested	Categorical	
Northern hardwood and mixed hardwood	Categorical	
Oak	Categorical	
Aspen	Categorical	
Pine	Categorical	
Forested wetland	Categorical	
Non-forested wetland	Categorical	

dataset into 5 categories: urban development, agriculture, forested, open, and water. We used the census block data to calculate the proportion of human population within these 5 categories to be 0.90, 0.07, 0.02, 0.01, and 0.0, respectively. These proportions were assigned to each of the reclassified LULC grid cells. We derived the number of people/LULC grid cell (i.e., number of people/30 m) by multiplying the grid cell proportion and the census block population estimates (see Eicher and Brewer 2001). We summed population density to calculate human population for each of the model grid cells at all target resolutions.

Landscape patterns. Landscape pattern metrics provide information on patch (i.e., LULC type) composition, diversity, and structure that may influence the ways in which bears travel and select various areas over the landscape. We used the Patch

Analyst extension (Rempel 2008) within ESRI's ArcView 3.3 (ESRI 2002) to calculate the number of patches, mean patch size, patch size coefficient of variation (CV), edge density, area-weighted mean shape index, Shannon's diversity index, and Shannon's evenness index for each of the model grid cells at all target resolutions. Mean patch size and CV have implications for food abundance (low patch size CV reflects homogeneity of land cover type sizes, suggesting relatively equitable distribution of food). The number of patches and Shannon's diversity index have implications for food variability (e.g., different land covers/land uses provide different foods and higher values of each suggest a greater variability). Edge density, area-weighted mean shape index, and Shannon's evenness index reflect landscape features and patterns that influence the way bears select areas (e.g., avoidance of areas with

significant landscape fragmentation is indicated by higher values of edge density, selection of areas with more escape and refuge cover is indicated by higher values of shape index, and selection of areas with concentrated food resources is indicated by lower values of Shannon's evenness index).

Bayesian discrete-choice model specification

We applied a discrete-choice function in the form of a multinomial logit that assumed that individual bears independently select a single patch of land (grid cell) from a 'choice set' of mutually exclusive patches (all grid cells in model area) that are all equally available (McCracken et al. 1998). The collection of all grid cells available to bears of each sex, S , depended on model resolution (females: 2,856 at 1-km² resolution, 1,467 [4 km²], 990 [9 km²] grid cells; males: 2,040 [1 km²], 1,290 [4 km²], and 1,088 grid cells [9 km²]). The probability of use of grid cell s by animal i was

$$p_i(s) = \frac{\exp(\beta_i x_s)}{\sum_{r \in S} \exp(\beta_i x_r)} \quad (1)$$

where:

X_s = a k -dimensional vector of covariate attributes (area of water, slope variability, area of agriculture land-use, etc.) characterizing grid cell s , and

β_i = a k -dimensional vector of covariate selection parameters for animal i .

The probability that the j th independent relocation of bear i occurs in grid cell s_{ij} was $p_i(s_{ij})$. For grid cell s_{ij} , the likelihood for all observed relocations was

$$\prod_{i=1}^m \prod_{j=1}^{n_i} p_i(s_{ij}) \quad (2)$$

where m represents all bears and n_i represents all independent relocations for bear i . Standard deviation across individuals was calculated as

$$\sqrt{\frac{\sum_{i=1}^m \left(\hat{\beta}_i - \bar{\beta}_i \right)^2}{m(m-1)}} \quad (3)$$

where:

$\hat{\beta}_i$ = selection parameter estimate
 m = number of bears

The goal of using Bayesian random effects models is to make probability statements on individual and population-level selection parameters given the observational data (radiotelemetry locations). In Bayesian methodology, all parameters (individual bear and population-level) must have a 'prior' distribution defined. Priors reflect our initial state of knowledge on the likely values of selection parameters (Sauer et al. 2005). Selection parameter values of interest (estimated mean and variance) are described by 'posterior' probability distributions. In each model iteration, individual bear selection parameters, sampled from prior distributions, were used in the discrete-choice function (Eq. 1) to modify individual bear posterior distributions according to an internal WinBUGS algorithm (Link et al. 2002). Because individual bears were considered to be random samples (i.e., random effects) from the whole population, the individual bear prior distributions were defined by population-level mean and user-defined variance. Population-level selection parameter priors were defined in this study by independent normal distributions with mean zero and variance 100 to express our ignorance of prior distribution (Thomas et al. 2006). Through this hierarchical information sharing, population-level selection parameters account for uncertainty in individual bear selection parameters via differing animal relocations and describe individual and population-level selection with valid error terms.

Using WinBUGS, we ran all models using 24,000 iterations in a single Markov chain with a burn-in of 4,000 iterations. Individual and population-level selection parameter estimates, posterior distributions, and validation values were calculated from the last 20,000 iterations. The number of burn-in iterations and parameter convergence were determined using suggestions from Raftery and Lewis (1992).

Model fit

We assessed goodness-of-fit of each model using a Bayesian P that estimated deviance between the observed dataset and the simulated dataset (from the MCMC samplings). We calculated deviance using

$$D(s_s, s_o) = 2 \cdot L(s_s | \theta) - 2 \cdot L(s_o | \theta), \quad (4)$$

where:

s_s = simulated data
 s_o = observed data

L = log-likelihood for the discrete choice model
 θ = vector of parameters

WinBUGS generated a simulated likelihood of selection at each grid cell based on parameter values at each iteration of the MCMC algorithm and compared that likelihood to observed likelihood from the data. Bayesian P was estimated by measuring the proportion of iterations in which the simulated likelihoods exceeded the observed likelihoods. A good model fit has $P \sim 0.5$ (equal proportion of simulated likelihoods greater and less than the observed likelihoods), whereas a poorly fit model has $P < 0.05$ or $P > 0.95$ (Thogmartin et al. 2004).

Evaluating selection parameter estimates

We evaluated covariate parameter significance by examining 95% Bayesian credibility intervals produced by WinBUGS. We interpreted Bayesian credibility intervals as bounded distributions within which 95% of potential parameter values will fall (Ellison 1996). If those distributions included zero, we interpreted covariate parameter estimates as not significant. We used Spearman's rank correlation analysis to test for correlations between significant covariate selection parameter estimates and mean bear age.

Mapping population-level habitat selection

To calculate a relative probability of selection for each grid cell, we used median values of population-level selection parameter estimates from the best fit (i.e., Bayesian P closest to 0.5) models and calculated the number of grid cells with selection probabilities greater than the probability of random-use. To apply our model to the entire NLP, we calculated selection likelihood for each grid cell by calculating habitat suitability of each grid cell using just the equation in the numerator of the discrete-choice function (Eq. 1). We divided the suitability value for each grid cell by mean grid cell suitability value across the NLP. After dividing each grid cell by mean suitability value, those grid cells with selection likelihood ≤ 1 were considered not-preferred and those with selection likelihood > 1 were considered preferred. Finally, preferred grid cells (> 1) for males and females were combined to illustrate preferable habitat to bears in the NLP.

Results

Observations of female bears varied from 30 to 326 ($\bar{x} = 76$); observations of male bears varied from 30 to 236 ($\bar{x} = 70$). Mean kernel home range for the 35 females was 227 km^2 ($SD = 810.2 \text{ km}^2$) and mean kernel home range for the 20 males was 606 km^2 ($SD = 740.3 \text{ km}^2$). Distributions of home range sizes were heavily skewed because of extreme home range sizes of a single male ($3,283 \text{ km}^2$) and female ($4,922 \text{ km}^2$). With the extreme cases removed, mean kernel home range size for females was 89.2 km^2 ($SD = 92 \text{ km}^2$) and mean kernel home range size for males was 465 km^2 ($SD = 424 \text{ km}^2$). The mean kernel home range of females was significantly smaller than males ($t = 3.718$, 18.946 df, $P = 0.001$).

Simulated data from the 4 km^2 female model was the best fit (Bayesian P closest to 0.50) to the observed data (1 km^2 : 0.65; 4 km^2 : 0.56; 9 km^2 : 0.61), whereas the best fit male model was based on 9 km^2 data (1 km^2 : 0.71; 4 km^2 : 0.66; 9 km^2 : 0.56). Both female and male models indicated that population-level locations of bears were negatively associated with water, small and medium roads, mean patch size, patch size CV, edge density, developed land-cover, and non-forested wetlands. They were positively associated with Shannon's diversity index, aspen, and forested wetlands. Locations of females were negatively associated with human population and positively associated with area-weighted mean shape index and northern hardwood and mixed hardwood. In contrast, locations of male were negatively associated with Shannon's evenness index (Table 2).

Among statistically significant covariates, median parameter estimates of individual bear selection were similar to the population-level selection parameter estimates of significant covariates. Most standard deviations of the individual selection parameter estimates for each covariate were smaller (females: 20/22 covariates, males: 21/22 covariates) than the population-level selection parameter estimates (Table 3). This is because the population-level estimates accounted for error associated with differing animal relocations (Thomas et al. 2006). In the female model, standard deviations of individual bear selection parameter estimates were highest for edge density and non-forested wetland and lowest for medium roads and developed land cover. In the male model, standard deviations were highest for human population and agriculture and lowest for Shannon's diversity index and aspen (Table 3, Fig. 2). Some

Table 2. Median, SD, and lower (2.5%) and upper (97.5%) credibility intervals of population-level selection parameters for covariates from the best-fit female (4-km² resolution) and male (9-km² resolution) American black bear habitat selection models based on data from 1991–2000. Covariates were measured across the northern Lower Peninsula of Michigan.

Covariates	Female, 4-km ² resolution				Male, 9-km ² resolution			
	Median	SD	2.5%	97.5%	Median	SD	2.5%	97.5%
Water	-1.236	0.342	-1.931	-0.557	-0.834	0.216	-1.277	-0.426
Slope deviation	-0.314	0.198	-0.709	0.074	-0.327	0.183	-0.691	0.032
Large road	-0.323	0.174	-0.674	0.020	-0.034	0.151	-0.341	0.258
Medium road	-0.252	0.111	-0.474	-0.037	-0.349	0.149	-0.648	-0.062
Small road	-1.295	0.446	-2.213	-0.441	-0.722	0.296	-1.325	-0.152
Human population	-1.154	0.452	-2.099	-0.322	-0.355	0.594	-1.581	0.796
Number of patches	-0.690	0.435	-1.545	0.167	0.394	0.431	-0.456	1.238
Mean patch size	-3.159	0.524	-4.290	-2.220	-1.650	0.451	-2.586	-0.792
Patch size coefficient of variation	-0.945	0.208	-1.361	-0.543	-0.799	0.274	-1.345	-0.262
Edge density	-2.128	0.439	-2.993	-1.263	-1.821	0.571	-2.943	-0.683
Area-weighted mean shape index	0.658	0.148	0.368	0.949	0.361	0.211	-0.048	0.781
Shannon's diversity index	0.994	0.398	0.231	1.801	1.244	0.492	0.339	2.261
Shannon's evenness index	-0.538	0.381	-1.314	0.192	-1.331	0.576	-2.520	-0.257
Developed	-7.159	1.339	-9.710	-4.237	-8.001	1.648	-10.970	-4.566
Agriculture	-2.879	3.149	-10.390	1.992	-6.696	5.595	-19.380	2.324
Upland non-forested	1.762	1.719	-1.881	4.987	-1.559	4.049	-10.710	5.447
Northern hardwood and mixed hardwood	4.323	1.700	0.876	7.587	6.326	3.787	-1.285	13.690
Oak	0.163	2.242	-4.842	3.994	0.451	3.450	-6.833	6.912
Aspen	4.443	1.628	1.160	7.665	6.886	3.321	0.499	13.460
Pine	2.156	2.060	-2.216	5.880	4.219	3.981	-4.243	11.600
Forested wetland	6.919	1.725	3.532	10.340	8.298	3.395	1.656	14.970
Non-forested wetland	-8.491	4.737	-20.060	-1.668	-8.381	4.405	-19.620	-2.334

individual bears for each model had outlying and extreme parameter estimates (Fig. 2). We identified 17 females and 4 males that had an outlying parameter estimate (defined as >1.5 times beyond the interquartile range, Fig. 2) for at least 1 parameter.

Mean male age was 4.0 years ($n = 19$), and mean female age was 5.3 years ($n = 35$). Male age was negatively correlated with covariate selection parameter estimates for small roads (Spearman's rank $r = -0.681$, $P = 0.001$) and developed land-uses ($r = -0.551$, $P = 0.015$), and positively correlated with medium roads ($r = 0.577$, $P = 0.01$). We found no significant correlation between female bear age and covariate selection parameter estimates.

Selection likelihood maps within the modeling region (i.e., aggregate home range) indicated that 15.7% (199/1,268) of 4-km² grid cells were selected more often than random by females and 25.6% (222/866) of 9-km² grid cells were selected more often than random by males. Selection likelihood maps of the entire NLP indicated that 11.2% (1,294/11,456) of 4-km² grid cells had female bear selection values

>1, with a maximum of 75 (that is, 75 times more likely to be selected than average suitability value throughout NLP), whereas 17.1% (857/5,006) of 9-km² grid cells had male bear selection values >1 with a maximum of 39 (Fig. 3). Combined likelihood maps for the NLP indicated that 22% of 4-km² grid cells represented selected habitats and 23.3% of 9-km² grid cells represented selected habitats for both sexes (Fig. 4).

Discussion

We assumed that bear relocations were spatially independent because bears can travel long distances between successive telemetry locations (approximately 1 week). We did not rigorously test this assumption. Swihart and Slade (1985) note that Schoener's ratio test may indicate location autocorrelation, even if the locations are actually independent, when the center of activity shifts over time. We believe that the bears in our study shifted their centers of activity over the multi-year duration of the study. Therefore, having not tested for

Table 3. Median and SD of covariate selection parameters for habitat selection models across all American black bears from the best-fit female (4-km² resolution) and male (9-km² resolution) models. Covariates were measured across the northern Lower Peninsula of Michigan, and were based on data from 1991–2000.

Covariates	Female, 4-km ² resolution		Male, 9-km ² resolution	
	Median	SD	Median	SD
Water	-0.754	0.136	-0.678	0.134
Slope deviation	-0.417	0.244	-0.350	0.154
Large road	-0.171	0.150	0.020	0.120
Medium road	-0.164	0.091	-0.347	0.117
Small road	-0.224	0.400	-0.694	0.253
Human population	-0.459	0.389	0.226	0.436
Number of patches	-0.318	0.417	0.389	0.264
Mean patch size	-2.409	0.433	-1.489	0.304
Patch size coefficient of variation	-0.706	0.201	-0.663	0.124
Edge density	-2.455	0.466	-1.189	0.404
Area-weighted mean shape index	0.484	0.139	0.256	0.124
Shannon's diversity index	0.876	0.336	0.285	0.051
Shannon's evenness index	-0.499	0.331	-0.431	0.130
Developed	-4.411	0.523	-6.469	1.686
Agriculture	-3.067	0.736	-8.032	1.923
Upland non-forested	1.619	0.611	0.525	1.367
Northern hardwood and mixed hardwood	3.217	0.645	6.687	1.170
Oak	-1.290	0.820	2.081	1.387
Aspen	2.953	0.646	5.598	0.975
Pine	2.539	0.655	5.466	1.280
Forested wetland	5.587	0.564	6.919	1.012
Non-forested wetland	-6.794	0.908	-7.785	1.712

independence, it is possible that telemetry locations were autocorrelated, which would influence parameter estimation and significance.

Although adjusted for unbalanced sample designs (differing numbers of relocations for each bear), these model results still should be interpreted cautiously because covariate collinearity was not explicitly accounted for in this analysis. If a set of covariates were significantly collinear, the selection parameter estimates may have been inflated because of insufficient information to distinguish between them. Additionally, standard errors of the affected selection parameter estimates (that is, correlated covariates) tend to be larger than if they are uncorrelated. These effects may influence the significance of selection parameter estimates (Graham 2003). Additionally, our analysis did not identify selection patterns separately by season or time of day (diurnal versus nocturnal). As a result, seasonally distinct selection patterns may have been obscured, and variance of covariate selection parameter estimates inflated over those from season-specific models. Rather, parameter estimates we report reflect overall patterns of habitat selection by the black bear population in the Northern Lower

Peninsula in Michigan for data collected over 10 years. Furthermore, we did not have access to night locations, but black bears may become more nocturnal when living near human settlements (Ayres et al. 1986, Beckmann and Berger 2003). We believe, however, that our analyses account for most of the variation in habitat selection because black bears are generally diurnal (Amstrup and Beecham 1976, Garshelis and Pelton 1980, Larivière et al. 1994).

Model results suggest that bears in the NLP select habitat attributes at a scale >1 km². Bears can travel long distances to exploit concentrated food sources such as soft and hard mast, human refuse, and agricultural crops (Garshelis and Pelton 1981, Rogers 1987). The different resolutions at which the Bayesian *P* was minimized for male and female bears may reflect gender-related differences in behavior (Gehring and Swihart 2003). Males typically travel much larger distances for mating opportunities than females (Rogers 1987) and probably interact with their environment at broader scales. Male home ranges were almost 3 times larger than female home ranges, further suggesting that males spatially perceive and interact with their

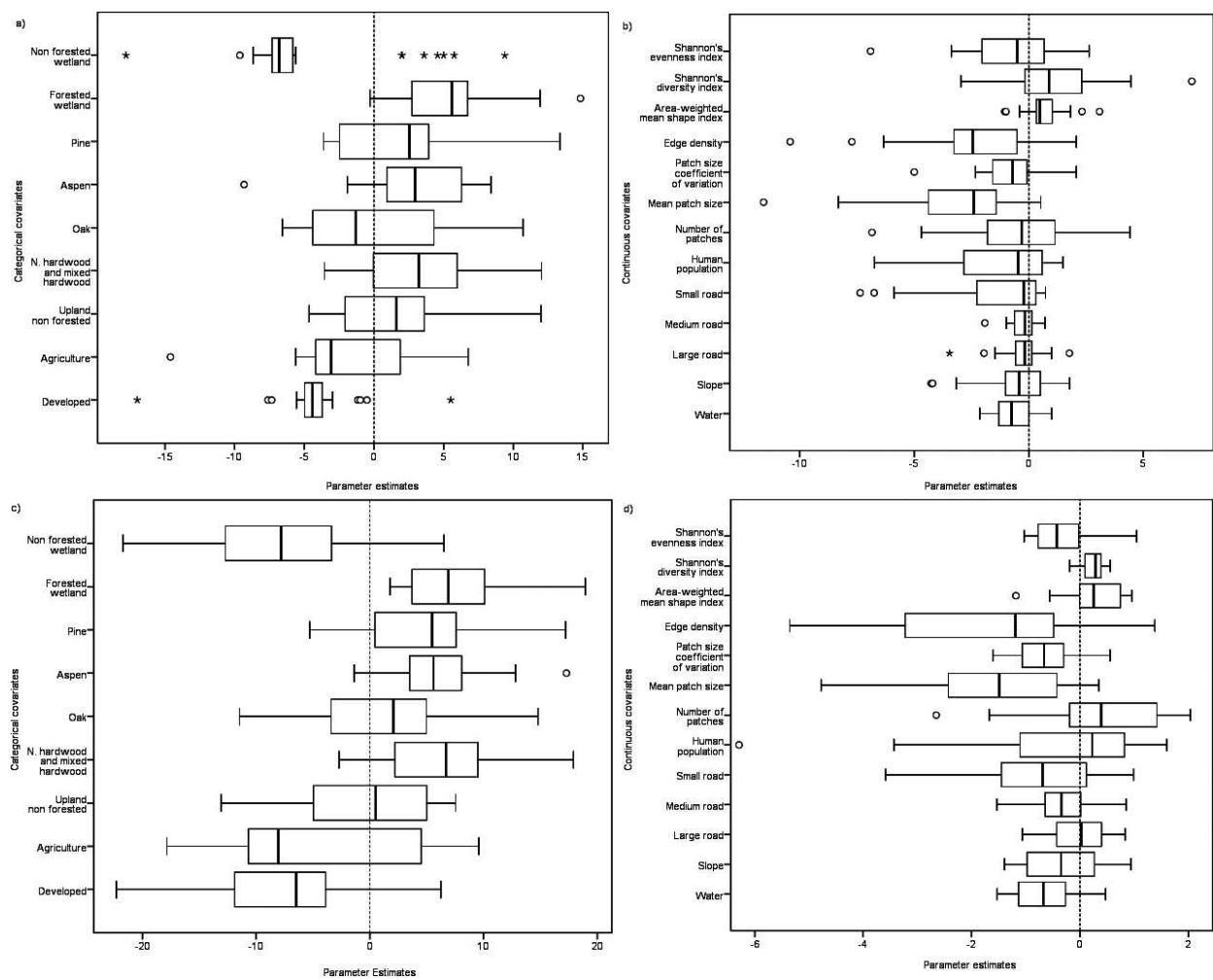


Fig. 2. Boxplots of individual parameters for habitat selection models for male and female American black bears from 1991–2000 data from the northern Lower Peninsula of Michigan, USA for (a) female 4-km² model categorical covariates, (b) female 4-km² model continuous covariates, (c) male 9-km² model categorical covariates, and (d) male 9-km² model continuous covariates. Boxes indicate first and third quartiles; line in box indicates median. Lines extending from boxes represent 1.5 times the interquartile range from the quartiles. Individual points represent outliers (>1.5 times the interquartile range from the quartiles); asterisks represent extreme outliers (>3 times the interquartile range from the quartiles).

surroundings differently than females. Traversing larger areas exposes males to a larger range of environmental attributes, which may explain greater heterogeneity in male population-level covariate selection. Females are more philopatric, and area selection is dictated more by necessity to choose den sites that reduce energy expenditure and promote cub growth (Lindzey and Meslow 1977). These characteristics may explain better performance of the female model at a finer resolution than the male model.

We summarized all environmental variables only for the area within each grid cell. Thus, probability of selection depended only on values of environmental variables within the grid cell and did not account for the landscape surrounding each grid cell (e.g., broad scale fragmentation). It is possible to summarize some variables within areas that are larger than the output spatial grid cells using a moving window analysis. Doing so may maintain a finer resolution (e.g., 1 km²) while acknowledging spatial characteristics of larger and varying sizes (i.e., multiple

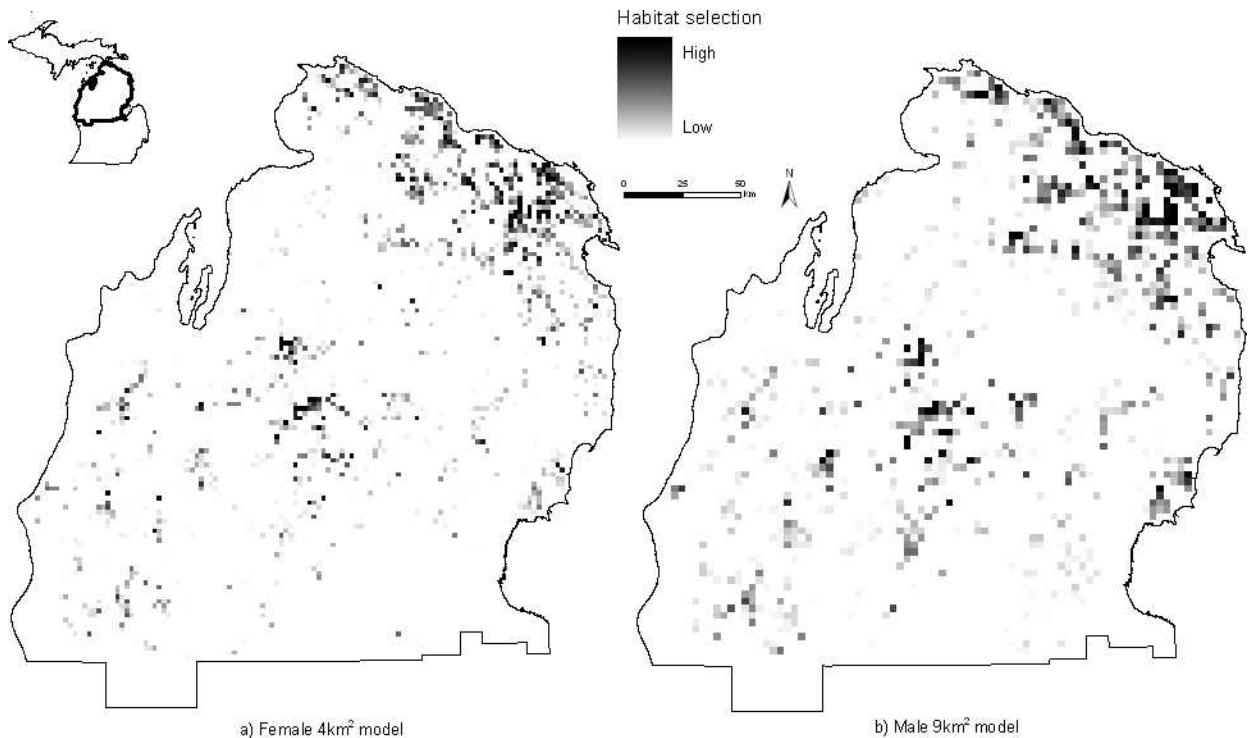


Fig. 3. Predicted likelihood of habitat selection for American black bears based on (a) 4-km² grid cells by female bears and (b) 9-km² grid cells by male bears in the northern Lower Peninsula of Michigan, USA using population-level parameter estimates from best-fit habitat selection model for each sex. Based on data from 1991–2000.

window sizes). Additionally, different covariates can be summarized at different resolutions and the effect of varying those resolutions can be tested.

The negative relationship between population-level bear presence and water is somewhat counter-intuitive, but may in part be due to collinearity, in which water bodies in the NLP are surrounded by comparatively large human populations with development and road networks which bears generally avoid (Bauer 1996). We found a negative association between population-level bear presence and medium and small road density in the NLP. Increased road density likely increases vehicular-related deaths and hunter access to bears (Schwartz and Franzmann 1992); hunting is the primary source of bear mortality in Michigan (Etter 2002). We were surprised to find no evidence that bears avoided large roads (interstate highways; Brody and Pelton 1989) but the density of large roads was much lower than the other 2 categories, and sample size may have limited our power to observe a significant negative relationship.

At the population level, bears appear to prefer small, similarly sized patches of various LULC types. Diversity of land-cover types provides for a variety of cover and food sources that bears require to meet their seasonal needs (Kindall and van Manen 2007). We speculate that edge density at the broad scale, as illustrated in these models, likely correlates with human-induced habitat fragmentation, thus explaining the negative association. Investigation of class-level patch metrics within forest types, instead of overall landscape patch metrics, would provide more detail on the relative role that human land uses and natural land covers have on bear habitat selection.

Population-level selection of aspen land cover was not surprising because bears often consume aspen catkins and leaves during spring (Rogers and Allen 1987). The negative relationship we found with non-forested wetlands at the population-level scale is contrary to research from Colorado (Hoover and Wills 1987), California (Grenfell and Brody 1986), and Washington (Lyons et al. 2003), where bears

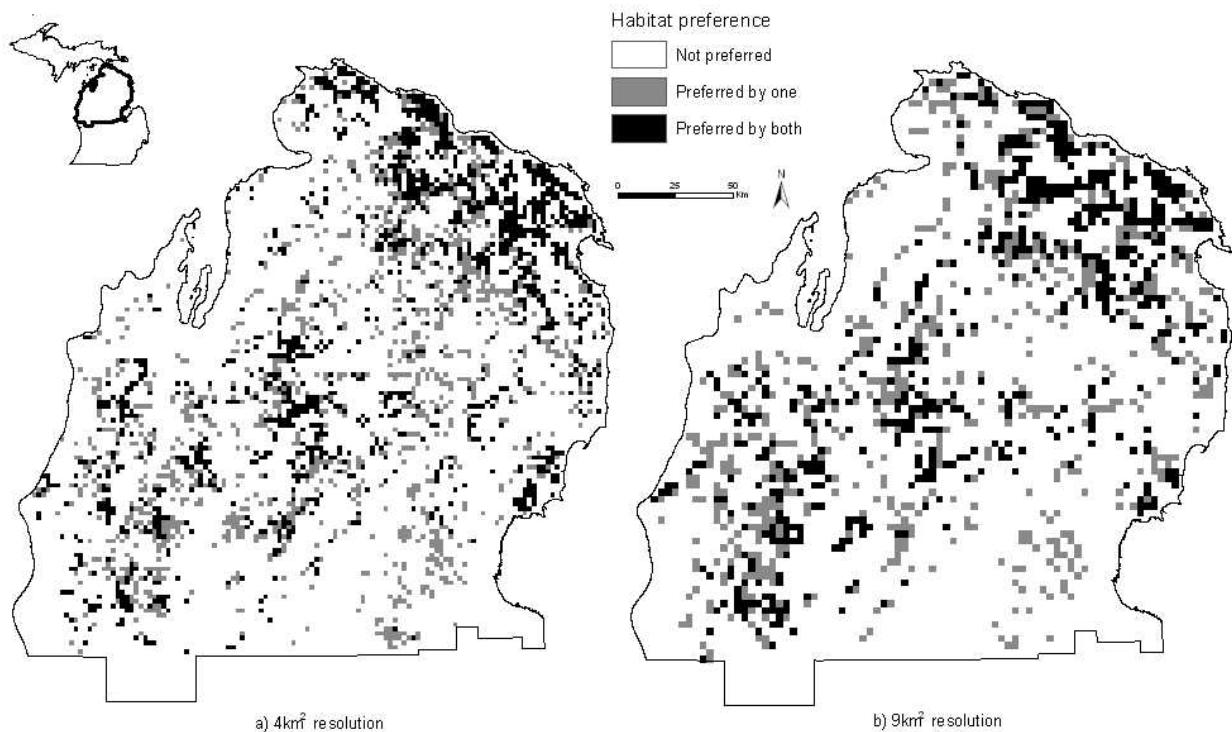


Fig. 4. Preferred habitat in the northern Lower Peninsula of Michigan, USA for American black bears of both sexes at (a) 4-km² grid cell resolution and (b) 9-km² grid cell resolution, from 1991–2000 data. Preferred habitat was calculated by combining areas with selection likelihoods >1 for each sex at the respective resolution.

selected wet meadows that provided herbaceous vegetation during spring. When collecting radiotelemetry data, we sometimes observed bears using the edges of non-forested wetlands. Due to large error associated with radiotelemetry locations, detecting use at this finer resolution was not possible.

Human population was negatively associated with females but not males. Bears generally select den sites away from possible disturbance (Tietje and Ruff 1980) and may become more nocturnal in response to human disturbance (Ayres et al. 1986). Area-weighted mean shape index and northern hardwood and mixed hardwood covariates were positively associated with females but not males. Increases in the area-weighted mean shape index (shape complexity) may indicate potential for escape and refuge cover in the landscape within the complex configurations of different patches. Black bears prefer areas with greater escape and refuge cover (Hugie 1979). Moreover, female bear presence was associated with northern hardwood and mixed hardwood communities across most of their range in North America (Landers et al. 1979, Maehr and

Brady 1984). These communities are important for production of hard mast and late ripening berries essential in bear's fall diets. Shannon's evenness index (0 = clumpy, 1 = even) was negatively associated with males but not significantly associated with females. This suggests that male bears demonstrate a strong behavioral inclination to find patches clumped together with abundant food sources. This behavior likely conserves search energy and travel time (Rogers 1987).

We identified 17 of 35 females and 4 of 20 males with at least 1 outlying parameter estimate. Five of those 17 females had relocation data concentrated in a single region within approximately 4 km of a lake in central Michigan. This region was dominated by wetlands and contained every other LULC type except human development. We interpret this to indicate that this region supported food and cover requirements of bears and represented high-quality habitat. This heavily selected region also had many patches of agricultural land nearby. It is very likely that bears in the NLP use agricultural crops for food. This is suggested by sightings and complaint

reports, as well as high variance in individual bear selection parameter estimates with some bears preferentially selecting for agricultural areas. A similar situation was reported in coastal North Carolina, where bears living in managed pine forests depended heavily on crops for food from nearby farms (Jones and Pelton 2003). Furthermore, heterogeneity in covariate selection, especially in males, suggests that bears may adaptively use a variety of habitats, including those near human land uses.

The negative correlations between bear age and selection parameter estimates for developed land-use and small road covariates indicated that older males avoided these landscape features more so than younger males. One possible explanation is that socially dominant older males may have relegated younger bears to marginal habitats (Gende and Quinn 2004, Rode et al. 2006), which include a preponderance of developed areas and small roads. Bear hunting pressure is likely greater near small roads, which hunters use to enter the field or run their dogs from (J. Belant, Mississippi State University, Starkville, Mississippi, USA, personal communication, 2009). In contrast, younger males avoided medium roads more so than older males. Despite vehicular mortality, older males may be using medium roads to traverse the landscape and secure resources more easily (less energy required for transit). An alternative explanation is that bears that did not avoid medium roads died earlier, leaving as the survivors those that did. Explicating these relationships more fully will require additional research that uses, among other things, bear age information from harvest records and more rigorous controls.

Incorporating random effects in our models provided measures of average bear population selection and selection variability among bears, both of which are important sources of information for bear managers. These measures improve our understanding of bear behavior and provide crucial insight when planning for future bear range expansion. Further, Bayesian random effects discrete-choice models are flexible enough to rigorously test hypotheses regarding bear-habitat relationships in many settings.

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