RESEARCH ARTICLE

# Predicting carnivore occurrence with noninvasive surveys and occupancy modeling

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**Abstract** Terrestrial carnivores typically have large home ranges and exist at low population densities, thus presenting challenges to wildlife researchers. We employed multiple, noninvasive survey methods—scat detection dogs, remote cameras, and hair snares—to collect detection–nondetection data for elusive American black bears (*Ursus americanus*), fishers (*Martes pennanti)*, and bobcats (*Lynx rufus*) throughout the rugged Vermont landscape. We analyzed these data using occupancy modeling that explicitly incorporated detectability as well as habitat and landscape variables. For black bears, percentage of forested land within 5 km of survey sites was an important positive predictor of occupancy, and percentage of human developed land within 5 km was a negative predictor. Although the relationship was less clear for bobcats, occupancy appeared positively related to the percentage of both mixed forest and forested wetland habitat within 1 km of survey sites. The relationship between specific covariates and fisher occupancy was unclear, with no specific habitat or landscape variables directly related to occupancy. For all species, we used model averaging to predict occurrence across the study area. Receiver operating characteristic (ROC) analyses of our black bear and fisher models suggested that occupancy modeling efforts with data from noninvasive surveys could be useful for carnivore conservation and management, as they provide insights into habitat use at the regional and landscape scale without requiring capture or direct observation of study species.

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## Introduction

Mammalian carnivores are notably sensitive to habitat fragmentation, disturbance, and exploitation by humans (Ginsberg 2001; Woodroffe 2001). As top-level consumers, carnivores also affect the biological structure and composition of ecosystems. Thus, the extirpation of a given carnivore species may result in cascading effects throughout the ecosystem (Crooks and Soulé 1999; Terborgh et al. 1999).

American black bears (*Ursus americanus*), fishers (*Martes pennanti*), and bobcats (*Lynx rufus*) occupy much of the northeastern United States, a landscape increasingly fragmented by roads, development, and other anthropogenic effects. The ability of resource managers to predict how these species respond to a changing landscape, and to identify habitat components that are most important for their persistence, may be of great consequence in the face of expanding human development and global climate change.

Recent advances in noninvasive survey methods (e.g., Long et al. 2008) and likelihood-based occupancy modeling (MacKenzie et al. 2002; MacKenzie and Bailey 2004; MacKenzie et al. 2006) now permit both the collection of detection–nondetection data from wide-ranging carnivores and the simultaneous estimation of site occupancy and detectability. Non-invasive survey approaches eliminate the need to capture or directly observe free-ranging species, and occupancy estimation can provide information about habitat suitability without having to estimate actual population parameters (e.g., abundance). Further, explicitly accounting for imperfect detectability is particularly important for studies of rare and elusive species (Thompson 2004) such as many carnivores.

We used detection dogs, remote cameras, and hair snares to survey black bears, fishers, and bobcats on sites distributed throughout Vermont. The objectives were to (1) collect detection–nondetection data suitable for occupancy estimation and modeling, (2) use this information to build models for predicting the occurrence of these species at the landscape scale, and (3) generate maps from the models illustrating the predicted probability of occurrence for each species across the state. Our primary goal was to produce predictive models that would be useful for wildlife managers and land-use planners, as opposed to testing specific hypotheses about habitat selection or preference.

## Methods

### Study area

Our study area included the entire state of Vermont (24,963 km$^2$), along with a few sites located immediately west of central Vermont's border with New York. Mean elevation was 370 m, ranging from 30 m along the shores of Lake Champlain to 1,339 m at Mount Mansfield—Vermont's highest peak. Recent changes in forest patterns have been dramatic. Up to 95% of the state was forested in 1750; by 1850, almost 75% of the forests had been cleared for timber and agriculture. Poor farming conditions prevailed, however, and roughly 79% of the state was again forested by 1980 (Thompson and Sorenson 2000). Currently, most of Vermont is dominated by hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), paper birch (*B. papyrifera*), and American beech (*Fagus grandifolia*).

Human density varied considerably across Vermont. For example, extremely rural areas in northeastern Essex County hosted 3.7 people per km$^2$, while Chittenden County, with 24% of the state's population, had a human density of 91 people per km$^2$ (U.S. Census Bureau 2005). Although primarily rural, the state has experienced ≥10% population growth per decade since the 1960s (U.S. Census Bureau 2005). Road density also varied substantially from an average of ~0.53 km/km$^2$ in Essex County to >1.55 km/km$^2$ in Chittenden County.

### Survey site selection

Carnivore surveys were conducted at sites distributed throughout the study area (Fig. 1) on lands owned by the State of Vermont, U.S. Forest Service, University of Vermont, or private citizens. To maximize the number of individuals detected and to minimize the chance that the same individual would be detected at multiple sites, we attempted to locate sites ≥5 km apart. In a few instances—such as when access was limited or topography was unsuitable for surveys—sites were located <5 km apart. Although it was possible that a single individual was detected on multiple (adjacent) sites, we assumed that this occurred rarely, and that most sites were sampled independently.

**Fig. 1** Map of 168 sites in Vermont and New York surveyed for target carnivores using detection dogs during May–August of 2003 and 2004. *Inset* shows transect size, shape, and assumed detection zone for detection dog surveys. A subset of sites was also surveyed with remote cameras and hair snares
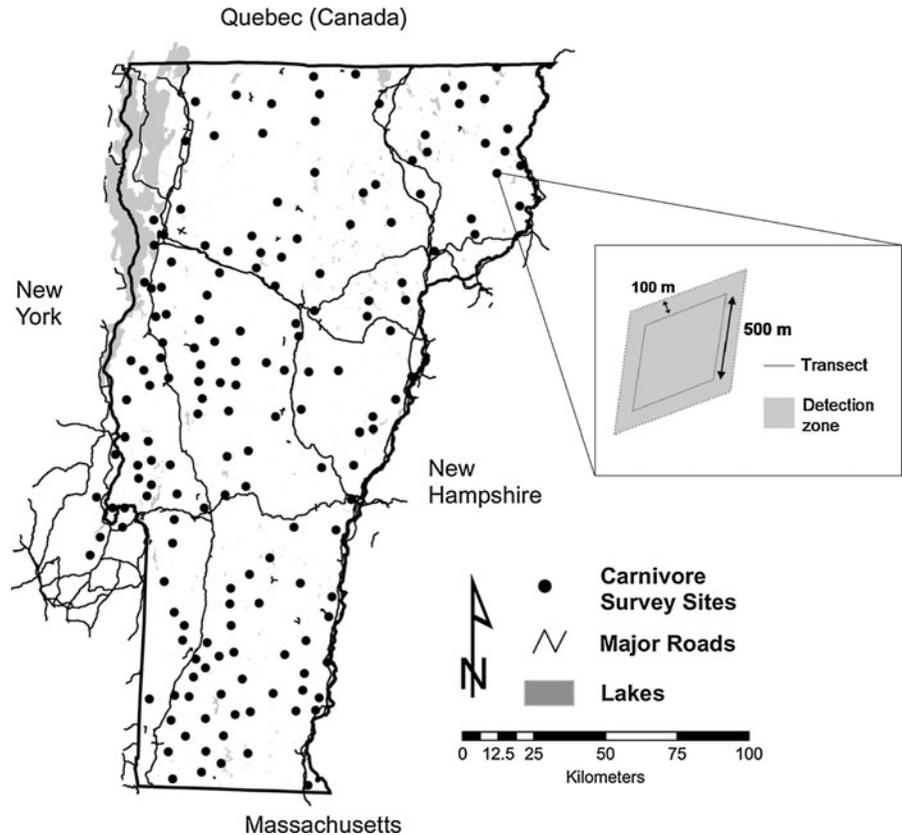
We used Geographic Information System software (ArcGIS; Environmental Systems Research Institute, Redlands, CA) and Hawth's Analysis Tools (www.spatialecology.com/htools/) to generate a large set of random points across the entire area to which we had access, and we constrained these points to be >5 km apart. We randomly selected a subset of remaining points as survey sites. We discarded sites in inaccessible areas (e.g., cliffs, bodies of water), or shifted them to the closest location that could be feasibly surveyed (usually within 1 km) when possible. The resulting 168 sites represented all major cover types and a broad gradient of human disturbance, forest fragmentation, land ownership categories, elevation, and topographic complexity.

Carnivore surveys

Surveys were first conducted at all sites with detection dogs, followed by remote camera and hair snare surveys at a subset of sites. A number of sites were also surveyed one or two additional times with detection dogs, enabling the estimation of detection probability. Long et al. (2007a) describe in detail the detection dog training, survey protocols, and criteria for assigning a species detection or nondetection at each site. Briefly, detection dog teams (i.e., dog, handler, orienteer) searched along a 2-km, diamond-shaped transect at each site (Fig. 1). We used scats collected inside the diamond or ≤100 m outside of the transect line (i.e., the detection zone; Long et al. 2007a) to establish detections and nondetections. DNA analysis was used to confirm the species for a subset of scats and to estimate a "probability of correct identification" metric (Long et al. 2007a), which was in turn used to help minimize the probability of incorrectly "detecting" a species (i.e., false positives). False negatives were addressed via the occupancy modeling approach described in "Modeling framework" below.

We conducted remote camera and hair snare surveys at a randomly selected subset of the 168 sites (*n* = 74; 44% of total sites; 50 in 2003, 24 in 2004) searched by detection dog teams (see Long et al. 2007b). In 2003, we baited camera and rub pad

sites with a commercial carnivore lure (Gusto; Minnesota Trapline Products, Pennock, MN), and hung a small nylon bag containing fish food pellets and molasses from an out-of-reach branch to attract bears. Rub pads were scented with a lure designed specifically for felids, but which was also known to attract ursids (J. Weaver, personal communication). In 2004, we also deployed two pieces of raw chicken at each site in an attempt to increase visitation by fishers. We left cameras and hair snares in place for 14 days and recorded a target species detection if (1) an identifiable photo was taken during the survey period, (2) large quantities of obvious (i.e., based on morphology) black bear hairs were found on a pad, or (3) hairs found on the snare pad were confirmed via genetic analysis to be from a target species.

## Modeling framework

We used likelihood-based occupancy modeling (MacKenzie et al. 2002; MacKenzie and Bailey 2004; MacKenzie et al. 2006) to estimate both site occurrence ($\psi$; probability that the species occurred at a site) and detectability ($p$; probability that the species was detected if present) from our detection–nondetection data. This modeling was conducted as a two-step process in which we first identified (during a previous analysis; Long et al. 2007a) variables that to some degree affected detection of the target species, and then included these variables as a constant set of detection covariates in our occupancy models (Kroll et al. 2006; Yates and Muzika 2006; Darrah and Krementz 2009). By explicitly modeling detection as a function of site- and survey-specific variables, the variables affecting site occupancy can be identified—and their effects estimated—with greater accuracy (MacKenzie et al. 2002).

For each site, we compiled an encounter history based on five surveys that we considered independent, corresponding to three dog surveys, one camera survey, and one hair snare survey. For example, a detection history of "10011" indicates that the target species was detected at this site during the first dog survey, missed during the second and third dog surveys, and detected by both the camera and hair snare surveys. This occupancy modeling approach accommodates sites with incomplete survey histories (e.g., a camera was not deployed), thus resulting in some detection histories with missing values (e.g.,

"10.11" indicates that the third detection dog survey was not conducted). We explored using the multiple methods modeling approach of Nichols et al. (2008) but concluded that a standard occupancy approach would be as appropriate and would perform similarly. The stated advantages of the multiple methods approach—no requirement of independence among methods, ability to compare detection probabilities among methods, and inference at multiple scales (Nichols et al. 2008)—are either already addressed by our design, or not relevant given our survey methods. Further, most of our sites (56%) were only surveyed via the detection dog method and thus would not take advantage of a true multiple methods framework.

## Selection of predictor variables

We attempted to limit the number of variables tested in our models to those that were both biologically meaningful and not strongly correlated with one another. Our intent was to minimize model overfitting, which can lead to models that perform poorly beyond the data used to create them, and to avoid excessive model testing and the "chasing" of significant variables—which risk inclusion of spurious or unimportant variables (Burnham and Anderson 2002). To this end, we developed a preliminary set of potential predictor variables by considering results of past studies and the natural history of each target species. We then reduced this set of variables by examining pair-wise correlations between variables and, in most cases, eliminating one variable from each highly correlated ($|r| > 0.80$) pair. In two cases (i.e., core area with forest, and core area with deciduous forest), we retained variables correlated beyond the cutoff because we were specifically interested in exploring effects of these variables in the models. We considered the resulting list of variables to be the "exploratory set" (Table 1) for initial analysis because we could not objectively reduce the set further based on biological or statistical grounds. Data sources and variable creation steps varied by layer. We conducted all manipulations of spatial data using ArcGIS (ESRI, Redlands, CA, USA) software.

## Modeling scale and covariate selection

All three target species are generally considered wide-ranging, and are likely influenced by resources

**Table 1** Description of variables considered during exploratory analysis for predicting occurrence of carnivores

| Functional group Covariate | Abbreviation | Description |
| --- | --- | --- |
| Forest cover | | |
| Forest (%) | %FOREST | Percent of cells classified as deciduous, coniferous, or mixed forest; or forested wetland |
| Coniferous forest (%) | %CONIFER | Percent of cells classified as coniferous forest |
| Deciduous forest (%) | %DECIDUOUS | Percent of cells classified as deciduous forest |
| Mixed forest (%) | %MIXED | Percent of cells classified as mixed forest |
| Forest configuration | | |
| Forest core (%) | %CORE | Percent of cells classified as >100 m from a forest and non-forest edge |
| Development/disturbance | | |
| Large roads (km/km$^2$) | LARGEROADS | Density (km/km$^2$) of category[a] 1–2 roads |
| Town roads (km/km$^2$) | MEDIUMROADS | Density (km/km$^2$) of category 3 roads |
| Small roads (km/km$^2$) | SMALLROADS | Density (km/km$^2$) of category 4 roads |
| Developed land (%) | %DEVELOPED | Percent of cells classified as either residential, commercial, industrial, or "other urban" |
| Residential land (%) | %RESIDENTIAL | Percent of cells classified as residential |
| Commercial, industrial, urban land (%) | %COMMMERCIAL | Percent of cells classified as either commercial, industrial, or "other urban" |
| Water | | |
| Wetland (%) | %WETLAND | Percent of cells classified as wetland |
| Forested wetland (%) | %FORESTEDWETLAND | Percent of cells classified as forested wetland |
| Water edge density (m/ha) | WATER | Amount of water edge divided by landscape area |
| Other | | |
| Conserved land (%) | %CONSERVED | Percent of cells classified as having at least a GAP class 3 stewardship level |
| Topographic ruggedness index (TRI) | RUGGED | Mean TRI value within the landscape |
| Predicted snowfall | SNOW | Mean predicted snowfall within the landscape |
| Latitude | NORTH | Northing at the center of the survey transect |

[a] Category corresponds to the specific road type as defined in the text. It is not synonymous with state class type

distributed at fairly large but potentially varying scales (Powell 1994; Campbell 2004). To accommodate the effects of scale on relationships between predictor variables and target species occurrence, we used "analysis window" areas of 3.1 and 78.5 km$^2$. These areas respectively corresponded with 1- and 5-km radius circles centered on the survey transect (hereafter referred to as 1- and 5-km scales or landscapes). Use of an additional 3-km radius circle was abandoned because it was correlated highly with both the 1- and 5-km scales. These scales were chosen not because they necessarily corresponded specifically with the home range size of ≥1 of the target species, but rather because they encompassed the average minimum and maximum home range sizes for all three target species (Litvaitis et al. 1986; Rogers 1987; Lovallo and

Anderson 1996a, b; Garant and Crête 1997; Arthur et al. 1989; Samson and Huot 2002).

We selected final variable-scale combinations to be used in the full "confirmatory" modeling by comparing univariate occupancy models representing all variables (at both scales) from the exploratory set (Table 1). These model sets comprised 28 models for black bears and 31 models for fishers and bobcats. Model ranking and evaluation were conducted with the information-theoretic method (see "Model development and selection" section). Variable-scale combinations appearing in the highest ranking models were selected first. Although we allowed variables at both scales into the final set, no single variable was permitted at both scales. Preliminary modeling exercises suggested that the relationship of fishers with

**Table 2** Model-averaged estimates, unconditional standard errors, and 95% confidence limits of coefficients of covariates in occurrence models comprising the 95% confidence set for each species

| Species Covariate | $\hat{\beta}$ | SE$\left(\hat{\beta}\right)$ | Lower CI $\hat{\beta}$ | Upper CI $\hat{\beta}$ |
|---|---|---|---|---|
| **Black bear** | | | | |
| INTERCEPT | 0.957 | 1.016 | −1.033 | 2.948 |
| %FOREST-5K | 3.059 | 1.444 | 0.229 | 5.888 |
| %DECIDUOUS-5K | 0.018 | 0.299 | −0.567 | 0.603 |
| %CORE-5K | 0.004 | 0.016 | −0.028 | 0.036 |
| %CONSERVED-5K | −0.009 | 0.390 | −0.773 | 0.756 |
| %WETLAND-5K | 0.140 | 0.510 | −0.860 | 1.140 |
| %DEVELOPED-5K | −1.847 | 0.754 | −3.324 | −0.370 |
| LARGEROADS-5K | 0.176 | 0.425 | −0.657 | 1.010 |
| **Fisher** | | | | |
| INTERCEPT | 1.531 | 0.466 | 0.618 | 2.444 |
| %FOREST-1K | 0.418 | 0.439 | −0.441 | 1.278 |
| %CONIFER-1K | 0.380 | 0.511 | −0.623 | 1.382 |
| %CORE-5K | −0.051 | 0.266 | −0.572 | 0.471 |
| %CONSERVED-1K | 0.253 | 0.377 | −0.487 | 0.992 |
| %WETLAND-1K | −0.442 | 0.680 | −1.776 | 0.891 |
| %RESIDENTIAL-5K | 0.572 | 0.723 | −0.845 | 1.989 |
| %COMMERCIAL-5K | −0.516 | 1.135 | −2.740 | 1.708 |
| NORTH | −0.073 | 0.228 | −0.520 | 0.374 |
| **Bobcat** | | | | |
| INTERCEPT | −0.731 | 0.691 | −2.084 | 0.623 |
| %FOREST-1K | 0.064 | 0.412 | −0.744 | 0.872 |
| %MIXED-1K | 1.087 | 0.636 | −0.160 | 2.334 |
| %CORE-5K | 0.065 | 0.382 | −0.683 | 0.813 |
| %CONSERVED-1K | 0.110 | 0.343 | −0.562 | 0.782 |
| %FORESTEDWETLAND-1K | 0.983 | 0.792 | −0.568 | 2.535 |
| LARGEROADS-5K | −0.362 | 0.619 | −1.575 | 0.851 |
| SMALLROADS-5K | 0.633 | 0.776 | −0.887 | 2.153 |

Coefficients and standard errors are in logit (log odds) space and relate to standardized covariate values

human development may be quite complex, and that the %DEVELOPED variable would be better expressed as separate components comprised of "residential" and a combination of "commercial," "industrial," and "urban" cover types. For univariate testing and all modeling hereafter, these two variables entered into fisher models as a pair. After univariate modeling, we were able to reduce the set of exploratory variables to a total of seven variable-scale combinations (hereafter covariates) for black bears and bobcats, and eight for fishers (Table 2).

Model development and selection

The occupancy-likelihood framework considers detection and occurrence simultaneously, thus yielding a dependency between estimates of $p$ and $\psi$. Because it would have been unrealistic to consider the large number of resulting models had we attempted to simultaneously model both $p$ and $\psi$, we modeled $\psi$ by fitting a set of candidate models for this parameter while including a general set of detection covariates for $p$ in all models (Kroll et al. 2006; Yates and Muzika 2006). These covariates were previously shown to affect species detection by detection dogs at the survey sites (black bears—topographic ruggedness, vegetation openness, year, temperature, humidity, wind, and precipitation; fishers—topographic ruggedness, vegetation openness, detection dog team, temperature, humidity, wind, and precipitation; Long et al. 2007a). As we had no data suggesting that site-specific variables would affect detectability by remote cameras

or hair snares, we did not include detection covariates for these devices.

We developed a set of 127 a priori candidate models for each species representing all combinations of $\psi$ covariates identified for the given species during exploratory modeling. Because %COMMERCIAL and %RESIDENTIAL always entered together, all combinations of covariates for fishers also resulted in 127 models. We considered each model to be a biologically plausible hypothesis for explaining presence–absence of the target species. We fit single-season occupancy models (MacKenzie et al. 2002) to the encounter histories for each species with program MARK (White and Burnham 1999). All continuous covariates were standardized to z-scores prior to analysis. No other transformations or interaction terms were included. Models that did not result in convergence, or for which convergence was suspect because of inestimable parameters (Cooch and White 2005), were eliminated from the candidate set. Models were ranked using the small-sample correction to Akaike's information criterion (AICc; Burnham and Anderson 2002). Akaike weights (Burnham and Anderson 2002) were used to evaluate the weight of evidence in favor of a given model being the best model in the candidate set. If no model received >90% of the weight, we extracted the 95% model confidence set for each species, recalculated model AIC weights, and calculated model-averaged estimates (Burnham and Anderson 2002) with spreadsheet software designed by B. Mitchell (www.uvm.edu/%7Ebmitchel/software.html) to allow interpretation of covariate effects across multiple models. We assumed that the 95% confidence set (i.e., set of models, considered in rank order beginning with the best model, whose summed Akaike weights = 0.95; Burnham and Anderson 2002) captured sufficient model information while also limiting the number of models contributing to final model-averaged estimates.

We evaluated model fit with program PRESENCE (Proteus Wildlife Research Consultants, Dunedin, New Zealand) by comparing the observed Pearson $\chi^2$ statistic from the most general model with $\chi^2$ statistics from 10,000 simulated parametric bootstrap datasets (MacKenzie and Bailey 2004). Finally, we addressed cases of poor model fit (i.e., model $\chi^2$ value >95% of the bootstrap values) by estimating an overdispersion factor ($\hat{c}$), inflating standard errors by a factor of $\sqrt{\hat{c}}$, and using a quasi-corrected AICc (QAICc) for model selection (Burnham and Anderson 2002).

## Model validation

Because an independent data set with which to validate our models was unavailable, we evaluated accuracy of final (model-averaged) models for black bears and fishers by calculating the area under the receiver operating characteristic (ROC) curve. ROC curves are obtained by plotting all sensitivity values (true positive proportion; 1—false-negative rate) on the y-axis against the false positive proportion (1—specificity [true negative proportion]) values on the x-axis (Fielding and Bell 1997; Pearce and Ferrier 2000). The area under this curve (AUC) is a threshold-free index of model classification performance and indicates overall ability of the model to accurately predict the data used to create it (Fielding and Bell 1997; Pearce and Ferrier 2000). AUC values range from 0.5 (i.e., no better than a null model) to 1.0 (i.e., perfect accuracy; Fielding and Bell 1997; Pearce and Ferrier 2000). Low detection rates can contribute to inaccurate or misleading AUC values, as the failure to detect a species at a given location is assumed by ROC analysis to represent a true absence. The probability of detecting black bears when they were present was 0.860 for a single dog survey, 0.997 for three dog surveys, and 0.998 for three dog surveys plus a camera survey (Long et al. 2007b). These values for detecting fishers were 0.840, 0.890, and 0.997, respectively (Long et al. 2007b). Given such high detection rates for these species, we assume that most failures to detect these species were true absences, and that use of AUC analyses for model validation is warranted. Bobcats had relatively low detection rates of only 0.670 even when three dog surveys were combined with remote camera and rub pad surveys (Long et al. 2007b), however, and AUC analyses were therefore not appropriate. We used web-based ROC analysis software (Eng 2005) to generate ROC curves and to calculate AUC values for black bears and fishers.

## Predictive mapping

For each model in the 95% confidence set for a given species, we calculated probability of occurrence for

each 30-km × 30-km grid cell in the study area using the model-specific coefficient estimates and covariate information for that grid cell. Grid cell values for 5-km scale covariates were generated at a 90-m resolution because of computer processing limitations. Grid cells were then multiplied by the weight of the specific model. This process was repeated for each model in the 95% set, and the resulting model-specific values for the grid cell were summed to yield a model-averaged probability of the target species occurring in that cell ($\psi$). Calculating a model-averaged $\psi$ for each cell resulted in a seamless map of predicted occurrence for each target species.

## Results

### Carnivore surveys

During May–August 2003 and 2004, five detection dog teams surveyed 168 sites (Fig. 1) a total of 220 times, with 135 sites surveyed once, 14 sites surveyed twice, and 19 sites surveyed three times. At 74 of the 168 sites, remote cameras and hair snares were also deployed. No sites were surveyed during both years. Mean nearest-neighbor distance between transects on adjacent sites was 6.9 km. Based on combined results of detection dog, camera, and hair snare surveys, raw detection rates were 60.1% (101/168 sites) for black bears, 61.9% (104/168 sites) for fishers, and 11.9% (20/168 sites) for bobcats. These values are naïve estimates of occupancy that do not account for probability of detection.

### Model selection

Univariate analyses identified covariates that varied across target species for final confirmatory modeling of species occurrence. Only covariates at the 5-km scale were selected for black bear modeling, whereas covariate sets for fishers and bobcats consisted of mixed scales (Table 2). Effect directions for all species were consistent across scales for a single variable. Thus, no single variable was included at both scales in a final set.

We detected no evidence of overdispersion in the data for any species (black bear: $\chi^2 = 107.4$, $P = 0.53$; fisher: $\chi^2 = 26.6$, $P = 0.21$; bobcat: $\chi^2 = 40.2$, $P > 0.99$). Model results for all species indicated

some level of model selection uncertainty (i.e., no model received >90% of the Akaike weight). Black bear models resulted in the least uncertainty, with 14 models comprising the 95% confidence set. Support for fisher and bobcat models was substantially divided, however, with the 95% confidence set composed of 57 and 66 models, respectively.

For black bears, %FOREST-5K, %DEVELOPED-5K, LARGEROADS-5K, and %WETLAND appeared in the top models (i.e., models where AICc difference [$\Delta_i$] was <2; Table 3). For fishers, all covariates except %CORE-5K were represented in the top models (Table 3). For bobcats, top models contained all seven covariates (Table 3).

Model-averaged results for black bears suggested that %FOREST-5K was an important positive predictor of bear occupancy (based on a 95% confidence interval that excluded 0), and %DEVELOPED-5K was an important negative predictor (Table 2). Confidence intervals on model-averaged coefficients for all other covariates strongly overlapped 0, indicating little direct effect on bear occupancy at a site. For fishers, all model-averaged coefficients overlapped 0 (Table 2), and therefore did not appear to directly influence species occurrence at the scales that we evaluated. For bobcats, 95% confidence intervals on model-averaged coefficients for all covariates overlapped 0 (Table 2). However, confidence intervals on the model-averaged coefficient for %MIXED-1K, and to some extent %FORESTEDWETLAND-1K, overlapped 0 only slightly (Table 2), indicating percent of mixed forest and forested wetland within 1 km of sites may have been related to bobcat occurrence.

Based on the 95% confidence set of models for each species, and adjusting for site- and visit-specific detection covariates, we estimated that actual occupancy at surveyed sites was 71.6% for black bears, 83.4% for fishers and 32.6% for bobcats. These estimates were 11.5%–20.7% greater than naïve estimates of occupancy.

### Model validation

Area under the receiver operating characteristic curve (AUC) was 0.90 for the black bear model based on the averaged 95% confidence set (Fig. 2), indicating considerable similarity between predicted and observed values. Applying the average model to each

**Table 3** Results of AIC-based model selection of probability of occurrence for black bears, fishers, and bobcats in Vermont

| | $\Delta_i$ | $w_i$ | $K$ | $-2 \log (\pounds)$ |
|---|---|---|---|---|
| **Black Bear** | | | | |
| %FOREST-5K − %DEVELOPED-5K | 0.00 | 0.258 | 15 | 252.76 |
| %FOREST-5K − %DEVELOPED-5K + LARGEROADS-5K | 1.56 | 0.118 | 16 | 251.87 |
| %FOREST-5K + %WETLAND-5K − %DEVELOPED-5K | 1.72 | 0.109 | 16 | 252.03 |
| **Fisher** | | | | |
| %FOREST-1K + %CONSERVED-5K + %COMMERCIAL-5K + %RESIDENTIAL-5K | 0.00 | 0.145 | 19 | 274.89 |
| %FOREST-1K + %COMMERCIAL-5K + %RESIDENTIAL-5K | 0.72 | 0.101 | 18 | 278.16 |
| %CONIFER-1K + %WETLAND-1K | 0.75 | 0.100 | 17 | 280.69 |
| %CONIFER-1K + %CONSERVED-5K + %WETLAND-1K | 1.00 | 0.088 | 18 | 278.43 |
| %CONSERVED-5K + %COMMERCIAL-5K + %RESIDENTIAL-5K | 1.14 | 0.082 | 18 | 278.58 |
| %FOREST-1K + %CONIFER-1K + %WETLAND-1K | 1.68 | 0.063 | 18 | 279.11 |
| %FOREST-1K + %CONIFER-1K | 1.86 | 0.057 | 17 | 281.81 |
| %CONIFER-1K + %WETLAND-1K + %COMIND-5K + %RESIDENTIAL-5K | 1.89 | 0.056 | 19 | 276.78 |
| %CONIFER-1K + %WETLAND-1K + NORTH | 1.94 | 0.055 | 18 | 279.38 |
| %FOREST-1K + %CONIFER-1K + %WETLAND-1K + %COMMERCIAL-5K + %RESIDENTIAL-5K | 1.95 | 0.055 | 20 | 274.26 |
| %FOREST-1K + %CONIFER-1K + %CONSERVED-5K + %COMMERCIAL-5K + %RESIDENTIAL-5K | 2.00 | 0.053 | 20 | 274.32 |
| **Bobcat** | | | | |
| %MIXE1K + %FORESTEDWE1K + SMALLROADS-5K + LARGEROADS-5K | 0.00 | 0.176 | 7 | 133.35 |
| %MIXED-1K + %FORESTEDWET-1K + SMALLROADS-5K | 0.53 | 0.135 | 6 | 136.06 |
| %MIXED-1K + %FORESTEDWET-1K | 1.35 | 0.090 | 5 | 139.03 |
| %MIXED-1K + %FWETLAND-1K + LGRDS-5K | 1.50 | 0.083 | 6 | 137.03 |
| %MIXED-1K + %CONSERVED-1K + %FWETLAND-1K + SMRDS-5K | 1.54 | 0.082 | 7 | 134.89 |
| %MIXED-1K + %CORR-5K + %FWETLAND-1K + SMRDS-5K | 1.69 | 0.076 | 7 | 135.04 |
| %FOREST-1K + %FWETLAND-1K + SMRDS-5K | 1.69 | 0.065 | 7 | 135.34 |

Included are top models (AIC$_c$ ≤ 2) for each species including AIC$_c$ difference ($\Delta_i$), Akaike weight ($\omega_i$; calculated from the 95% confidence set of models), number of parameters in model ($K$), and $-2$ log-likelihood ($-2 \log (\pounds)$)

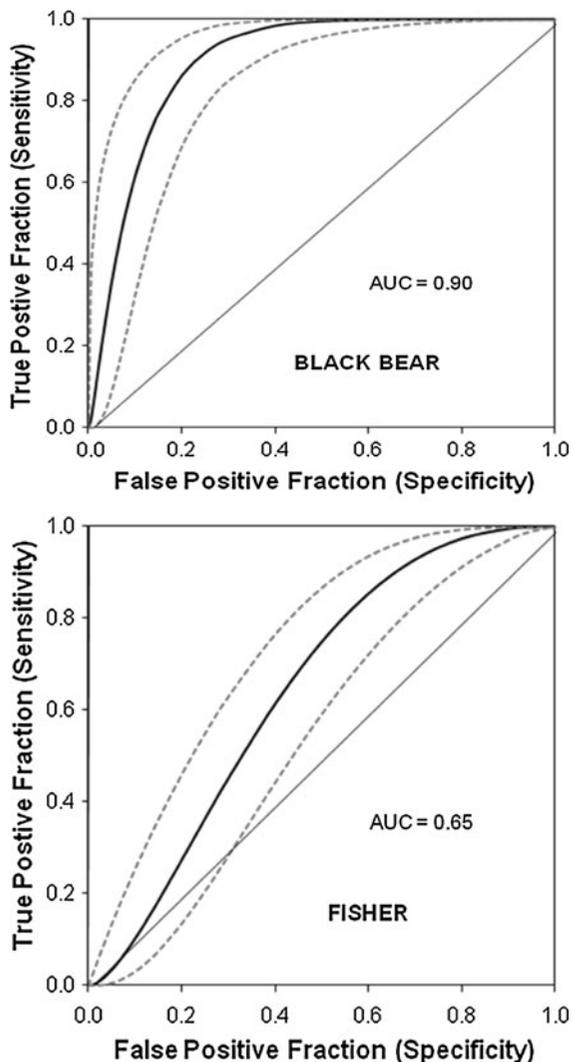The AUC was low (0.65; Fig. 2) for the fisher model obtained by averaging the 95% confidence set. Sensitivity was high for this averaged model (97%), but specificity was low (19%). Although only three sites where fishers were detected were predicted to be unoccupied by the final model, 52 sites where fishers were not detected were expected to be occupied. Although less accurate than the bear model, the averaged fisher model performed substantially better than a null model (AUC = 0.5) for predicting fisher presence.

Predicted distribution

The map derived from the model-averaged results for black bears predicted occurrence (i.e., probability of occurrence ≥0.50) throughout a high percentage of the state (Fig. 3). Areas with predicted occurrence <0.50 coincided with the Champlain Valley, extreme
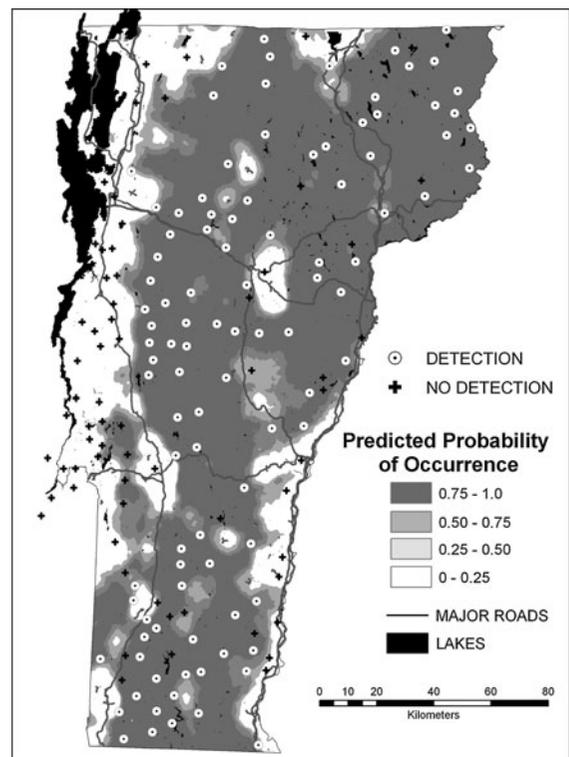
Fig. 2 Receiver–operator-characteristic (ROC) curves that resulted from averaging the 95% confidence sets of all models for black bears and fishers. Area-under-curve (AUC) = 1.00 for a model that perfectly predicts occupancy at surveyed sites, and AUC = 0.5 for a model that predicts no better than a null model. Dotted lines represent upper and lower 95% confidence intervals

site surveyed, and based on a detection–nondetection cutoff for predicted occupancy of 0.5, only five sites where actual detections occurred were predicted to be unoccupied by the model, whereas 35 sites without detections were predicted to be occupied. In these cases, bears may have been present but undetected by the survey methods. At this cutoff, sensitivity (i.e., ability to correctly predict species presence) was 95%, and specificity (i.e., ability to correctly predict species absence) was 69%.



Fig. 3 Predicted probability of black bear occurrence based on model-averaging of the 95% model confidence set. *Circles* indicate sites where black bears were detected, and *crosses* indicate where they were not detected, during surveys conducted in May–August of 2003 and 2004
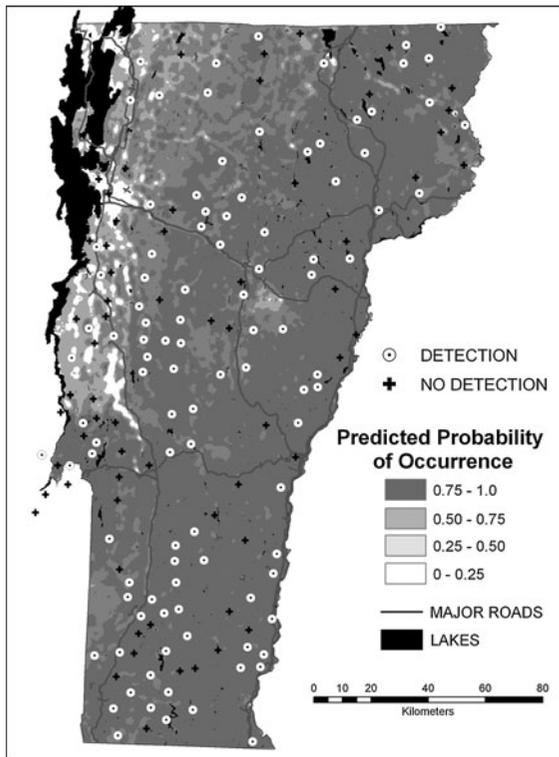
**Fig. 4** Predicted probability of fisher occurrence based on model-averaging of the 95% model confidence set. *Circles* indicate sites where fishers were detected, and *crosses* indicate where they were not detected, during surveys conducted in May–August of 2003 and 2004
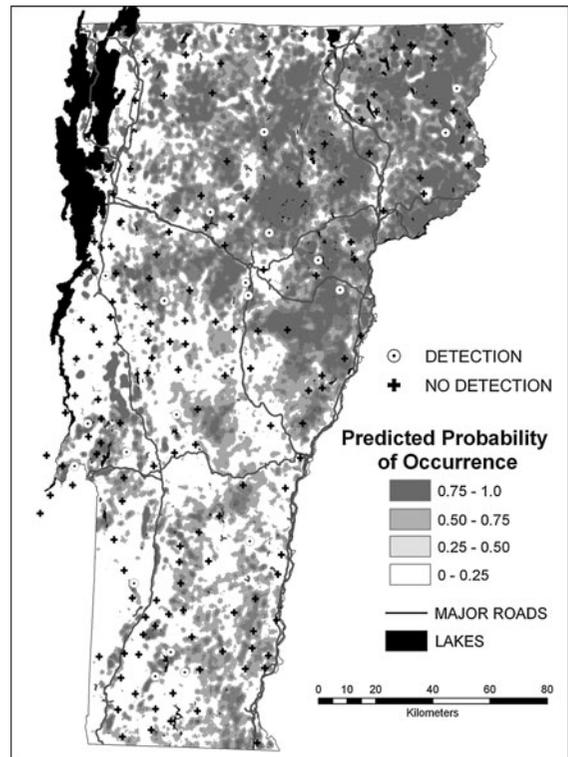


**Fig. 5** Predicted probability of bobcat occurrence based on model-averaging of the 95% model confidence set. *Circles* indicate sites where bobcats were detected, and *crosses* indicate where they were not detected, during surveys conducted in May–August of 2003 and 2004

western Vermont, and areas within 5–15 km of large-town centers.

Fishers were predicted to occur throughout much of Vermont (Fig. 4), with the Champlain Valley comprising the only substantial area with predicted occurrence values <0.50. A pocket of lower predicted fisher occurrence also coincided with major wetland complexes in the extreme northeastern part of the state.

Areas of predicted bobcat occurrence were more restricted (Fig. 5), with the highest predicted occurrence in the east-central and northeastern regions. Predicted bobcat occurrence throughout much of the remainder of the state was less contiguous, consisting largely of scattered "islands" of high predicted value.

## Discussion

We combined noninvasive survey methods with occupancy estimation and modeling to develop

distribution models that performed well for predicting the occurrence of black bears in Vermont. Black bear models contained only coarse-scale (5-km) variables, whereas bobcat and fisher models contained both 1- and 5-km scale variables. Models developed for fishers resulted in relatively high rates of commission error, and were therefore less informative than those for black bears and bobcats. Because of a low probability of detecting bobcats when they were present it was impossible to accurately validate bobcat models.

Black bear

Site occupancy by black bears was positively associated with percent forest and negatively associated with percent human development. This outcome was not surprising. Although black bears use many types of habitats, their general reliance on forests is consistent throughout their range (Hall 1981), and most of their life requisites are obtained directly from

forested habitats or microhabitats within a forested matrix (Mitchell et al. 2002). Further, although black bears are known to cross roads and areas with low human population densities (Brody and Pelton 1989), they are generally considered sensitive to direct human interaction. An intensive study of radio-collared bears at Stratton Mountain, Vermont (Hammond 2002) documented that adult black bears avoided houses during all seasons. Therefore, the development covariate in our models may have effectively represented human activity.

The small number of models in the 95% confidence set and clear predictive ability of the average black bear model were likely due to the relative simplicity of both the habitat requirements of bears in Vermont and the distribution of bear habitat. Areas meeting the ideal model requirements for bear occupancy (i.e., high percent forest, low percent development) were fairly contiguous, and few areas existed where high and low predicted occurrence values were interspersed. Indeed, the predictive occurrence map derived from model-averaging identified high probability of occurrence values for bears throughout much of the state, with the exception of towns, cities, and the Champlain Valley—all of which contain a relatively small percentage of forest.

### Fisher

In our analysis, no individual covariate had an important effect on the occurrence of fishers, and the number of models appearing in the 95% confidence set was large when compared with our black bear results. This outcome, as well as the relatively poor predictive power indicated by a low AUC value, suggests that (1) our models did not contain the variables that reflect why fishers occur where they do in Vermont, (2) fishers are highly varied in their resource needs across the large area for which we attempted to develop models, or (3) fisher habitat needs in this region are too general to allow for successful predictive modeling. Researchers interested in predicting occurrence of fishers in the Northeast should consider these explanations when initiating future modeling efforts. Further, efforts to model at a more local scale, and methods designed to test hypotheses relating to specific biological needs of fishers, may ultimately result in models that are more predictive than those we were able to produce.

### Bobcat

Although no variables stood out as having strong effects on occurrence of bobcats, coefficients for %MIXED-1K and %FORESTEDWETLAND-1K overlapped 0 only slightly, suggesting a possible relationship to bobcat occupancy in our study area. Results from other studies in the Northeast and elsewhere suggest that bobcats locate their home-ranges based more on prey availability than on land cover (Litvaitis et al. 1986; Lovallo and Anderson 1996a, b; Kamler and Gipson 2000). In Vermont, mixed forests containing high-stem-density conifer habitat preferred by snowshoe hares (*Lepus americanus*), as well as mast-producing deciduous species that support relatively high densities of other prey (e.g., squirrels [Sciuridae]), could represent optimal bobcat habitat. Similarly, lowland forested wetlands may support relatively large or diverse prey populations, especially in areas where upland mixed forests are less common.

The large number of models in the 95% confidence set may be a result of bobcats having been detected at only 20 (11.9%) of the 168 sites, and that estimates of the probability of detecting this species with either dogs or cameras was ≤0.27 for an individual survey (Long et al. 2007b). Further, most sites were surveyed only once or twice. Simulation studies indicate that both low detection rates and low probability of detection can result in difficulties when modeling occupancy, and suggest that a minimum of three surveys be conducted at each site to accurately estimate detection probability and occupancy (Tyre et al. 2003; MacKenzie and Royle 2005).

### Model application

Our surveys were conducted during summer only; thus, predictions from the resulting models should be limited to this season. This restriction may be important in attempting to identify important habitat components for each of the target species. Black bears commonly move long distances from summer ranges to access seasonally available hard mast resources in the fall (e.g., Samson and Huot 2002). Similarly, both bobcats and fishers shift their use of habitat and prey during the winter (e.g., Arthur et al. 1989; Lovallo and Anderson 1996a, b; Kamler and Gipson 2000). In addition to exhibiting seasonal

differences in habitat use, all three target species likely require specific micro-habitats for reproduction and other activities (e.g., denning, rearing of young). This study was not designed to model these types of resource requirements.

The ability to efficiently and effectively sample species—especially those characterized as rare, wide-ranging, or elusive—continues to challenge wildlife researchers. Carnivores meet all of these criteria, and are also often of management and conservation concern. Increasing levels of human development require that land-use planning decisions be made across large regions, and be evaluated in part based on their potential consequences for wildlife populations (Theobald et al. 2000). Further, efforts to evaluate functional landscape connectivity for species, or conversely, to identify barriers to species movement, are being conducted at regional scales and require accurate distribution maps (e.g., Beier et al. 2006). By combining effective noninvasive survey techniques with statistical approaches incorporating detection probability into occupancy estimation, we produced models to predict the occurrence of black bears, fishers, and bobcats at a statewide scale.

Our main objective was to predict species occurrence accurately across a large region. Guisan and Zimmermann (2000) note that predictive geographical modeling has gained importance as a tool for evaluating the effects of accelerated land use and other environmental change on species distribution. Further, Betts et al. (2009) observe that "Models developed for prediction may include covariates whose functional link to the response is not obvious but which are excellent predictor variables. Quality coefficient estimation and quality prediction do not necessarily coincide…" Our models provide managers and planners with a tool for understanding how carnivores are distributed across the Vermont landscape and for informing future decisions concerning land-use.

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