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Original investigation

Describing habitat suitability of bobcats (*Lynx rufus*) using several sources of information obtained at multiple spatial scales

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ABSTRACT

We investigated habitat use of bobcats (*Lynx rufus*) across spatial scales in New Hampshire, USA, by integrating independent sources of information into one statewide model of habitat suitability. First, statewide distribution of bobcats (second-order selection) was estimated using observations of bobcats solicited from the public. Probability functions indicated that areas where bobcats were not detected (no sightings) were characterized by high elevations and deep snow during winter. That pattern was corroborated by camera traps that were distributed among high and low-elevation landscapes. Second, bobcats equipped with GPS collars in two study areas were used to determine habitat use within established home ranges (third-order selection). Resource-selection probability functions developed from locations of marked bobcats indicated they selected forests, shrub/scrub, and wetlands, and avoided developed areas, agricultural areas, and open water relative to availability. Bobcats also avoided areas with high road densities and selected areas close to forest edges, and preferred rugged south-facing slopes. Finally, these measures of bobcat distribution were combined to obtain fine-scale estimates of bobcat habitat suitability across New Hampshire. A comparison of models of habitat suitability to an index of bobcat abundance (effort-corrected detections of bobcats by hunter) indicated that the hierarchical model (second-order multiplied by third-order of selection) provided a better description of statewide bobcat habitat than either single-scale analyses. As a result, we recommend caution when extrapolating information on the distribution of a species obtained at a limited spatial scale.

Introduction

The distribution of a species is often a consequence of processes acting at different spatial scales (e.g., Alberdi et al., 2014). Identifying the factors that limit a species and applying them at appropriate spatial scales can improve our ability to develop conservation plans (Hurlbert and Jetz, 2007). GPS-based telemetry provides information on fine-scale habitat associations, but extrapolating that information to a larger spatial extent (e.g., region or statewide) can result in misinterpretation of the occurrence of a species if the scales of processes are not considered (Laforge et al., 2016). On the other hand, information based on incidental observations (Quinn, 1995; Palma et al., 1999) or organized surveys (Linde et al., 2010; Cooper et al., 2012) can identify features that are expressed at large spatial scales but offer no information on fine-scale resource use. By combining information on habitat suitability obtained at multiple spatial scales, we may obtain a more complete description of the factors that limit the distribution of a species (Graf et al., 2005; Hortal et al., 2010; DeCesare et al., 2012).

We were interested in understanding the environmental factors that affect the distribution and abundance of bobcats (*Lynx rufus*) in New Hampshire, a region in the northeastern United States where populations of bobcats have undergone substantial changes in recent decades (Litvaitis et al., 2006). Since 1989, bobcats have been protected in New Hampshire and harvest seasons have been closed. However, recent sightings and incidental vehicle collisions indicate that bobcats have become more abundant and widespread in the state (Litvaitis et al., 2006; Broman et al., 2014; Mahard et al., 2016). Although New Hampshire is contained within the geographic range of bobcats (Anderson and Lovallo, 2003), the state presents a range of environmental conditions from coastal plain to alpine habitats that are likely to affect bobcats distribution and abundance (Litvaitis et al., 2006). Regional variation in snowfall in particular may be especially relevant to the distribution of bobcats in New Hampshire because snow depth affects their mobility (Marston, 1942; McCord, 1974) and prey acquisition (Petraborg and Gunvalson, 1962), and ultimately can limit bobcat survival (Litvaitis et al., 1986a) and density (Fox, 1990).

Previously, Broman et al. (2014) compared bobcat telemetry locations from southwestern New Hampshire to a subset of statewide observation-based locations of bobcats by developing logistic models for each data set that described habitat associations. They found that the observation-based locations substantially oversampled habitat features where bobcats were easily detected (e.g., near roads, agricultural fields, and close to human developments). On the other hand,

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telemetry-based models from the southwestern portion of the state could not be easily extrapolated to the rest of the state due to environmental diversity at large spatial scales. Attempts to correct for observer bias by applying a weighing factor did not resolve the contradictions between data sources (Broman et al., 2014). Therefore, neither data source was adequate for describing both fine and large-scale habitat associations.

Despite those limitations, we contend that observations obtained throughout New Hampshire may still provide useful information on features that vary at a relatively large spatial scale and are therefore less affected by the distribution of observers. For example, variation in snow depth within an individual bobcat home range is modest in comparison to the variation that occurs at a regional or statewide scale, and thus, could potentially be explored with a coarser sampling method. On the other hand, the distribution of prey within a home range can be affected by local land uses (e.g., timber harvests) and have substantial influence on individual bobcat movement patterns (Litvaitis et al., 1986b), necessitating a more detailed sampling method.

Our objective was to examine the utility of combining information on broad or coarse-scale habitat associations based on observations of bobcats and information on fine-scale habitat suitability based on selection patterns by transmitter-equipped individuals within established home ranges. We predicted that a hierarchical model (sensu Johnson, 1980) that combines both approaches would yield a better description of bobcat distributions or habitat suitability than either approach taken separately. Such an approach would first consider coarse-scale factors that affect home-range placement (second-order selection) and then how characteristics of home ranges affect individual movement patterns (third-order selection). To evaluate our prediction, we compared habitat suitability based on second-order selection, third-order selection, and hierarchical selection (product of second and third-order selection) to an index of bobcat abundance (effort-corrected detections of bobcats by hunters distributed throughout New Hampshire; Mahard et al., 2016).

Materials and methods

Study areas

New Hampshire (24,200 km^2) is located at the northeastern edge of the geographic range of bobcats (Fig. 1). Topographic elevations range from sea level, along the southeastern coast up to 1917 m on the summit of Mount Washington, the highest mountain in the northeastern United States. This variation results in a large gradient of snow depths throughout the state, with areas in the White Mountains and northern portion of the state receiving substantially more snow than southern and coastal areas (Fig. 1).

Historic and contemporary land-use patterns also have had a profound influence on wildlife populations. After European settlement, New Hampshire was dominated by agriculture and only 47% was forested by the mid 1800s (Litvaitis, 1993). Subsequent farm abandonment from the mid 19th to the early 20th century resulted in reforestation and large areas of early-successional habitats that benefitted bobcats and their prey (Litvaitis, 1993). By the 1960s, however, 87% of the state was forested (Sunquist and Hewes, 2010) and many forests matured into closed-canopy stands that supported few prey (especially lagomorphs) causing bobcat populations to decline precipitously (Litvaitis, 1993, 2001). In recent decades, forest coverage has decreased to 78% as a consequence of expanding human populations (Justice et al., 2002). In particular, urban and suburban developments have become most pronounced in southern and coastal regions of the state. These regions also include dense transportation corridors (Sunquist and Hewes, 2010; Litvaitis et al., 2015) in comparison to other portions of the state (Fig. 1).

Telemetry-study areas were established in southwestern (1862 km^2) and southeastern portions (2033 km^2) of the state to investigate habitat selection by marked bobcats (Fig. 1). The southwestern area included more varied terrain and a higher mean elevation (308 m) than the southeastern area (186 m). Both areas contained a mix of forest types. Dominant overstory species included eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), American beech (*Fagus grandifola*), yellow birch (*Betula allegheniensis*), paper birch (*Betula papyrifera*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), and white oak (*Quercus alba*). Wetlands, farmlands, and varying levels of development also characterized both areas.

Course-scale habitat selection

To investigate environmental factors influencing bobcat distribution throughout the state, we used bobcat locations that were opportunistically collected by the public throughout the state from 2007 to 2013 and reported to New Hampshire Fish and Game Department or our project website (http://mlitvaitis.unh.edu/Research/BobcatWeb/bobcats.html). Reliability of incidental observation can be a concern, where animals can be misidentified or their locations incorrectly plotted (e.g. McKelvey et al., 2008; Broman et al., 2014). To address those concerns, observations were initially evaluated by the description or photograph submitted by the observer. Next, the physical location of each sighting was scored on a scale of 1–3, where a score of 1 indicated that the location was the address of a residence (verifiable on Google Earth) or geographic coordinates were reported. Observations that included sufficient information to estimate the location (e.g., direction and distance from an obvious landmark or highway intersection) were given a score of 2. If only a general location was reported (e.g., within the township of Newmarket) or a modest description was provided (e.g., along the shore of Long Lake), the observation was given a score of 3. Only observations with scores of 1 or 2 were used in our analysis.

To reduce observer bias and focus on large-scale features, we restricted our evaluation of observation-based locations to a comparison of elevation and mean or maximum snow depths (during November to March) among regions with and without bobcat detections. Although snow and elevation are correlated at a statewide scale, snow depths are higher in the north regardless of elevation (Fig. 1). We sampled available and used habitats in a fashion similar to methods used by Graf et al. (2005). For available habitats, we buffered roads by the maximum distance an observation was reported from a road (3.8 km). Then, each observation-based location was buffered by the radius of the maximum home range of our marked bobcats (9.6 km; Reed, 2013). Maximum home-range size was used to insure that all possible areas suitable for home range placement were considered. Next, 10,000 random points were generated throughout the state. Points contained within home-range buffers were considered occupied and those that fell outside of the buffer were considered unoccupied. This sampling scheme reduced the likelihood of autocorrelation where a single bobcat may generate many observations. Resulting locations were then used in Type I design (Manly et al., 2002) in which used and available features were sampled for the state and individual animals were not identified. Given the coarse-scale of our habitat analysis, screening of observations, the commonality of bobcats, and the sampling scheme utilized, we be-

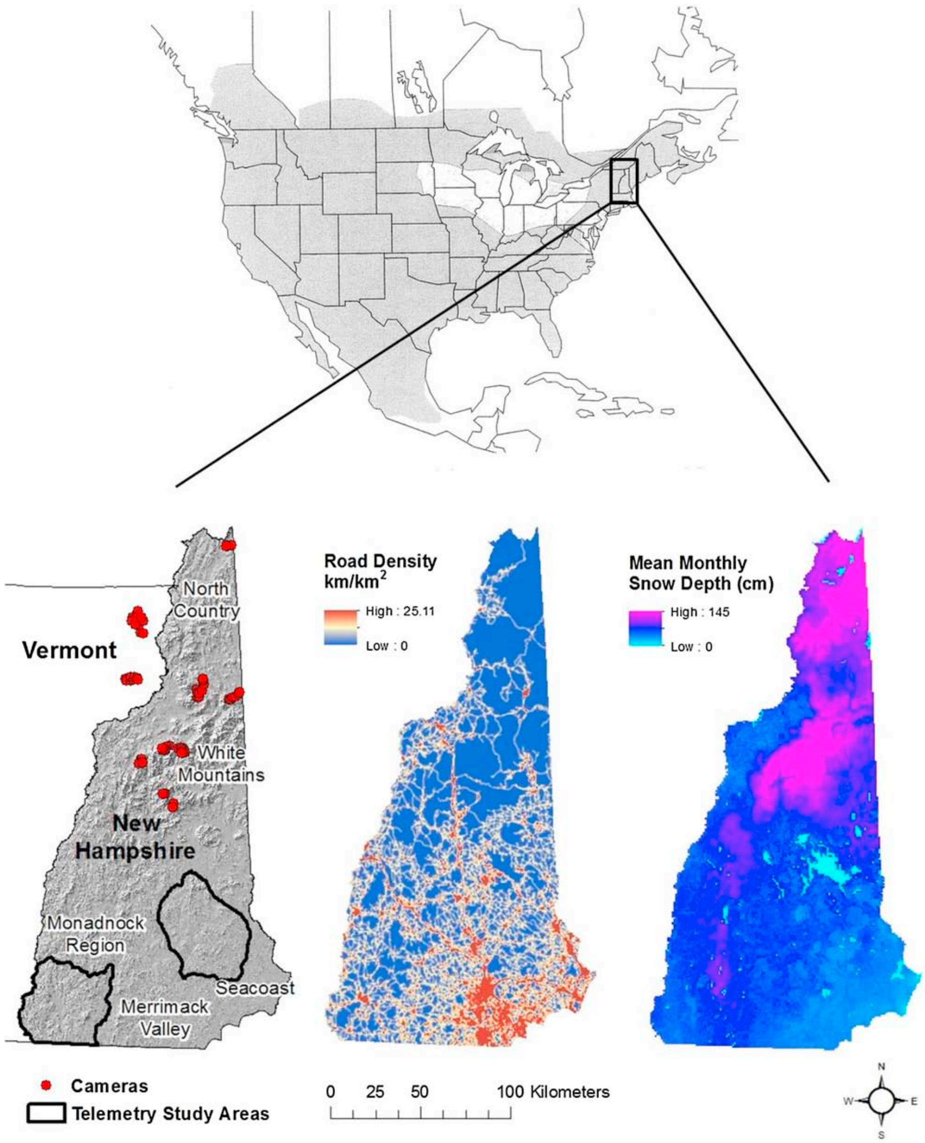

Fig. 1. Top: Geographic range of bobcats (adapted from Hansen, 2007). Bottom left: Study areas where bobcats were monitored in southwest (2009–2010) and southeast New Hampshire (2010–2011) and locations of camera traps in northern New Hampshire and northeastern Vermont. Bottom middle: Road density generated with a 1-km^2 moving window. Bottom right: mean monthly snow depth from November–March 2007–2012.

lieve this approach was appropriate for describing the statewide distribution of bobcats (second-order habitat selection).

We quickly accumulated locations of bobcats from all portions of the state; however, there was an apparent bias against the most northern townships, likely due to low human populations in that region. To assess the impact of sampling disparity, we used information obtained from remotely-triggered cameras that were distributed in the White Mountain National Forest, northern townships, and wildlife reserves in nearby northeastern Vermont as part of a study to monitor mesocarnivores (Fig. 1; Sirén, 2014). This region is especially relevant for understanding the role of snow depth on bobcats because it reaches the statewide maximum there (Fig. 1). The region also includes the historic (Litvaitis et al., 1991) and recent ranges of Canada lynx (*Lynx canadensis*) in New Hampshire (Sirén, 2014). Lynx have morphological adaptations to deep snow that enable them to occupy habitat where bobcat movements are hindered (Peers et al., 2013).

Sixty-one remotely-triggered cameras were set along elevational (335–1452 m) and latitudinal (43.906–45.232°) gradients during January–April 2014. A combination of 5 brands/models were used, including 43 infrared (Bushnell Trophy Cam, n = 24; Moultrie i990, n = 15; Moultrie M80, n = 2; and Reconyx HC500 Hyperfire, n = 5) and 18 incandescent flash cameras (ScoutGuard SG565FV-8M, n = 18). Cameras were spaced 1–3 km apart, comparable to previous camera-trap studies of bobcats (Kelly and Holub, 2008) and lynx (Moen and Lindquist, 2006; Nielson and McCollough, 2009), and separated by 2 × 2 kmgrids to investigate occupancy for multiple species (Shannon et al., 2014). Each camera site included a compact disc hung from a tree limb as a long-range visual attractant. Commercial skunk lure and feathers were placed on a wooden snow-depth stake that was positioned 3–5 m from the camera. Each camera was set for >45 d and checked once every 1–4 weeks to download images, refresh attractants, and to ensure cameras were working properly. Detections of carnivores were considered independent when recorded >1 h apart.

Camera detections were organized into daily occasions and for each occasion we tallied presence/absence and used these data in an occupancy modeling framework (MacKenzie et al., 2002) to estimate daily detection probability (p) and site occupancy (ψ) with the 'unmarked' package (Fiske and Chandler, 2011) in R (R Core Team, 2012). Occupancy was modeled for bobcats using maximum snow depth at the camera site.

Home range and fine-scale habitat selection

Eighteen bobcats (13M:5F; ages = yearling to 10-years old) were trapped during the winters of 2008–09 and 2009–2010 in the southwestern and southeastern portions of the state, respectively (Fig. 1). Adults (>1 yr, based on body weight and tooth wear and subsequently verified from an extracted tooth) were fitted with either Sirtrack drop-off collars (Internal Release, 220 g, Sirtrack Limited, Havelock North, New Zealand) or Lotek collars (Wildcell, 270 g, Lotek Wireless, Newmarket, Ontario, Canada). Sirtrack collars were retrieved after collar release, or the bobcat was recaptured if the release mechanism failed. Lotek collars sent locations via short message services (SMS) to a ground station located at the University of New Hampshire. Collar weight was <5% of body weight of all bobcats and recaptured bobcats were in good physical condition. Study animals were handled in accordance with the University of New Hampshire Institutional Animal Care and Use Committee (Protocol #081201).

Home ranges were generated using a fixed-kernel density estimator (Seaman and Powell, 1996) with least squares cross-validation within the Home Range Extension (Hooge and Eichenlaub, 1997) of ArcView 3.3 (Environmental Systems Research Institute, Redlands, CA, USA). Home ranges were modeled at 95% utilization distributions (UD) with a minimum of 30 locations/bobcat.

Location error, habitat-induced GPS fix bias, and autocorrelation are important considerations when using GPS-based telemetry to investigate habitat associations (Nielsen et al., 2002; Frair et al., 2004, 2010; Lewis et al., 2007; Hebblewhite et al., 2007). Tests in nearby Maine revealed that the average error for Lotek and Sirtrack GPS collars was 20.5 m and 15 m during leaf-on seasons and 14 m and 11.8 m during the leaf-off seasons, respectively (Mallett, 2014); all of these location errors are within the finest resolution (30 m) used for habitat layers. Further, the overall fix success was 87% and 80% for Lotek collars and 95% and 100% for Sirtrack track collars during leaf-on and leaf-off seasons, respectively (Mallett, 2014). All locations generated from 3D fixes were kept, and locations generated from 2D fixes were kept if the dilution of precision was less than or equal to 5.0 (Lewis et al., 2007).

Hebblewhite et al. (2007) recommend weighting locations when GPS bias is >10%. Given the different study areas and types of collars, GPS locations were weighted to assess potential effects of habitat-induced GPS-fix bias using the linear logistic model coefficients for forest (closed conifer = 1.83; deciduous = 1.1; mixed forest = 0.27) and slope (percent slope = 0.03; percent slope * conifer = 0.046; percent slope * deciduous = 0.056; percent slope * mixed = 0.014) obtained from Frair et al. (2004). Spatial autocorrelation was accounted for by using mixed effects models to estimate resource selection probability functions (Gillies et al., 2006; Lele and Keim, 2006). Resulting locations served as *used* points in model generation and an equal number of *available* points were randomly generated within individual home ranges. These points were then used to determine third-order habitat selection patterns (Manly et al., 2002).

Developing suitability models

We considered probability of bobcat occurrences (second-order selection) and use of specific sites within homes ranges (third-order selection) to be measures of habitat suitability. For incidental observations, two snow depth layers were compiled from the National Operational Hydrologic Remote Sensing Center (NOHRSC) and the Snow Data Assimilation System (SNODAS; NOHRSC, 2004). These layers consisted of an average of the maximum monthly snow depth and an average of the mean monthly snow depth from November through March in 2008–2012 (Table 1). Snow depths were then used in conjunction with the observation-based locations to model second-order habitat selection (Table 1). For the telemetry locations,

Table 1
Habitat variables, justification for inclusion, data source, and resolution for GIS layers used to model habitat selection of bobcats in New Hampshire at second and third order.

Habitat Variable (units)	Justification	Source	Resolution
Second-order selection			
Snow – max (mm)	Avoidance of deep snow depth	SNODAS[c]	1 km
Snow – mean (mm)	Avoidance of deep snow depth	SNODAS[c]	1 km
Elevation (m)	Lower productivity at high elev.	DEM[d]	30 m
Third-order selection			
Land Cover[a]	Represents habitat	NLCD 2006[e]	30 m
Elevation (m)	Avoidance of deep snow depth	DEM[d]	30 m
Aspect (flat, north, south)	Sun exposure influences snow	DEM[d]	30 m
Slope (degrees)	Terrain for dens, escape cover	DEM[d]	30 m
VRM[b]	Terrain for dens, escape cover	DEM[d]	30 m
Distance to edge (km)	Prey densities, travel corridors	NLCD 2006[e]	30 m
Distance to stream (km)	Prey densities, travel corridors	GRANIT[f]	30 m
Distance to road (km)	Avoidance of roads	GRANIT[f]	30 m
Road density (km/km[c])	Avoidance of roads	GRANIT[f]	30 m
Traffic Density (unit/km[c])	Avoidance of roads	GRANIT[f]	30 m

[a] Collapsed into development, deciduous forests, coniferous forest, mixed-woods, shrub/scrub, agriculture, wetlands, and open water (Fry et al., 2011).

[b] Vector ruggedness measurement (Sappington et al., 2007).

[c] Snow Data Assimilation System.

[d] USGS Digital Elevation Model.

[e] 2006 National Land Cover Dataset.

[f] New Hampshire Geographically Referenced Analysis and Information Transfer System.

selection was based on 10 variables (Table 1) known to effect bobcat habitat selection in the region (Donovan et al., 2011; Broman et al., 2014).

Resource-selection probability functions (RSPF; Manly et al., 2002) were used to model habitats at both orders of selection. RSPF were fitted using generalized linear models and the R package Resource Selection (R Core Team, 2012) for second and third order, respectively (Lele et al., 2013). Typically, RSPF are approximated with the proportional RSF by exponentiating the parameters fitted with the logistic function (Johnson et al., 2006). Lele (2009; also see Lele and Keim, 2006) demonstrated that the stable estimations of parameters in RSPF can be obtained by using weighted distributions. The advantages of this approach are a potentially better fitting model, compared to the exponential RSF, and output values represent the true probability of selection.

Second-order habitat models were fitted using the three explanatory variables (elevation, snowmean, and snowmax) into single variable models because of collinearity. Models were then re-fitted using quadratic terms when the relationship between selection and the variable was non-linear. The best model was selected using Akaike's Information Criterion (Akaike, 1973) adjusted for small sample sizes (AICc; Burnham and Anderson, 2002). The top second-order model was generated using a used-versus-unused design, and standard logistic regression validation techniques were used, including confusion matrices, Kappa statistic, and Receive Operating Characteristic (ROC) curves (Boyce et al., 2002).

Third-order habitat selection models were developed using logistic regression (Hosmer and Lemeshow, 2000). First, to avoid collinearity, all continuous variables were compared using Pearson's correlation coefficient and one of each pair of correlated ($r > 0.7$) variables was excluded from the analysis. Next, univariate models were fitted for all variables and only those found statistically relevant ($P < 0.25$) were retained (Hosmer and Lemeshow, 2000). Next, variables were standardized to aid in model convergence and then fitted in a multivariate logistic model using a manual forward-stepping procedure (Hosmer and Lemeshow, 2000) starting will a null model that only contained land cover variables. Each variable was added to the null model sequentially according to its univariate strength, measured by Wald statistics. To determine if a variable was retained, likelihood-ratio tests between sequential models were utilized ($P < 0.05$) and each subsequent model was nested in the previous one. Variables excluded after univariate tests were then added to the model to determine if they improved model fit. During model fitting, attention was paid to any large changes or reversals of sign in the coefficient estimates to insure stability. This stepwise process was chosen (as opposed to AICc) because we weren't testing a specific hypothesis in regards to environmental variables, as the candidate variables had been shown to be important predictors in previous studies. The top third-order model was tested using k-fold cross-validation (Boyce et al., 2002; Johnson et al., 2006).

Model extrapolation and validation

The two final models were then mapped using the Raster Calculator tool in ArcMap 10.0 (ESRI, Redlands, CA). All habitat variables present in the RSPF were represented by raster layers in ArcMap 10.0. The model equation was then used to extrapolate the RSPF for New Hampshire at both orders of selection. Continuous variables were capped at the minimum and maximum values measured, so that models were not extrapolated outside the observed data (DeCesare et al., 2012). We then combined scales by multiplying second- and third-order habitat selection models to generate a map of suitability for the entire state (Johnson et al., 2004). We felt this approach represented habitat suitability at local and landscape scales throughout New Hampshire.

Habitat suitability scores among WMUs were not normally distributed, so we calculated Spearman's ρ to identify the model (second order, third order, or combined scales) that was the best correlate of bobcat density under the assumption that bobcat abundance should increase with habitat suitability. Correlations were calculated and plotted in R (R Core Team, 2012). Hunter-detection rates of bobcats collected from 2009 to 2013 were used as an index of relative abundance (described by Mahard et al., 2016). Briefly, licensed hunters were surveyed by members of New Hampshire Fish and Game Department and the number of bobcat sightings/1000 hunter outings was partitioned among Wildlife Management Units (WMUs) that comprise the state. Kindberg et al. (2009) found that effort-corrected indices based on hunter surveys were a reliable proxy of carnivore abundance. WMUs range from 398 to 2407 km^2 ($\mu = 1041$ km^2) and thus have the potential of containing multiple bobcats. Hunter effort was low in the White Mountain region, so we combined the four WMUs in that region (see Mahard et al., 2016 for details). Average habitat suitability of each WMU based on second-order selection, third-order selection, or combined models was the predictor variable. The resolution of second-order and third-order suitability rasters differed, so resolution of the third-order model was decreased to be equivalent to the second-order model. All spatial analyses for the regressions were carried out in QGIS (QGIS Development Team, 2016).

Results

Course-scale habitat selection

A total of 729 sightings from 72% of the 259 townships in the state were reported to the project website between December 2007 and January 2013. After screening, 665 were assigned GPS coordinates and these locations were buffered with the largest home-range radius of our marked bobcats (9.6 km; Reed, 2013). The model with average monthly mean snow depth with a quadratic term was considered the best model as judged by AICc (Table 2). A receiver operating characteristic (ROC) curve showed an Area Under the Curve (AUC) score of 0.90, suggesting a good predictive model. However, the model received a moderate kappa statistic of 0.51 (±0.013) because of the high rate of false positive. Probability of bobcat use declined with increased snow depth (Fig. 2). The model predicted well for used sites (sensitivity = 0.96 ± 0.002), but poorly for unused sites (specificity = 0.50 ± 0.013).

Fourteen independent detections of bobcats occurred at 6 of the 61 camera-trap sites during 4367 trap nights. Detections were confined to low elevation sites (368–429 m) that were characterized by a shallow snowpack (44–72 cm). The null estimate of detection proba-

Table 2
Models for second-order selection that used incidental observations (2007–2013) and average monthly (November–March) maximum snow depth (Snow_Max) and average monthly (November–March) mean snow depth (Snow_Mean) to explain bobcat distributions in New Hampshire.

Model	K	AIC$_c$	ΔAIC$_c$	AIC$_w$	log(L)
Snow_Mean^2	3	4703.82	0.00	1.00	−2348.91
Snow_Mean	2	4761.66	57.84	0.00	−2378.83
Snow_Max^2	3	4995.55	291.73	0.00	−2494.77
Snow_Max	2	4998.28	294.46	0.00	−2497.14
Elevation^2	3	5236.30	532.48	0.00	−2615.15
Elevation	2	5546.02	842.21	0.00	−2771.01

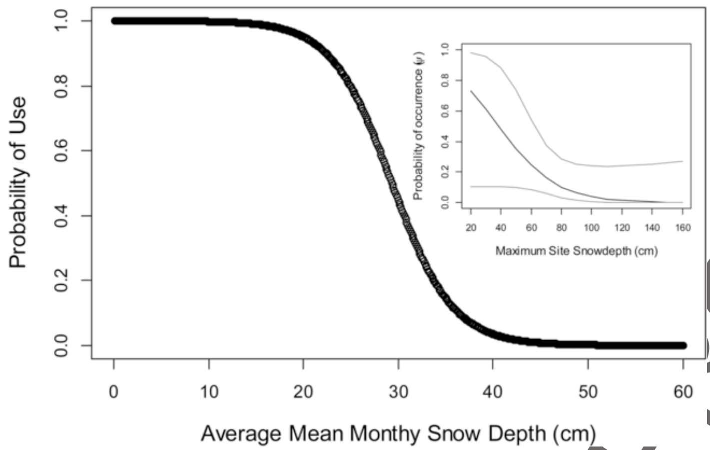

Fig. 2. Probability of habitat use by bobcats in New Hampshire (based on incidental observations) in comparison to the average monthly mean snow depth between November –March 2007–2012. Inserted figure depicts bobcat occupancy (with 95% confidence bands) in relation to maximum snow depth based on 14 detections of bobcats during 6221 camera-trap nights in northern New Hampshire and nearby Vermont from 9 January to 15 April 2014.

bility (p) was low ($p = 0.02$, 95% C.I. = 0.01–0.04), but typical for bobcat studies (Long et al., 2011; Schuette et al., 2014; Shannon et al., 2014). There was little evidence that site covariates influenced detection probability, except that p was directly proportional to Julian day (p = 0.505) and tend date (p = 0.495); i.e., detection probability increased later in the winter and after traps were tended, respectively. Bobcat occupancy (ψ) was affected by snow depth at the camera site ($\beta = -0.05 \pm 0.03$, P = 0.08)and there was obvious agreement between camera detections and incidental observations in their response to snow (Fig. 2). Because of the relatively small number of camera-trap detections, we considered these observations as confirming the pattern revealed by statewide observations and did not incorporate camera detections in our models of selection.

Home range and fine-scale habitat selection

Bobcats were monitored for 54–286 days ($\bar{x}$ = 206), with 89–1138 locations/individual ($\bar{x}$ = 503).The 95% UD home ranges averaged 23.8 km^2 (range = 14.1–54.4) for females and 81.6 km^2 (range = 16.4 –292.1) for males. Additional details are provided in Reed (2013).

GPS-fix biases were not included in the final third-order selection model because no large changes in coefficients were observed when they were applied. K-fold cross validations with 5 folds were all highly correlated (Table 4) for the top model. Spearman correlations ranged from $\rho = 0.952$ ($P < 0.001$) to $\rho = 0.988$ ($P < 0.001$), indicating that bin number and area-adjusted frequency of used points were highly correlated. All slopes (b_1) were significantly different from 0, indicating the model performed better than neutral model where use would be equal to availability. All slopes were not significantly different from 1, indicating the model was proportional to use. Additionally, none of the intercepts (b_0) were significantly different from zero (Table 4), which is expected for a model that was proportional to use. Model fit for expected vs. observed regressions was 0.634–0.774. Bobcats selected forests, shrub/scrub, and wetlands, and avoided developed areas, agricultural areas, and open water relative to availability (Table 3). They also showed avoidance of areas with high road densities and selected areas closer to forest edges. They preferred more rugged and steeper sloped areas, with southern facing slopes. Finally, there was selection for areas closer to streams, but no significant relationship to elevation at this order of selection.

Statewide suitability versus relative bobcat abundance

Resulting models of second- and third-order selection were combined by multiplying them together which changed the resolution of habitat suitability in New Hampshire (Fig. 3). Although suitability

Table 4
Spearman rank correlations between and expected versus observed regressions for the best RSPF model used to describe bobcat habitats in New Hampshire. The model was validated with k-fold cross-validation utilizing five folds.

Fold	Rank Correlation		Expected vs. Observed Regression			
	ρ	P	b_0	b_1	R^2	P
1	0.988	<0.001	0.020	0.796	0.774	<0.001
2	0.976	<0.001	0.038	0.624	0.634	0.006
3	0.964	<0.001	0.016	0.836	0.735	0.002
4	0.964	<0.001	0.031	0.689	0.670	0.004
5	0.952	<0.001	0.020	0.795	0.730	0.002

Table 3
Parameter estimates from the best third-order habitat selection model. Models were generated using GPS-location data from 18 collared bobcats in New Hampshire from 2009 to 2011.

Habitat Variable	β estimate	SE	P value
(Intercept)	0.32	0.16	0.045
Agricultural field	−0.02	0.13	0.888
Deciduous forest	0.06	0.06	0.321
Developed	−0.50	0.10	<0.001
Evergreen forest	0.11	0.08	0.162
Open water	−0.76	0.24	0.002
Shrub/scrub	0.67	0.32	0.035
Wetlands	2.29	0.68	0.001
Aspect-flat	−1.50	0.40	<0.001
Aspect-south	0.19	0.05	<0.001
Distance to forest edge	−0.23	0.03	<0.001
Vector ruggedness measurement (VRM)	0.15	0.06	0.013
Slope	0.10	0.03	0.004
Road density	−0.27	0.03	<0.001
Elevation	0.00	0.06	0.987
Distance to stream	−0.07	0.03	0.026

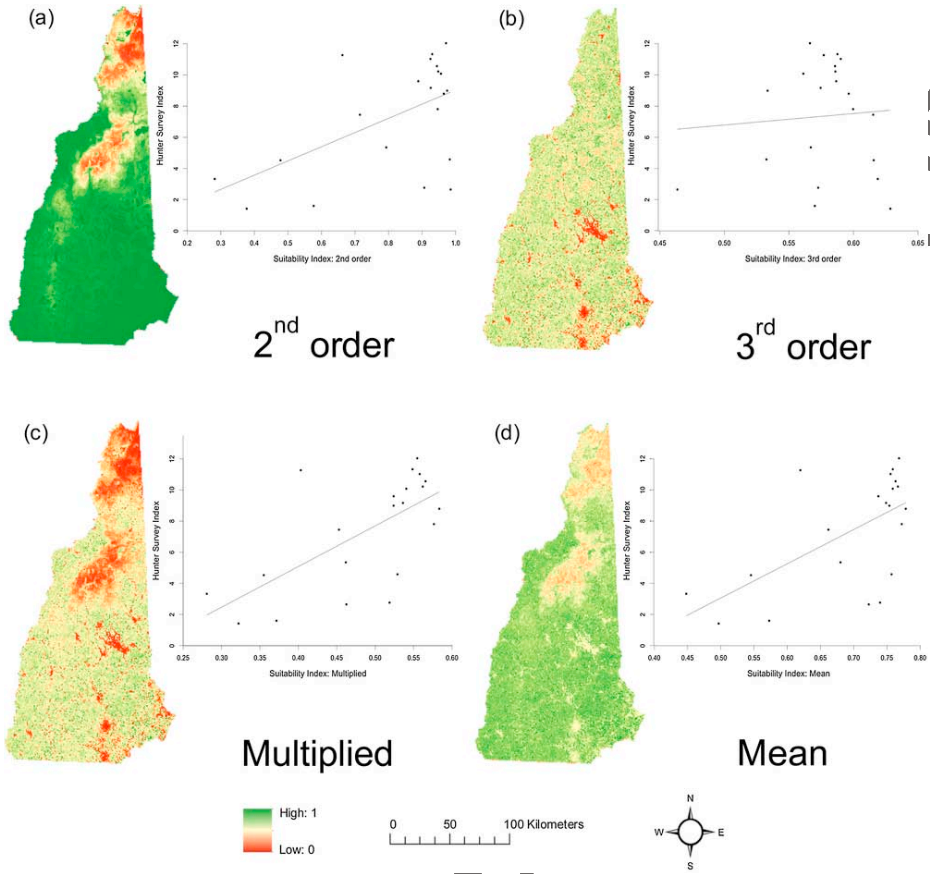

Fig. 3. Statewide maps illustrating bobcat habitat suitability in New Hampshire based on (a) incidental observations collected from 2007 to 2013 (second-order selection), (b) suitability based on GPS-telemetry locations collected from 2009 to 2011 from 18 collared bobcats (third-order selection), (c) suitability based on a hierarchical model (combined second and third-order selection), and (d) suitability based on the average of second and third-order models.

was highest in the southern part of the state according to the second-order model (Fig. 3a), regions with intensive development and highway corridors were considered poor habitat and rectified by the inclusion of the third-order selection model (Fig. 3b). Conversely, the second-order model modified third-order suitability in the northern part of the state especially in areas with deep snowpack (Fig. 3c).

The hierarchical suitability model produced by multiplying second and third-order models (Fig. 3c) was the best correlate of bobcat detection rates ($\rho = 0.62$, $P = 0.003$). Individually, suitability values of the second-order model were weakly but not significantly correlated to bobcat detections ($\rho = 0.32$, $P = 0.160$; Fig. 3a), whereas the third-order model showed no relationship to bobcat detections ($\rho = -0.09$, $P = 0.704$; Fig. 3b).

Discussion

By using several sources of information on bobcat-habitat associations collected at different spatial scales, we were able to produce a statewide map of suitability that differed substantially from efforts relying on a single source. Such an approach acknowledges the intrinsic linkages that may exist among scales of habitat selection (Bergin, 1992; Luck, 2002). If we had only applied an extrapolation of our telemetry-based model, northern portions of the state comprised of highly suitable habitat (e.g. wetlands, scrub/shrub, and forest edges) would have been depicted as having high suitability even at high elevations with deep winter snow cover (Fig. 3b). Likewise, a habitat map based on incidental sightings depicted the entire southern portion of New Hampshire to be suitable habitat despite the presence of high-volume roads and urban development (Fig. 3a). When the models were combined, suitability dropped substantially for areas in southern New Hampshire where road density and development are substantially greater than other portions of the state (Fig. 3c). Comparing our suitability models to relative abundance supported our prediction that a hierarchical model of bobcat-habitat suitability was substantially better at predicting abundance than single-scale analyses.

We were somewhat surprised by how influential the effect of snow depth was on bobcat distribution. Measuring responses to snow depth is difficult at a fine scale because there is relatively little heterogeneity of this feature within a bobcat home range. At a regional or statewide scale, snow depth and overall winter severity can change habitat suitability drastically and apparently affect bobcat abundance. Such a pattern is supported by research in other northern regions. In New York, bobcats were found to have much smaller home ranges in the southern Catskills region ($\bar{x} = 36.0\ km^2$ and $\bar{x} = 31.0\ km^2$, for males and females respectively) compared to those in the northern Adirondack Mountains ($\bar{x} = 325.7\ km^2$ and $\bar{x} = 86.4\ km^2$; Fox, 1990). In nearby Maine, Litvaitis et al. (1986a) monitored physical condition of harvested bobcats (based on body weight and fat reserves) in comparison to winter severity. Juvenile and female bobcats in particular were in poor condition during periods of deep snow and low temperatures. Adult male bobcats seemed less affected, possibly because they are capable of securing a wider range of prey (Litvaitis et al., 1986a). Yet even adult males were susceptible to starvation during extended periods of deep snow (Major, 1983). As a result, bobcat densities in northern regions of New Hampshire are likely lower than other regions because of the limitations imposed by snow. However, extrapolation of the telemetry-based model indicated that the northern portion of the state contains suitable habitat. Only when snowfall is taken into consideration does this region become one the poorest areas in the state (Fig. 3a). Bobcat density in northern townships may be dynamic in response to variation in annual snowfall. Historic harvest records indicated that the region did periodically support more bobcats, especially when widespread timber harvesting generated habitats for snowshoe hares (*Lepus americanius*) in the early 1960s (Litvaitis et al., 2006). If second and third-order selection models are averaged (Fig. 3d), we may obtain a depiction that reflects that pattern. However, the mean suitability model did not correlate to statewide detections of bobcats as well as the hierarchical (multiplied) model did ($\rho = 0.59$, $P = 0.005$ versus $\rho = 0.62$, $P = 0.003$).

Extrapolating our incidental-sightings model as the only source of information could have lead to inaccurate conclusions by depicting the entire southern portion of New Hampshire to be suitable habitat (Fig. 3a). This region, influenced by the coastal climate, seemed to represent the best habitat. However, when the telemetry-based model was added, low lying and relatively snow-free areas overlap highly-developed areas, causing those areas to be of low suitability (Fig. 3c, d). As a result, we believe by using incidental sightings coupled with telemetry data, we were able to generate a realistic impression of statewide bobcat suitability.

Our application of incidental observations to characterize features of carnivore habitat is not unique. For example, McDonald et al. (2008) used a 1-km buffer around hunter sightings to investigate habitat overlap of several species of mesocarnivores. In that study, hunters were not randomly distributed yet their detections of carnivores did provide an efficient method to investigate habitat associations. There are obvious concerns about using presence-only information to determine the distribution patterns of a species (e.g., Elith and Leathwick, 2009; Yackulic et al., 2013), but such information is often the only available data. Because observations from the public did not include non-detections of bobcats, we cannot be certain that portions of northern New Hampshire with low human density and limited access were adequately surveyed. However, our solicitation of bobcat observations by the public was widely distributed by media outlets throughout the state and we even received sighting reports from neighboring states by people travelling through New Hampshire. Additionally, low densities in the northern portion of the state were corroborated by our camera-trap surveys. Detections in these areas demonstrated bobcats were present on the landscape, but were using areas with lower snow depths. This independent survey demonstrated a similar relationship to the one observed with our incidental observations.

This study provides a method for reliably including data collected by citizen scientists in habitat suitability analyses. By relating citizen sightings of bobcats to a large-scale variable like snow cover, we were able to limit the impact of known observer biases (human population density, road density, observer motivation; Broman et al., 2014) and validate a meaningful model parameter. The resulting second-order selection model was supported by a camera survey and proved to be an integral component in the accuracy of our optimal habitat suitability model for bobcats in New Hampshire. Citizen science has been an increasingly important tool in ecological research (e.g., Silvertown, 2009) as it allows for efficient large scale data collection that would be otherwise prohibitively time- and labor-intensive. It can be especially effective in predator conservation studies because these charismatic species tend to draw large numbers of volunteers, but also because greater citizen involvement and education can help eliminate the stigma of fear often associated with predator species cohabiting near urban areas (Zinn and Pierce, 2002). To date, we have solicited nearly 1000 sightings on our citizen reporting website where visitors also learned about bobcat ecology and the results of our research. Additionally, we were informed by citizen scientists of novel foraging strategies used by bobcats in winter (staking prey at backyard bird feeders) that may enhance juvenile bobcat survival in human-dominated landscapes (Broman et al., 2014).

In contrast to the course-scale information obtained by incidental observations, habitat selection by transmitter-equipped bobcats was a poor predictor of statewide bobcat abundance when considered alone. Although GPS telemetry has greatly enhanced our understanding of spatial ecology through increased location data per individual, the high cost often compromises the sample size of transmitter-equipped animals (see Hebblewhite and Haydon, 2010 for review). This may be problematic when evaluating habitat suitability due to individual differences (Gillingham and Parker, 2008; Latham et al., 2011), and variation of habitat and climate within a species range or regional distribution (D'Eon and Serrouya, 2005; Dettki et al., 2003). Yet there are clear advantages to incorporating the detailed information obtained from marked animals (Loe et al., 2012). Thus, investigators should consider the sampling design and region of interest or application when determining habitat suitability with telemetry-based data.

In conclusion, we believe that by combining models developed at multiple spatial scales, we substantially improved our understanding of bobcat habitat requirements in New Hampshire. Each model, considered independently, would have led to inaccurate conclusions about the animal's needs. By integrating our models, we developed a map of habitat suitability that can be used across a region with differing environmental conditions and thus more appropriately inform conservation and management decisions.

Uncited reference

USDA Forest Service (2001).

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