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Quantifying home range habitat requirements for bobcats (*Lynx rufus*) in Vermont, USA

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ABSTRACT

We demonstrate how home range and habitat use analysis can inform landscape-scale conservation planning for the bobcat, *Lynx rufus*, in Vermont USA. From 2005 to 2008, we outfitted fourteen bobcats with GPS collars that collected spatially explicit locations from individuals every 4 h for 3–4 months. Kernel home range techniques were used to estimate home range size and boundaries, and to quantify the utilization distribution (UD), which is a spatially explicit, topographic mapping of how different areas within the home range are used. We then used GIS methods to quantify both biotic (e.g. habitat types, stream density) and abiotic (e.g. slope) resources within each bobcat's home range. Across bobcats, upper 20th UD percentiles (core areas) had 18% less agriculture, 42% less development, 26% more bobcat habitat (shrub, deciduous, coniferous forest, and wetland cover types), and 33% lower road density than lower UD percentiles (UD valleys). For each bobcat, we used Akaike's Information Criterion (AIC) to evaluate and compare 24 alternative Resource Utilization Functions (hypotheses) that could explain the topology of the individual's UD. A model-averaged population-level Resource Utilization Function suggested positive responses to shrub, deciduous, coniferous forest, and wetland cover types within 1 km of a location, and negative responses to roads and mixed forest cover types within 1 km of a location. Applying this model-averaged function to each pixel in the study area revealed habitat suitability for bobcats across the entire study area, with suitability scores ranging between −1.69 and 1.44, where higher values were assumed to represent higher quality habitat. The southern Champlain Valley, which contained ample wetland and shrub habitat, was a concentrated area of highly suitable habitat, while areas at higher elevation areas were less suitable. Female bobcat home ranges, on average, had an average habitat suitability score of near 0, indicating that home ranges consisted of both beneficial and detrimental habitat types. We discuss the application of habitat suitability mapping and home range requirements for bobcat conservation and landscape scale management.

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1. Introduction

Home range and habitat use are two crucial components of predator ecology, and are aimed at interpreting an animal's occurrence in space and time (Kernohan et al., 2001). The distribution of resources is the predominant factor in influencing where individuals occur on the landscape (Litvaitis et al., 1986; Azevedo and Murray, 2007). These resources include an appropriate prey base, mates, refugia from competitors and predators, and appropriate denning and rearing sites for young.

Understanding home range and habitat requirements is often critical for managing wide-ranging predators, which usually occur at low densities and are often of conservation and management concern. Because they occur on such a large scale across the landscape, they encompass numerous habitat types, geographic features, non-habitat, and potential barriers that could restrict access to their preferred resources (Jaeger and Fahrig, 2004). Additionally, these species illicit strong emotional responses from the public, and create a demand for information on habitat requirements and management plans.

Kernel home range analysis (Silverman, 1986; Seaman and Powell, 1996; Worton, 1989) provides an opportunity to estimate

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not only home range size and boundaries, but also habitat requirements of species (Marzluff et al., 2004). Kernel home-range analysis involves obtaining numerous, independent, x–y coordinates where animals occur, fitting a probability distribution such as a bivariate normal distribution over each coordinate, and then summing these distributions across all points to yield an estimate of home range size.

In addition to providing an estimate of home range size and boundaries, kernel home range analysis provides an estimated probability density function (Silverman, 1986), also known as the Utilization Distribution (UD; Worton, 1987; Kernohan et al., 2001). The UD is a probability map that explains where the individual is most likely to occur within the home range boundary (Kernohan et al., 2001; Marzluff et al., 2004). Thus, the UD illustrates the animal's use of space across its entire home range, instead of the individual x–y locations. Within the home range, probabilities of use are rarely uniform; some areas are used much more than other areas (Marzluff et al., 1997), resulting in a home range topographic map, consisting of peaks that represent frequently-used (core) areas and valleys that represent less-used areas.

Conservation and management decisions could be aided with knowledge of how various environmental resources influence the topology of the UD. Resource Utilization Functions (RUFs) offer an opportunity to quantify this association. A RUF is a mathematical equation that estimates the association between the UD percentile (use) and the level of a given spatially defined resource at the same location in the home range, such as the slope of the land, distance to a road, or the landcover type. The dependent variable in a RUF is the UD percentile at any given location within the home range, and the independent variables in a RUF are the spatially corresponding resource levels. The goal of the analysis is to find a RUF that best explains the peaks and valleys within a given UD (see Fig. 1, from Marzluff et al., 2004 analysis on stellar's jays).

The bobcat (*Lynx rufus*) is an excellent example to illustrate the uses of kernel home range and UD analysis for conservation and management decisions. Like other medium-sized carnivores, bobcats have large home ranges (95.7 km^2; Litvaitis et al., 1986). They are reclusive, solitary hunters, and utilize a wide range of habitats in their role as generalist predators (Hansen, 2007). In Vermont, bobcats currently are well-distributed across much of the state and occupy a variety of habitats. However, upon the completion of the State Wildlife Action Plan in 2003, the bobcat was identified as a species of greatest conservation need because its large home-range requirements and life-history characteristics make it vulnerable to habitat loss, habitat fragmentation, and road mortality (see also Crooks, 2002).

Because bobcats occur across heterogeneous landscapes, a primary challenge in guiding conservation and management decisions has been to determine if specific features or resources in the landscape shape habitat use for the species as a whole. Such information is vital because management objectives often target populations, not individuals within a population. By understanding how individuals vary in their use of different habitat types within home ranges, managers will be better equipped to make decisions for the population on the whole.

Our objectives were to: (1) Estimate the home range size for bobcats in our study area; (2) across all bobcats studied, compare levels of various resources between UD peaks (upper UD percen-

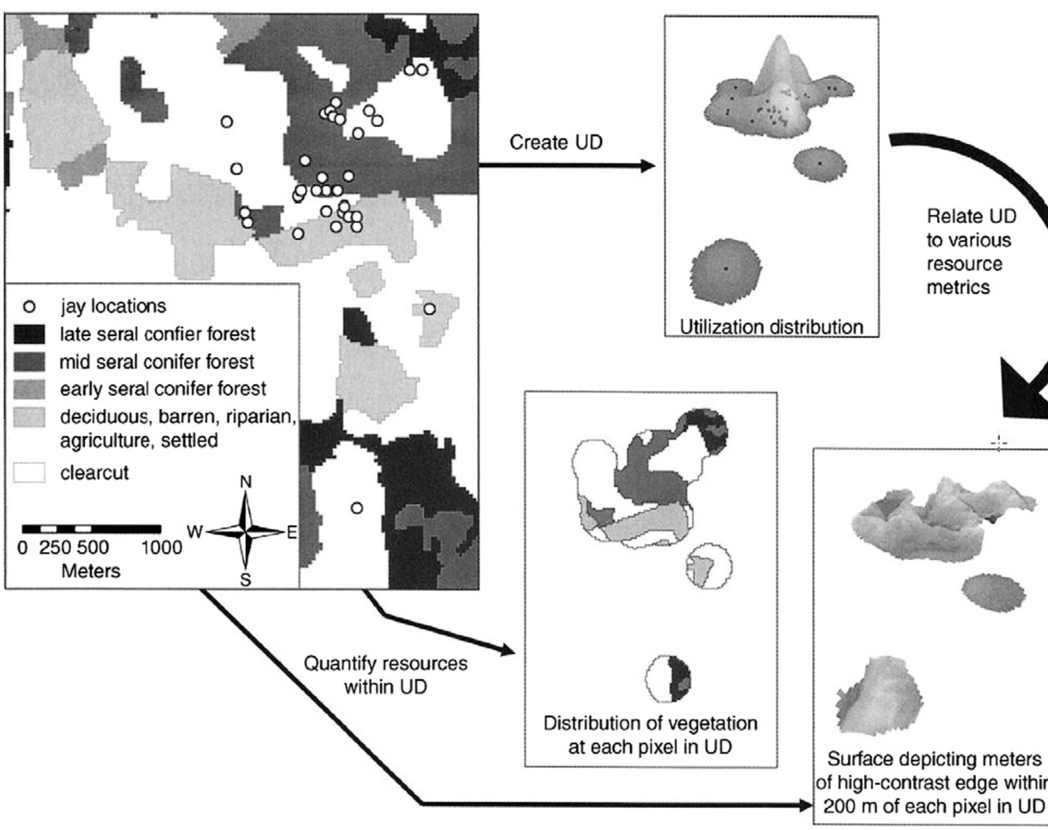

Fig. 1. Calculation of a Resource Utilization Function for a single Steller's Jay (source: Marzluff et al. 2004). First, the jay's location estimates (upper left) are converted into a three-dimensional utilization distribution (UD; upper right) using a fixed-kernel home range estimator. The height of the UD indicates the relative probability of use within the home range. Greater heights indicate areas of greater use, as inferred from regions of concentrated location estimates. Second, resource attributes are derived from resource maps within the area covered by the UD. For example, we calculated a continuous resource measure (contrast-weighted edge density; lower right; highest at interfaces between late-serial forest and clearcuts or urban areas) and a categorical resource measure (vegetative land cover; lower left) at each grid cell center within the area of the UD. The height of the UD (relative use × 100) is then related to these local (e.g., vegetation cover; lower left) and landscape (e.g., contrast-weighted edge density; lower right) attributes on a cell-by-cell basis with multiple regression techniques that adjust the assumed error term for spatial autocorrelation.

tiles or core areas) and UD valleys (lower UD percentiles or rarely used areas within home ranges); (3) within the home range of each bobcat, evaluate 24 alternative Resource Utilization Functions (e.g., amount of scrub-shrub habitat) to determine which RUF best describes the association between the height of the UD and levels of a spatially defined resource; and (4) derive a model-averaged RUF to map habitat quality across the study area and identify minimum home range habitat requirements for female bobcats.

2. Study area

Our study area was located in the Champlain Valley of northwestern Vermont, including Chittenden (1606 km^2), Addison (2093 km^2), Lamoille (1202 km^2), and Washington (1800 km^2) counties (Fig. 2). The western edge of the study area was Lake Champlain. We chose this study area because it contained a gradient of landscape fragmentation, and because it included diverse habitat types (coniferous forest, deciduous forest, agriculture, and wetlands) and elevation (high, rocky mountainous regions to low valleys and lake front). In addition to the diversity of habitat types, the area was dissected by four main throughways and burgeoning development from the Burlington area.

3. Methods

3.1. Field methods

To estimate bobcat home ranges and habitat use in Vermont, bobcats were captured with two different trapping techniques in accordance to the University of Vermont's Animal Care and Use protocols (permit 05-036). Traps were operated from February 2005 to January 2008 and individual captures spanned both breeding and non-breeding seasons. In Vermont, bobcats mate in late March or early April, and kittens are born in late May or June and are weaned about 2 months later. During warmer trapping months, padded foot hold traps (Victor 3 Softcatch) were used in blind trail and lure sets and checked daily. Bobcats caught by this method were sedated using a syringe pole. In the winter and in areas of high human use and activity, Safe Guard cage traps were used to trap bobcats. Cage traps were 48 in. long, 18 in. wide and 22 in. tall. Cage traps were baited with partial beaver carcasses and both visual and scent lures, and were checked every 24 h. Animals caught by this method were sedated by hand injection.

Captured bobcats were immobilized with ketamine and xylezine at a 5 to 1 ratio according to the mass of the animal

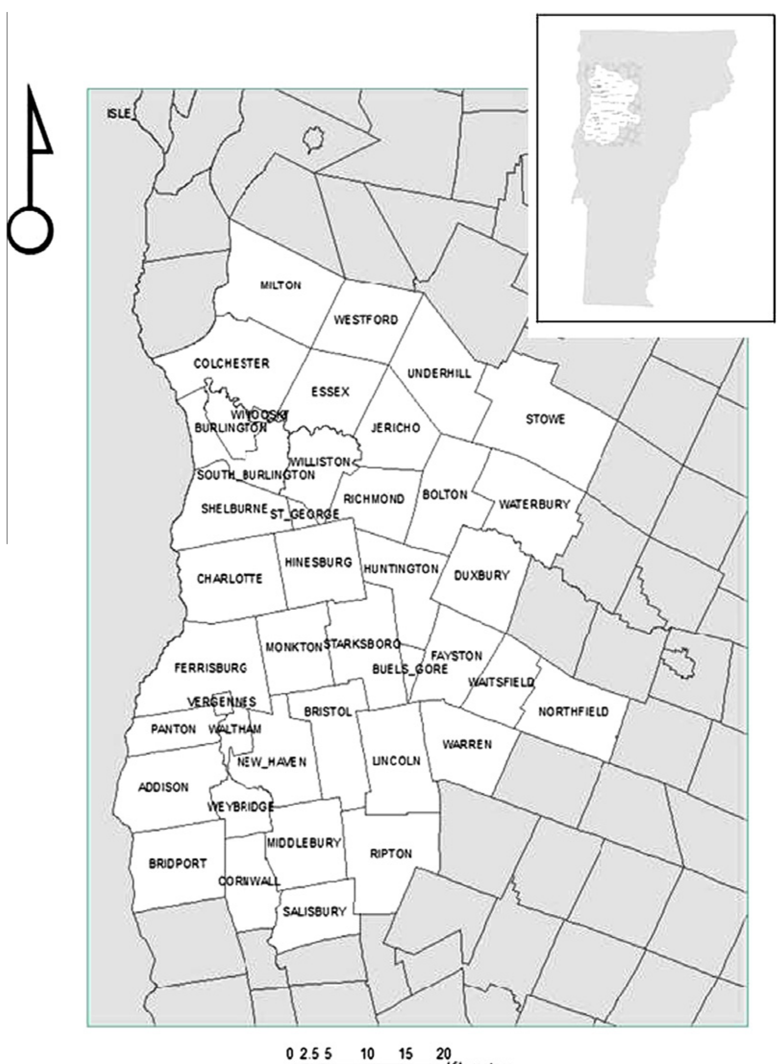

Fig. 2. Study area occurred within Chittenden (1606 km^2), Addison (2093 km^2), Lamoille (1202 km^2), and Washington (1800 km^2) counties in Northwestern Vermont. Lake Champlain acted as the western boundary while the town of Milton acted as the northern most boundary, Northfield the eastern most boundary, and Salisbury the southern boundary.

(15.2:3 mg/kg). While the bobcats were sedated, care was taken to monitor the animal's capillary refill, respirations per minute, and body temperature to avoid over heating in summer and hypothermia in winter. Eye salve was applied to keep the animal's eyes moist while under sedation. Measurements taken included age (approximated based on tooth wear and size), weight, length, girth, and overall condition of the animal.

Male and female adult bobcats were ear tagged and outfitted with ATS G2004 or Lotek 3300S store-on-board GPS collars that allowed for remote monitoring of habitat use and movement over time and space. Collars did not exceed 2% of the animal's total body weight and therefore should not have affected the reproduction, behavior, survivorship, or condition of medium- to large-sized terrestrial mammals (Withey et al., 2001).

GPS collars were programmed to record the location of individuals every 20 min during crepuscular and nocturnal periods (1600–930 h), when bobcats are most active, every other day for 130 days. These data are highly correlated temporally and were used to assess movement patterns (Abouelezz et al., submitted for publication). On the alternate days, locations were collected every 5 h for a full 24 h. For each location obtained, collars recorded temperature, activity information, time, and date. Given this schedule, the maximum number of locations per collar was 4992. However, not every attempt resulted in a successful location fix (see below).

Each GPS collar also contained a "mortality" switch that indicated a dead animal or dropped collar, and a VHF transmitter for real-time tracking of actively-collared animals. The VHF transmitter allowed the use of ground and aerial telemetry to relocate collared individuals on a daily basis. In cases where an animal had not been relocated for more than 48 h, an aerial survey was conducted to relocate the individual. When the collar reached 130 days, the collar self-released and was retrieved.

3.2. Objective 1: Home range estimation

For each bobcat, we ordered all location fixes by their time stamp, and then used location data that were separated by minimally by 4 h to maintain temporal independence. Although many researchers conservatively use locations separated by 24 h (Dieffenbach et al., 2006), we chose 4-h intervals to provide a more accurate estimation of the UD (Marzluff et al., 2004) while at the same time minimizing observations that are highly auto-correlated (Swihart and Slade, 1985). Across all bobcats sampled and all GPS fixes (including those not used in the home range analysis), the maximum distance a bobcat moved within a 4 h period was roughly 4.5 km. Given an average home range size of $\sim$57 km^2 (see Section 4), a bobcat in the middle of its home range would be able to access any area within the average home range within a 4 h period.

Data were uploaded into ArcGIS and shape files were created for each animal. Shape files were imported to the program Animal Space Use (Horne and Garton, 2006) to estimate the UD for each animal while correcting for GPS collar detection bias. Collar bias, the differential success rate of collars in obtaining location data in different habitats and terrain, can significantly bias the UD and subsequent habitat selection analyses (Frair et al., 2004, 2010). In an experimental study, Frair et al. (2004) estimated the effects of collar type (ATS versus Lotek), forest habitat (mixed, deciduous, and coniferous), slope, and the interactions among these variables. We used the coefficients estimated by Frair et al. (2004) to weight the observations for each bobcat analyzed in Animal Space Use. We computed the probability that a collar would successfully acquire a GPS location based on the following linear logistic model coefficients: Intercept = 3.86; Closed Conifer Habitat = -1.83; Deciduous Habitat = -1.1; Mixed Forest Habitat = -0.27; ATS collar type = -0.45; Lotek GPS collar = reference; Percent Slope = -0.03; Percent Slope $\times$ Conifer = 0.046; Percent Slope $\times$ Deciduous = 0.056; Percent Slope $\times$ Mixed = -0.014. These coefficients illustrate that GPS units located in forest landcover types (conifer, deciduous, and mixed forest) have lower probability of acquiring a GPS location than other locations. Although the coefficients from Frair et al. (2004) were estimated from data collected in Alberta, CA, we assumed they would be applicable to Vermont given that canopy cover within forested landcover types in Vermont were similar to those reported in Frair et al. (2004) Table 1 (Donovan, unpublished data; see also Hebblewhite et al., 2007). Each acquired observation was weighted as described by Horne et al. (2007) to reduce collar detection bias. Likelihood cross-validation was used to estimate the smoothing parameter for kernel home range estimation (Horne and Garton, 2006).

The primary output of Animal Space Use was the UD, which consisted of pixilated grid containing probabilities of space use across the home range (Fig. 1). Pixels with high probability values indicated locations where a bobcat was most likely to occur, pixels with low probability values indicated locations less likely to be used by the bobcat, and pixels with 0 probabilities were not included in the home range. We converted the pixel probabilities to percentiles for analysis, which aided interpretation. Probabilities of 0 were in the 0th percentile, and the highest probabilities within the home range were the 100th percentile.

Home range sizes were calculated by multiplying the number of pixels within the UD that had probabilities greater than zero by the UD pixel area, and converting the area to km^2.

3.3. Objective 2: Analysis of resources within UD peaks versus valleys

We mapped the levels of 18 resources across the entire study area. Resource levels were derived from remotely sensed data (see Table 1 and below for more detailed description). Three resources levels were derived from Digital Elevation Maps (DEM), which had a 30 m $*$ 30 m pixel resolution. Slope and aspect (flat, north-, south-, east-, and west-facing slopes) were quantified for each pixel throughout the study area. For the third resource, we used the program LCaP (Theobald, 2007) to assign a topographic position index (TPI) to each pixel in the study area. Pixels were classified to one of five categories (ridge, upper slope, lower slope, flats, and valley), based on the elevation of a given pixel and its position relative to the average elevation of pixels in a surrounding annulus (300 m and 600 m defined the inner and outer rings). Twelve additional resources were derived from National Land Cover Data (NLCD, 2001), which had a 30 m by 30 m pixel resolution (Table 1). We considered six land cover types (resources) to represent collective bobcat habitat: deciduous forest, coniferous forest, forest wetland, mixed forest, scrub-shrub, and wetland. In addition, we mapped forest edge cells across the study area by reclassifying all forest cover types as "forest" and determining if a forested cell had at least one non-forest neighbor (ArcGIS Neighborhood Analysis tool). We reclassified hay, grass, pasture, and row crops in the original NLCD layer into one resource category called "agriculture" (Table 1). We considered three land cover types to represent development: low-, medium-, and high-intensity development (NLCD, 2001). The final resource derived from the NLCD layer was a measure of land cover variety, which counted the number of unique, reclassified land cover types within a specified area of analysis (90 m, 300 m; Table 1).

Roads and streams are potentially important resources shaping bobcat home range and habitat use, and are linear map features. We used 1:5000 orthophotographs from the E911 road maps layers (Vermont Center for Geographic Information) to map class 1 and 2 roads (combined), as well as to map class 3 roads across the study area. We used Vermont Hydro DEM maps (Vermont Hydrography

Table 1
Descriptions for the 18 resources that were spatially quantified for each bobcat home range, the map resolution, and the source data from which it was created.

Resource category	Resource name	Description	Resolution	Data source
Slope	Slope	Measures degree slope for each pixel in the study area	24 m^2	DEM 24
Aspect	Aspect	Estimates aspect of each pixel in study area, categorized into five groups (flat, north, south, east, west)	24 m^2	DEM 24
Topographic position	TPI	Assigns topographic classification (ridge, upper slope, lower slope, flats, and valley) for each pixel in the study area	24 m^2	DEM 24
Bobcat habitat	Deciduous	Estimates whether a individual pixel is deciduous forest cover	30 m^2	NLCD 2001
Bobcat habitat	Coniferous	Estimates whether a individual pixel is coniferous forest cover	30 m^2	NLCD 2001
Bobcat habitat	Forest wetland	Estimates whether a individual pixel is wetland forest cover	30 m^2	NLCD 2001
Bobcat habitat	Mixed forest	Estimates whether a individual pixel is mixed forest cover	30 m^2	NLCD 2001
Bobcat habitat	Scrub Shrub	Estimates whether a individual pixel is scrub-shrub forest cover	30 m^2	NLCD 2001
Bobcat habitat	Wetland	Estimates whether a individual pixel is wetland cover	30 m^2	NLCD 2001
Forest edge	Forest edge	Determines whether a pixel occurs along a forest edge	30 m^2	NLCD 2001
Agriculture	Agriculture	Combined hay, grass, pasture, and row crop land cover classifications	30 m^2	NLCD 2001
Developed	Low development	Included single family homes, constructed materials, and vegetation	30 m^2	NLCD 2001
Developed	Medium Development	Included row housing, apartment complexes, and commercial and industrial buildings and infrastructure	30 m^2	NLCD 2001
Developed	High development	Included areas where people live or work in high numbers	30 m^2	NLCD 2001
Variety	Variety	Measures the number of different land cover types surrounding each pixel in the study area for a given scale of analysis	30 m^2	NLCD 2001
Road density	Roads 1 and 2	Density of class 1 and 2 roads within a given area of analysis	1:5000	E911
Road density	Roads 3	Density of class 3 roads within a given area of analysis	1:5000	E911
Stream density	Streams	Density of streams within a given scale of analysis	l:5000 and l:24000	Orthophotographs 1993 and 2003

Dataset) to map streams across the study area. We used Spatial Analyst to calculate the density of roads and streams within a specified area of analysis (Table 1).

To compare the resource levels in the upper UD percentiles (home range "peaks" or core areas) and lower UD percentiles (home range "valleys"; Objective 2), we first extracted locations of all "peaks" and "valleys" for each bobcat. Locations in the home range with kernel probabilities in the top 20th percentile were considered "peaks," whereas locations with kernel probabilities in the bottom 20th percentile were considered "valleys." We quantified each of the 18 resource levels in peaks and valleys for each bobcat home range. Next, to meet analytical requirements, we reduced the resources from 18 to 5 by combining different resources. The five resources were: bobcat habitat, development, agriculture, stream density, and road density. "Bobcat habitat" was combined deciduous, coniferous, forest wetland, mixed forest, scrub-shrub, and wetland habitat. "Development" was combined low, medium, and high development land cover types. For each bobcat, the proportion of bobcat habitat, development, and agriculture was computed for each home peak and valley. Additionally, the density of combined class 1, 2, and 3 roads was computed, as was stream density. We analyzed the differences in resource levels (peak resource level minus valley resource level) in a MANOVA to investigate if the differences in the mean proportions were equal to 0 for all five area types simultaneously; a 0.10 level of significance was used due to low sample size. Paired *t*-tests were then carried out for each of the five types separately. Analyses were done using S Plus.

3.4. Objective 3: Resource Utilization Functions (RUFs)

Objective 3 focused on differential use of areas within each bobcat's home range, with a goal of understanding how the levels of various resources may shape the UD surface and how these relationships varied among individuals. For each bobcat, we evaluated 24 Resource Utilization Functions (Table 2), and then used model selection procedures to evaluate the strength of evidence for each model (Burnham and Anderson, 2002).

The RUFs focused on the same set of resources described for Objective 2. However, with few exceptions, most of the RUF analyses did not use the actual pixel resource value as the independent (predictor) variable. Instead, for each pixel in the study area, we evaluated and mapped the percentage of each resource within a 90-m, 300-m, and 1-km buffer surrounding each pixel, effectively changing the extent at which resource levels are mapped (Fig. 3). By evaluating the same resource measured under different scales, we attempted to gain insight into how bobcats may perceive the distribution of resources (Wiens, 1989). Fine scales (90 m) were evaluated to determine if bobcats may use specific landcover pixels within a home range, such as a forest edge (Abouelezz et al., submitted for publication). Courser scales (e.g., 1 km) were also evaluated because bobcats are wide ranging carnivores, and as such may utilize locations in their home range that maximize access to multiple habitat types for hunting, cover, or loafing.

We followed RUF methods outlined by Marzluff et al. (2004), which involved overlaying each bobcat's UD with resource maps, selecting a sample of points within the home range based on a grid, and running a regression or multiple regression analysis (i.e., a particular model of a Resource Utilization Function) while adjusting for spatial autocorrelation of pixels within the UD (see Fig. 1 for description). The dependent variable was the pixel's UD percentile, and the explanatory variables were resources thought to be related to bobcat's habitat, landscape, and behavior. Multiple, explanatory resources were considered for analysis based on literature review; we assessed the correlations among these candidates and evaluated RUFs that (1) represented a hypothesis explaining bobcat habitat use within home ranges and (2) did not include correlated explanatory variables to minimize multicollinearity. The 24 RUFs are described below:

3.4.1. Slope and aspect

Model 1 and 2 related the UD percentile with the bobcat's home range to the aspect and slope associated with each pixel. We hypothesized that aspect would be important as cats often sun themselves, and cats may prefer steep, rocky ledges for refugia and denning.

Table 2
The 24 Resource Utilization Functions (models) analyzed for each bobcat, the hypothesis and rationale for inclusion, and description of explanatory variable(s) in each model.

Model	Hypothesis	Variable Name (s)	Description
1. Aspect	Ledge	North, South, East, West, Flat	Describes the aspect of each pixel within the home range.
2. Slope	Ledge	Slope	Slope measures degree slope of each pixel in the home range.
3. Habitat 90 m	Habitat	Habitat 90 m	% Conifer, deciduous, mixed forest, wetland, forest wetland, and shrub habitat (combined) within 90 m of a probability point
4. Habitat 300 m	Habitat	Habitat 300 m	% Conifer, deciduous, mixed forest, wetland, forest wetland, and shrub habitat (combined) within 300 m of a probability point
5. Habitat 1 km	Habitat	Habitat 1 km	% Conifer, deciduous, mixed forest, wetland, forest wetland, and shrub habitat (combined) within 1 km of a probability point
6. Habitat 1 km components	Habitat	Conifer 1 km, mixed 1 km, wetland 1 km, shrub 1 km, deciduous 1 km	Measures % of each cover type within 1 km of a probability point
7. Roads 90	Roads	Road density 90 m	Density of class 1, 2, and 3 roads (combined) within 90 m of a probability point
8. Roads 300	Roads	Road density 300 m	Density of class 1, 2, and 3 roads (combined) within 300 m of a probability point
9. Road 1 km components	Roads	Road density 1 & 2 combined, road density 3	Density of class 1, 2 roads, plus density of class 3 roads within 1 km of a probability point
10. Agriculture 90 m	Agriculture	Agriculture 90 m	Combined hay, grass, pasture, and row crop classifications within 90 m of a probability point
11. Agriculture 300 m	Agriculture	Agriculture 300 m	Combined hay, grass, pasture, and row crop classifications within 300 m of a probability point
12. Agriculture 1 km	Agriculture	Agriculture 1 km	Combined hay, grass, pasture, and row crop classifications within 1 km of a probability point
13. Development 90 m	Development	Development 90 m	% Low, medium, high development (combined) within 90 m of a probability point
14. Development 300 m	Development	Development 300 m	% Low, medium, high development (combined) within 300 m of a probability point
15. Development 1 km	Development	Development 1 km	% Low, medium, high development (combined) within 1 km of a probability point
16. Development 1 km components	Development	Developed low, developed medium, developed high	Measures % of each development type separately within 1 km of a probability point
17. Stream density 300 m	Streams	Stream density 300 m	Density of streams within 300 m of a probability point
18. Stream density 1 km	Streams	Stream density 1 km	Density of streams within 1 km of a probability point
19. Forest edge 90 m	Forest edge	Forest edge 90	Proportion of forest edge habitat within 90 m of a probability point
20. Forest edge 300 m	Forest edge	Forest edge 300	Proportion of forest edge habitat within 300 m of a probability point
21. Forest edge 1 km	Forest edge	Forest edge 1 km	Proportion of forest edge habitat within 1 km of a probability point
22. Topography	Topography	Topographic index (TPI)	Assigns topographic classification to probability point
23. Variety 90 m	Diversity	Variety 90 m	Measures the number of different land cover types within 90 m of a probability point
24. Variety 300 m	Diversity	Variety 300 m	Measures the number of different land cover types within 300 m of a probability point

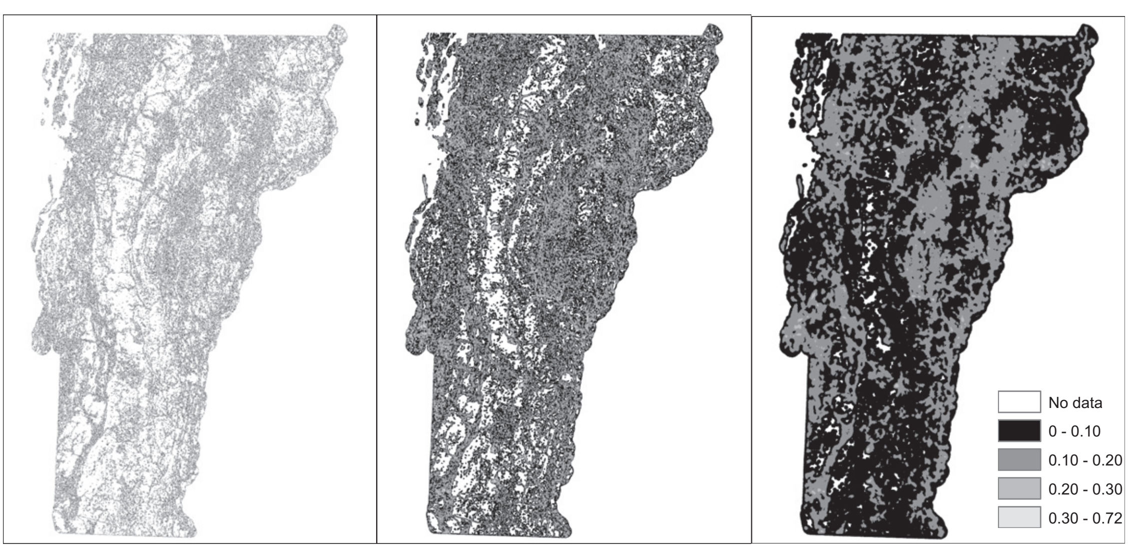

Fig. 3. Percent forest edge was mapped at (a) 90 m, (b) 300 m, and (c) 1000 m buffer surrounding each pixel in the study area. At a 300 m buffer, for instance, the value of a pixel in the map is the proportion of neighboring pixels within 300-m that were classified as forest edge. The effect of increasing the buffer "blurs" the resource level at each pixel because it accounts for a wider range of conditions evaluated.

3.4.2. Habitat

Models 3–6 related the UD percentile within a bobcat's home range to amounts of "bobcat" habitat. Bobcat habitat collectively consisted of six different land cover types from the National Land Cover Data (NLCD, 2001): deciduous forest, coniferous forest, forest wetland, mixed forest, scrub-shrub, and wetland (Table 2). We felt these types most accurately described foraging locations and prey species habitats. Models 3–5 evaluated the relationship between total habitat and UD percentile, but measured habitat at different spatial scales (90-m, 300-m, and 1-km respectively). Model 6

(Habitat 1 km Components) evaluated the amount of habitat within a 1 km radius from a pixel but evaluated each of the six land cover types separately (Table 2).

3.4.3. Road density

Models 7–9 related the UD percentile to levels of road density. We hypothesized that cats would avoid roads with high traffic volume (categories 1 and 2), but potentially use less traveled dirt roads (category 3). Models 7 and 8 evaluated whether the UD percentile was related to total road density when calculated at a 90-m radius (Model 7) and a 300-m radius (Model 8). Model 9 (Road Density 1 km components) evaluated the density of roads within 1-km of each pixel in the UD but considered category 1 and 2 roads separately from category 3 roads (Table 2).

3.4.4. Agriculture

Models 10–12 related the UD percentile to levels of agricultural habitat within 90-m (Model 10), 300-m (Model 11), and 1-km (Model 12) radius of each pixel in the UD (Table 2). Agricultural resources were thought to be important for bobcats in Chittenden and Addison counties of our study area because large, abandoned farm dumps and forest hedgerows potentially acted as refugia to bobcats in areas of large open landscapes where there was little cover otherwise and may have provided hunting opportunities.

3.4.5. Development

Models 13–16 related the UD percentile to levels of development (combined low, medium, and high intensity) within 90-m (Model 13), 300-m (Model 14), and 1-km of each pixel within a cat's UD (Model 15). Models 13–15 considered the percentage of all three development types collectively. Model 16 evaluated the amount of development within a 1 km radius from a pixel, but evaluated each of the development categories separately (Table 2).

3.4.6. Streams

Models 17 and 18 related the UD percentile to the density of streams. Based on the literature (Beier and Barrett, 1993; Noss et al., 1996) and our own observations, bobcats are known to use streams and other linear features in the landscape as travel paths. We evaluated the density of streams within 300-m (Model 17) and 1-km (Model 18) from each pixel in the UD (Table 2).

3.4.7. Forest edge

Models 19–21 related the UD percentile to the proportion of forest edge habitat within 90-m (Model 19), 300-m (Model 20) and 1-km (Model 21) of a pixel within the UD (Table 2). We hypothesized that edge habitat offered more prey and hunting opportunities while providing cover for bobcats. Edge habitats tend to be denser, shrub-like habitats.

3.4.8. Topographic position

Model 22 related the UD percentile to the topographic position of each pixel within the UD. This model evaluated how bobcats exploited the full topographic landscape in their habitat use. We hypothesized that bobcats frequently used ridge habitat, but we also were interested in the potential usage of river ways (valleys).

3.4.9. Land cover heterogeneity

Finally, Models 23 and 24 related the UD percentile to the number of NLCD cover types within 90-m and 300-m of each pixel in the UD (Table 2). Bobcats are prey generalists, and therefore, may use areas containing many different habitat types in their search of food.

We assessed each of these 24 models (RUFs) for each bobcat (Marzluff et al., 2004), which estimated the association between the UD percentiles and spatially corresponding covariates. Data were analyzed in S+, which fit a single or multiple-regression model to the percentiles in the UD while correcting for spatial autocorrelation. This correction was essential because, by definition, points near each other had similar percentiles as a result of the kernel home range estimate procedure. S+ corrected for spatial autocorrelation by assuming that the correlation was a function of the Euclidean distance between two locations (Handcock and Stein, 1993), where the covariance among the observations was a function of distance from one another times the common (uncorrected) variance. We used a spatial neighborhood of 5 pixels and moving average covariance structure, which is analogous to a moving-average time series model (Kaluzny et al., 1997).

We used Akaike's Information Criteria (AIC; Burnham and Anderson, 2002) to rank each model in the model set for each bobcat and obtain model weights. AIC was calculated as $-2 * \log$ likelihood + $2 * K$, where K was the number of parameters in the model. The ΔAIC for a model was the model's AIC minus the minimum AIC in the model set for a particular bobcat. Models with $\Delta\text{AIC} < 4$ were considered to support the observed field data; models with $\Delta\text{AIC} > 10$ were considered to be unsupported by the data (Burnham and Anderson, 2002). We then examined the model coefficients (betas) for any variable in a supported model to make inferences about habitat use within the home range. To aid interpretation of the results, we revisited the correlation analysis from Objective 3 to determine if any of the RUF variables analyzed were correlated with other variables, including those not modeled. This was done on an individual basis.

3.5. Objective 4: Derive a population-level RUF and map potential high quality habitat across the study area, and identify minimum habitat requirements for breeding females

Following the procedures of Marzluff et al. (2004), we developed a population-level RUF, which generalized the results of individual bobcats to the population level. We focused our efforts on the two models that were best supported by the bobcats analyzed (Habitat 1-km Components and Road Density 1-km Components; see below). We averaged the effect sizes (betas) for each of these variables in these models ($n = 8$ variables, the intercept plus: % conifer, % mixed forest, % deciduous forest, % wetland, % forest wetland, class 1 and 2 road density, class 3 road density as measured at a 1 km scale), weighted by each bobcat's model AIC weight, to derive population-level responses to each of these resources. Then, we quantified the habitat suitability for each pixel throughout the study area by measuring the level of each of the seven resources within 1 km of that location, multiplied by the corresponding model-averaged beta coefficient. This procedure resulted in a habitat suitability score for each pixel in the study area. Finally, we computed the total habitat suitability score within female bobcats' home ranges, which we assumed represented the minimum threshold of habitat required by breeding females for management purposes.

4. Results

4.1. Field data results

Fourteen bobcats were available for home range analysis: 10 males and 4 females, of which 10 wore ATS collars and 4 wore Lotek collars (Table 3).

4.2. Objective 1: Home range size

We calculated the average home range size by sex ($n = 10$ males, $n = 4$ females), and by breeding season (within the breeding

Table 3
Bobcat identification, physical characteristics including sex, weight, and approximate age at capture (determined by tooth condition and wear), collar type, total number of GPS location points used to estimate the home range, whether or not an animal was collared during breeding season, and home range size (km^2). Data were from individuals captured in Vermont, USA between 2005–2008.

Cat	Sex	Wt. at capture (kg)	Age	Collar type	GPS points	Breeding season	HR (km^2)
B1	M	12.3	Adult	ATS	22	N	29.4
B4	F	8.6	Young adult	ATS	105	N	7.0
B11	M	7.3	Young adult	ATS	33	N	3.9
B15	F	11.8	Adult	ATS	165	Y	23.9
B20	M	14.9	Adult	ATS	129	Y	218.2
B21	F	8.2	Adult	ATS	105	N	26.2
B23	F	12.7	Adult	ATS	275	N	34.5
B24	M	12.7	Adult	ATS	29	N	37.3
B29	M	16	Adult	Lotek	1391	Y	140.7
B30	M	14.9	Adult	Lotek	900	Y	49.3
B32	M	11.3	Adult	ATS	160	Y	65.5
B37	M	14.1	Adult	ATS	498	Y	69.6
B41	M	13.6	Adult	Lotek	528	N	28.7
B42	M	11.8	Adult	Lotek	357	N	67.4

season and outside the breeding season). Across individuals, 22 to 1391 data points were used to estimate the kernel home ranges (average = 335 data points; Table 3). Home range sizes were not well-explained by the number of sampling points used to estimate the home range ($R^2 = 0.12$), and sample locations used in home range analysis appeared to represent the minimum convex polygon home range based on the full sample of GPS locations, including those not used to estimate kernel home ranges. The average home range size for bobcats in our study area was 57.3 km^2 (Table 3). Male home ranges averaged 70.9 km^2 while females averaged 22.9 km^2 (Table 3). Five of the 10 males were collared during breeding season and had an average home range size of 108.6 km^2. The five males collared outside the breeding season had an average home range size of 33.3 km^2 (Table 3). Three of the four females were collared during the breeding season and had an average home range of 28.2 km^2. The one female collared outside the breeding season had a home range of 7.0 km^2 (Table 3).

4.3. Objective 2: Comparison of resources within UD peaks versus valleys

Percent agriculture, percent development, percent bobcat habitat, and stream and road density collectively differed between home range peaks (upper 20th percentile of UD probabilities) and valleys (lower 20th percentile of UD probabilities; MANOVA Wilks Lambda $F = 3.25$, $p = 0.056$). Subsequent paired t-tests identified stream density as the only resource type without significant differences between upper and lower UD percentiles (Fig. 4, $p < 0.03$ for all tests). Across bobcats, upper percentiles, or UD peaks, had 18% less agriculture, 42% less development, and 26% more forest, scrub/shrub and or/wetland habitat than lower percentiles (UD valleys). Upper percentiles had 33% lower road density than lower percentiles.

4.4. Objective 3: Resource Utilization Functions (RUFs)

We ran our model set ($n = 24$ models) for all 14 bobcats individually, ranking each RUF model for each individual bobcat using Akaike's Information Criterion (Burnham and Anderson, 2002). We calculated the AIC and Delta AIC to determine the support for each model in the model set and then ranked the models accordingly. For every bobcat, each top ranked model carried all the weight in the model set. Habitat 1 K Components (Model 6) was the top-ranked model for 12 of the 14 bobcats (Table 4), indicating that the amount of forest, scrub/shrub, and/or wetland habitat within 1 km of a location within a home range was very important in shaping the UD for bobcats in our study. Ten of 12 bobcats showed increased use of locations in the home range that had higher levels of shrub habitat surrounding it, and eleven out of 12 bobcats showed increased use of location that had higher levels of wetland habitat surrounding the location (Table 5). Eleven of 12 bobcats had positive responses to deciduous and/or evergreen forest. In addition, nine of 12 bobcats had negative coefficients for the

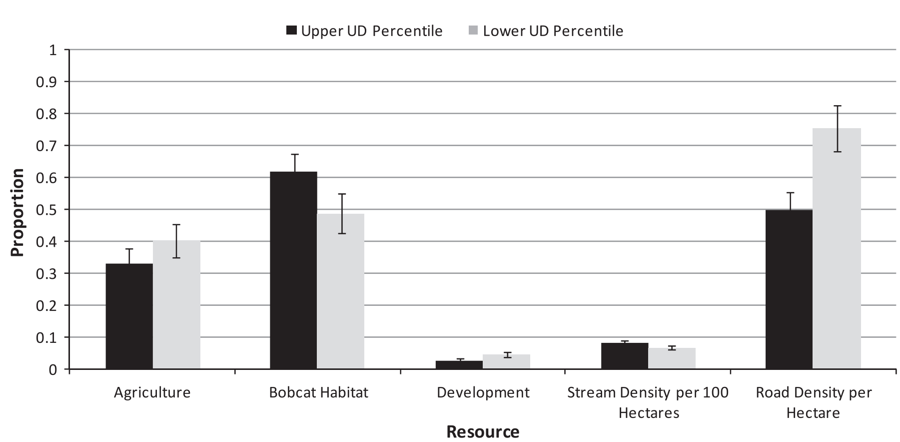

Fig. 4. Average percent agriculture, bobcat habitat, and development and average stream and road density within the upper 20th UD percentiles (UD peaks) and lower 20th UD percentiles (UD valleys); see Table 1 for definitions of each resource.

Table 4
Model rankings for each of the 24 Resource Utilization Functions (models) evaluated to explain the surface of the home range Utilization Distribution for bobcats in northwestern Vermont. *K* is the number of parameters estimated for each model. Models ranked 1 were the top-ranked model and in each case carried all of the AIC weight in the model set.

Model name	Model number	Bobcat													
		B1	B4	B11	B15	B20	B21	B23	B24	B29	B30	B32	B37	B41	B42
Aspect	1	11	21	8	12	12	13	2	11	13	18	8	12	10	15
Slope	2	15	5	×	12	21	15	6	13	13	18	16	12	17	15
Habitat 90 m	3	10	21	15	12	15	15	16	19	9	15	10	12	11	15
Habitat 300 m	4	2	11	8	12	7	9	2	5	3	7	×	12	4	×
Habitat 1 km	5	3	8	4	12	2	8	5	19	2	9	6	5	2	15
Habitat 1 km Components	6	1	1	1	5	1	1	1	1	1	1	1	1	1	×
Road density 90 m	7	13	15	17	12	15	15	20	13	17	18	×	8	13	7
Road density 300 m	8	16	15	14	12	15	9	9	13	9	12	16	6	17	7
Road Density 1 K Components	9	5	2	2	1	5	3	×	2	3	8	12	2	3	1
Agriculture 90 m	10	18	11	×	12	21	15	18	13	13	15	16	23	13	7
Agriculture 300 m	11	18	11	8	8	8	15	9	×	9	15	10	12	13	6
Agriculture 1 km	12	12	8	6	12	6	13	9	19	8	9	3	8	17	2
Development 90 m	13	22	8	18	12	8	12	16	13	13	9	19	12	17	7
Development 300 m	14	17	14	×	8	8	7	15	8	7	4	7	8	13	5
Development 1 km	15	8	3	×	3	4	5	7	4	6	2	19	4	8	4
Development 1 km components	16	7	×	×	2	2	4	×	×	5	2	8	3	6	3
Stream density 300 m	17	18	21	4	12	15	15	4	6	17	18	19	8	17	7
Stream density 1 km	18	18	15	×	6	8	15	7	3	17	18	13	12	12	15
Forest edge 90 m	19	14	4	8	12	15	15	9	11	17	13	×	23	17	7
Forest edge 300 m	20	6	6	8	6	15	6	×	13	17	6	2	12	7	7
Forest edge 1 km	21	4	15	8	4	12	2	9	×	12	5	4	6	5	15
Topographic position	22	22	15	16	8	21	15	18	7	17	18	13	12	17	7
Variety 90 m	23	22	6	6	12	12	15	14	9	17	13	13	12	17	15
Variety 300 m	24	9	15	3	8	21	9	×	9	17	18	5	12	8	15

mixed forest classification within the model, indicating a decrease in use of this forest type with an increase of the resource.

Two of the 14 animals had the Roads 1 km Components (Model 9) as top-ranked model (Table 5). These two bobcats showed differential use of different road types. B15, a female, had a negative beta coefficient for class 1 and 2 (higher volume and freeways) roads but little response to class 3 roads (low volume and dirt roads; Table 5). However, B42's coefficients were just the opposite. B42 (a male) had a negative coefficient for class 3 roads and a near-zero coefficient for class 1 and 2 roads (Table 5).

The correlation matrix indicated many strong correlations (rho > 0.5) between variables across models, which is important for interpreting the results of the top-ranked model. The Habitat 1 km Components model had significant, positive correlations between many of its variables (Deciduous 1-km, Coniferous 1-km, Mixed 1-km, Wetland 1-km, and Scrub Shrub 1-km) and variables assessed in other models, including Forest Edge at all scales (10 of out 10 bobcats). Seven out of 10 bobcats had positive correlations between Variety 300 and Deciduous 1 km, Wetland 1 km, and Scrub Shrub 1 km. Therefore, in a broad sense, bobcats were using areas in the home range that had high levels of surrounding habitat, but these areas also tended to have high levels of forest edge and a variety of land types, and low levels of agriculture and development.

4.5. Objective 4: Determine habitat requirements at the level of the population and map potential high quality habitat across the study area

We developed a population level RUF by averaging the beta coefficients from Models 6 and 9 (Habitat 1 km Components and Road Density 1 km Components; Table 5). This RUF was applied to every pixel in the study, and resulted in a habitat suitability score for each pixel in the study area that ranged from -1.69 to 1.44, where higher values represented higher quality habitat. The resulting map indicated the habitat quality for bobcats based on percent scrub-shrub, deciduous, coniferous, forest wetland, and wetland habitat, and also based on road density within 1 km of the pixel. These values were then categorized into quantiles for ease of interpretation in mapping (Fig. 5). The southern Champlain Valley in the southern portion of the study area region had, by far, more high quality habitat than anywhere else in the study area, while the spine of the Green Mountains has the least amount of quality habitat. Female bobcat home ranges, on average, had a total habitat suitability score of near 0, indicating that home ranges consisted of both beneficial and detrimental habitat types.

5. Discussion

5.1. Home range size and habitat use

Based on our results, Vermont bobcat home ranges averaged 70.9 km^2 for males and 22.9 km^2 for females, with fluidity in size between breeding and non-breeding seasons. These results are fairly comparable to other studies on bobcats (Fuller et al., 1985; Litvaitis et al., 1986; Lovallo and Anderson, 1996; Lovallo, 2002). Some researchers attribute this size difference to females being influenced more heavily by prey abundance and energetic demands, and male being more influenced by breeding demands (Kamler and Gipson, 2000).

Our study provides insight into how bobcats use the space within home ranges differentially, and how resources shape the home range UD. We examined 24 alternative RUFs for each bobcat individually, and then tested for consistency in the correlations between resource level and use among individuals. We learned that bobcats frequently used areas that had a high proportion of habitat, particularly shrub and wetlands, within 1 km of any given location in the home range. This result was consistent across individuals even though individuals varied in age, sex, and the season in which the collars were deployed. Not only do these types of habitat tend to have denser understories, offering better cover, but they also have greater prey density as well. These same types are often less likely to successfully acquire a GPS fix than more open habitats (Frair et al., 2010); thus our results are conservative. Other investigators conducting research on bobcat habitat use throughout the species' range previously suggested that these habitats

Table 5
Beta and standard errors for all variables of the top ranked models (Habitat 1 km Components, Road Density 1 km Components) for each bobcat. In all cases, the top ranked model carried 100% of the AIC weight.

Bobcat	Habitat 1 km										Road density			
	Shrub		Deciduous		Mixed		Wetland		Evergreen		Roads 1 and 2		Roads 3	
	Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE
B1	1.2518	0.1805	0.9403	0.0822	−3.5216	0.3152	2.3975	0.0869	0.8755	0.21	×	×	×	×
B4	2.3135	0.9352	0.8555	0.0487	0.8555	0.0487	1.9006	0.2327	1.1516	0.1096	×	×	×	×
B11	7.3165	0.8013	−3.5017	0.121	−0.8698	0.4592	4.5176	0.3115	2.3743	0.2566	×	×	×	×
B15	×	×	×	×	×	×	×	×	×	×	−0.3315	0.0112	0.0249	0.0108
B20	0.9007	0.2322	0.2755	0.0219	0.3372	0.0364	0.3356	0.114	−0.5245	0.0858	×	×	×	×
B21	9.5465	0.1956	0.425	0.0319	−0.0215	0.0344	2.0971	0.2069	0.0114	0.0314	×	×	×	×
B23	0.8737	0.3529	0.376	0.0438	−0.2349	0.1444	0.9435	0.0498	0.3622	0.1357	×	×	×	×
B24	−8.8399	0.9054	−0.2756	0.0543	−0.2979	0.0573	0.5438	0.6434	−0.1643	0.0825	×	×	×	×
B29	0.0523	0.3443	0.6727	0.0378	0.5174	0.0949	0.1765	0.0825	−0.2484	0.0863	×	×	×	×
B30	1.2636	0.1631	2.0442	0.0889	−1.8809	0.1847	−0.2642	0.0898	−0.0695	0.1298	×	×	×	×
B32	1.8631	0.1073	0.5412	0.0466	−3.468	0.2606	0.9446	0.0722	1.0081	0.1762	×	×	×	×
B37	−0.7751	0.1731	−0.4738	0.0327	−0.5338	0.0503	1.3006	0.1062	1.9029	0.0732	×	×	×	×
B41	1.4595	0.156	0.693	0.0701	−2.0428	0.2572	2.3967	0.0717	0.2414	0.1758	×	×	×	×
B42	×	×	8	×	×	×	×	×	×	×	0.0339	0.0065	−0.1323	0.0059
Average	1.44	0.38	0.21	0.06	−0.93	0.16	1.44	0.17	0.58	0.13	−0.15	0.01	−0.05	0.01
Std Dev	4.41	0.31	1.33	0.03	1.48	0.14	1.31	0.17	0.90	0.06	0.26	0.00	0.11	0.00

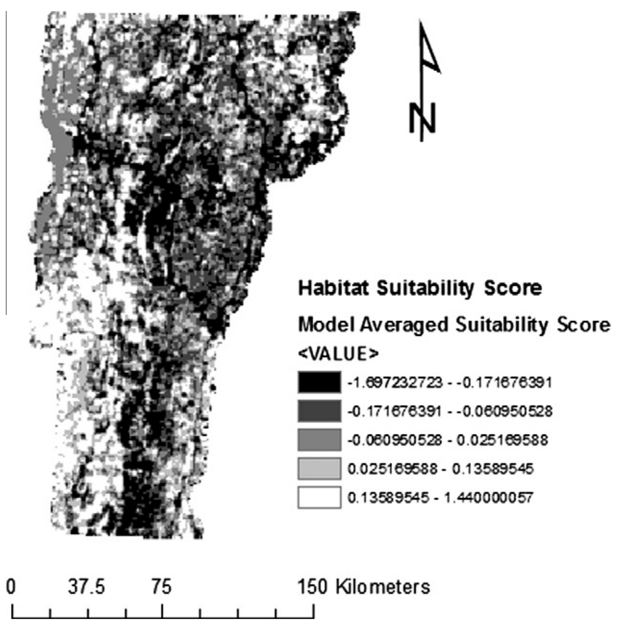

Fig. 5. Quantile map of bobcat habitat quality across the study area where inference is strongest (Fig. 2), and across the state were inference is weaker, based on averaged beta coefficient estimates across cats for Model 6 (see Table 5). Highest quality habitats are depicted in white; lowest quality habitats are depicted in black.

are important to bobcats (Litvaitis et al., 1986; Kolowski and Woolf, 2002). However, by analyzing these resources at multiple spatial extents (level of resource in a 90 m window versus a 300 m window versus a 1 km window), our results suggest that bobcats are not pinpointing locations within their home range that match these habitats *per se*; rather they use those areas that have high concentrations of these habitats within 1 km of a location. This result is not surprising for a mobile species that has great ability to access resources on a landscape, and uses multiple habitat types for hunting, breeding, and refuge.

Our study provides important insights for bobcat ecology and management, and more generally for management of wide-ranging carnivores. We documented average home range requirements in terms of habitat suitability, and provided spatially explicit information on habitat suitability throughout the study area. An important caveat is that by using the averaged coefficients across animals, individual level variation is largely lost in order to predict habitat use for the population as a whole, and furthermore that averaged coefficients will undoubtedly vary across the species' range (Anderson and Lovallo, 2003). Nevertheless, the general methodology we used can be applied for conservation and landscape-scale habitat management anywhere. The process involved first computing the overall suitability of each pixel throughout the study area based average responses to important variables (in our case, road and habitat conditions within 1 km of that pixel). Given these pixel-based suitability scores, the next step involved calculating the total suitability of pixels within the average female's home range, which provided a quantitative estimate of minimum habitat requirements per breeding female in our study. A key assumption is that locations with high suitability scores are also high in quality for bobcats, which in turn reflects fitness in those habitats.

These two pieces of information are useful for management and conservation from a variety of standpoints; linking the pattern of habitats (resources) on a landscape to populations of target wildlife species is of particular interest (Boyce and McDonald, 1999). In their review article of the use of Resource Selection Functions, Boyce and McDonald (1999) describe how Resource Selection Functions (RSFs) can be used to link spatially defined resource patterns to population size, where RSF's assess the use of resources with respect to their availability. Here, our RUFs provide information that can be used to link the spatial distribution of resources with population size. If home range area requirements can be duly estimated, each pixel in the suitability map provides not only a suitability score, but also can be evaluated to determine if the area surrounding it (akin to the female home range size) provides enough critical habitat for a potential female's home range (pseudo home range) to occur. The result is binary (yes or no), and indicates all locations within the study area that meet the minimum habitat threshold for potential breeding female occurrence and therefore providing information about the capacity of the landscape to support a breeding population (K. McGarigal; pers. comm.). Because female bobcats maintain non-overlapping home range (Bailey, 1974; Berg, 1981; Lawhead, 1984; Anderson, 1987), assessment of the non-overlapping pseudo home ranges can be used to approximate the landscape's carrying capacity of female bobcats per town, county, or across the entire study area.

While this process allows for estimating changes in the number of pseudo home ranges in response to a changing landscape, it does not ensure that actual population targets will be met. First, even if additional habitat is created to support additional breeding females, individuals must be able to access those new habitats. For example, Dickson et al. (2005) use movement data to provide information on how cougars (*Puma concolor*) are affected by roads, an unnatural linear feature. The study found that this species avoids crossing paved roads, but will use dirt roads as travel corridors. Abouelezz et al. (submitted for publication) analyzed the GPS data collected in this study to determine habitat preference of bobcats when they are moving. They found that, for movement purposes, forested land cover and scrub/rock land cover were most preferred cover types while developed land cover types were least preferred. Furthermore, the preference for forest and scrub depended on the surrounding landscape; bobcats moved quickly through forest and scrub habitats that are surrounded by other habitat types (e.g., development or agriculture), but moved slowly through these habitats when the surrounding area was likewise forested (Abouelezz et al., submitted for publication). Thus, if a conservation goal is to provide landscape connectivity, then linear strips of forest and/or scrub may facilitate access to locations that are rich in bobcat habitat suitability.

Second, attention must be given to the current locations of breeding females (not pseudo locations). Females often settle relatively close to their natal range, with juvenile males dispersing longer distances (Sunquist and Sunquist, 2002; Anderson and Lovallo, 2003). Thus, if a goal is to increase the number of breeding bobcats in an area, evaluating landscape options should consider both habitat suitability and distance to existing females, which are the source of new recruits. Such information can allow managers to use their limited resources to their fullest potential when planning for the conservation of this medium carnivore.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.06.026.

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