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Bobcats (*Lynx rufus*) as a Model Organism to Investigate the Effects of Roads on Wide-Ranging Carnivores

John A. Litvaitis[1] · Gregory C. Reed[1] · Rory P. Carroll[1] · Marian K. Litvaitis[1] · Jeffrey Tash[1] · Tyler Mahard[1] · Derek J. A. Broman[1] · Catherine Callahan[2] · Mark Ellingwood[2]

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Abstract We are using bobcats (*Lynx rufus*) as a model organism to examine how roads affect the abundance, distribution, and genetic structure of a wide-ranging carnivore. First, we compared the distribution of bobcat-vehicle collisions to road density and then estimated collision probabilities for specific landscapes using a moving window with road-specific traffic volume. Next, we obtained incidental observations of bobcats from the public, camera-trap detections, and locations of bobcats equipped with GPS collars to examine habitat selection. These data were used to generate a cost-surface map to investigate potential barrier effects of roads. Finally, we have begun an examination of genetic structure of bobcat populations in relation to major road networks. Distribution of vehicle-killed bobcats was correlated with road density, especially state and interstate highways. Collision models suggested that some regions may function as demographic sinks. Simulated movements in the context of the cost-surface map indicated that some major roads may be barriers. These patterns were supported by the genetic structure of bobcats. The sharpest divisions among genetically distinct demes occurred along natural barriers (mountains and large lakes) and in road-dense regions. In conclusion, our study has demonstrated the utility of using bobcats as a model organism to understand the variety of threats that roads pose to a wide-ranging species. Bobcats may also be useful as one of a group of focal species while developing approaches to maintain existing connectivity or mitigate the negative effects of roads.

Keywords Fragmentation · Genetic structure · Vehicle collisions

✉ John A. Litvaitis
john@unh.edu

[1] Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA

[2] New Hampshire Fish and Game Department, Concord, NH 03301, USA

Introduction

Efforts to sustain populations of wide-ranging species in contemporary landscapes are confronted with substantial challenges (Crooks and Sanjayan 2006). Among these are the consequences of high-traffic volume roadways that may include elevated mortality rates as a result of collisions with vehicles (Beckman et al. 2010), habitat loss (Forman et al. 2002), and potential legacy effects of isolation and disruption of gene flow (Forman et al. 2003). Mammalian carnivores may be especially vulnerable to the effects of roads because they range over relatively large areas and are therefore likely to encounter roads often (Riley et al. 2006; Jansen et al. 2010).

Our focus is to understand factors that influence bobcat (*Lynx rufus*) populations in New Hampshire, a region in the northeastern United States where this species has undergone dramatic changes in abundance during the past 50 years (Litvaitis et al. 2006). Since 1989, bobcats have been protected in New Hampshire. In recent years, incidental sightings and road mortalities suggest that bobcats are becoming more abundant in New Hampshire (Broman et al. 2014), similar to reports from other regions of North America (Roberts and Crimmins 2010).

An initial examination of environmental features associated with remnant populations of bobcats revealed that large tracts of forests or wetlands that were not fragmented by highways or primary roads were important predictors of occupied habitats (Litvaitis et al. 2006). However, more recent observations indicate that bobcats are re-colonizing portions of the state that contains dense road networks with substantial traffic volumes (Broman et al. 2014). In comparison to other wide-ranging carnivores, such as coyotes (*Canis latrans*) and cougars (*Felis concolor*), Crooks (2002) indicated that bobcats are intermediate in their demographic responses to roads and they are able to persist in fragmented landscapes if there are habitat linkages. On the other hand, Riley et al. (2006) found that multi-lane highways can impose artificial home-range boundaries and functionally decrease gene flow.

Bobcats in New Hampshire encounter a wide range of conditions that range from sparsely settled regions with limited roads to intensively developed landscapes that contain interstate highways (Litvaitis et al. 2006; Broman et al. 2014; Reed 2013). As a result, we considered this species to be a suitable *model organism* to investigate a variety of demographic and genetic responses to roads (Simmons et al. 2010). In this paper, we synthesize results of several completed investigations and provide additional information on the effects of roads on bobcats in New Hampshire. First, we consider the risk factor roads present based on collisions with vehicles. We then evaluate the habitat degradation caused by roads and the potential barriers they pose to regular movements and to juvenile dispersal. Next, we consider the long-term or legacy effects of roads that can affect gene flow and subsequently population structure. We conclude with an evaluation of bobcats as a focal or umbrella species that may be useful in developing ways to mitigate the detrimental effects of roads on a range of species.

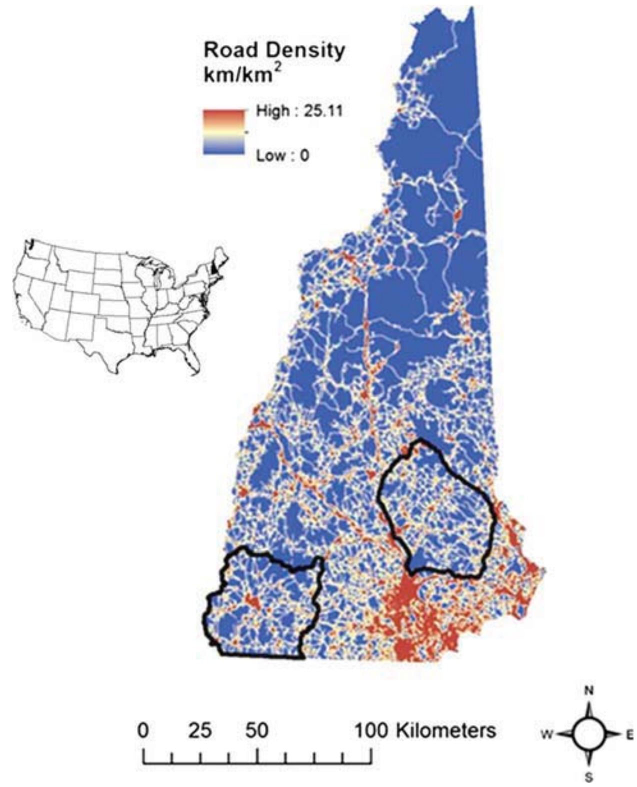

Fig. 1 Location of New Hampshire within the contiguous United States. Statewide map includes location of study areas where transmitter-equipped bobcats were monitored (*bold outlines*) and road density

Methods

Study Areas

New Hampshire (24,200 km^2) is located at the northeastern edge of the geographic range of bobcats. Elevations range from sea level, along the Atlantic coast, to 1917 m on the summit of Mt. Washington. Climate, including snow depth during winter, also varies substantially across the state. Historic and contemporary land-use patterns in the region have a profound influence on wildlife populations. After European settlement, New Hampshire was dominated by agriculture and only 47 % was forested in the mid 1800s (Litvaitis 1993). Subsequent farm abandonment in the mid nineteenth to early twentieth century resulted in widespread forest regeneration (Litvaitis 1993) and by the early 1960s, 87 % of the state was forested (Sundquist and Hewes 2010). In subsequent decades, expanding human populations reduced forest coverage to 78 % (Justice et al. 2002). Urban and suburban developments are currently most pronounced in the southeastern portion of the state, and this region contains several transportation corridors that may hamper animal movements (Fig. 1).

Telemetry study areas were established in southwestern (1862 km^2) and southeastern (2033 km^2) portions of the state to investigate habitat selection by marked samples of adult bobcats (Fig. 1). Road densities were 1.1 and 1.2 km/km^2 in the southwest and southeast study areas, respectively. Both areas contain a mix of forest types and dominant overstory species include eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghe-niensis*), paper birch (*Betula papyrifera*), northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*). Wetlands, farmlands, and varying levels of development also characterize these areas.

Roads as a Risk Factor

New Hampshire Fish and Game Department personnel documented bobcat-vehicle collisions. We examined the distribution of mortalities recorded between 2008 and

2013, a period when the frequency of incidental observations suggested that bobcat distribution and abundance were increasing (Broman et al. 2014). Road mortalities were recorded by township, eliminating our ability to consider local habitat features or road-specific factors (e.g., traffic volume) that were associated with individual collision sites. As a result, we used Spearman-rank correlations to compare collision rates (bobcats killed/100 km^2 of township area) during 2008–2013 to the density (km/km^2) of all roads and density of high-traffic volume roads (i.e., Class 1 = state and interstate highways and Class 2 = major primary roads) within individual townships.

To further explore bobcat-vehicle collisions on specific roadways, we relied on the predictive model developed by Hels and Buchwald (2001). The basic equation incorporates species-specific information on the rate of movement while crossing a road, traffic volume, and approximate size of the impact or kill zone to estimate the probability that an individual animal will be killed while crossing a particular road (P_{killed}), where

$$P_{\text{killed}} = 1 - \left(e^{-Na/v}\right),$$

N = vehicles per minute, a = width of kill zone (m), and v = velocity of animal moving through kill zone (m/min).

This approach has been applied to several taxa, including amphibians (Hels and Buchwald 2001), reptiles (Gibbs and Shriver 2002; Aresco 2005), and mammals (van Langevelde and Jaarsma 2004).

We restricted our modeling to six counties in the southeastern portion of the state, where road densities and traffic volume are among the greatest in the state. Annual average daily traffic volume (AADT; vehicles per day) was obtained for approximately 2400 road segments where electronic vehicle counters were deployed by New Hampshire Department of Transportation. Because not all roads were included in these inventories, we developed a multivariate linear regression model to predict traffic volumes for road segments that lacked traffic information [see Litvaitis et al. (2006) for details of this procedure]. We also examined the distribution of traffic in a 24-h day because bobcats are not active during all periods of the day, and considered bobcats most vulnerable to vehicle collisions at night (1800–0600 hours). To generate a daily distribution of traffic volume, we randomly selected three counting stations (road segments) in each county that had hourly traffic volume information available. Because each station had traffic data for multiple days, we calculated the average across days for each hourly increment. Estimates of the kill zone (per lane) were based on the area of impact with the vehicle and the size of bobcats, and are similar to the approach used by Hels and Buchwald (2001). For all simulations, we assumed that bobcats crossed the road perpendicular to the direction of traffic, and that all collisions were fatal. The kill zone per lane for bobcats (2.40 m) was calculated as the average width of a car or truck plus twice the body length of a bobcat. Finally, travel speed while crossing roads for bobcats (540 m/min) was based on the animal moving quickly but not at maximum speed. It is important to acknowledge that our modeling approach does not consider avoidance responses by either bobcats or drivers that may affect collision rates.

To illustrate the application of collision models in landscape situations, we used Arcview neighborhood statistics function (moving window analysis) and interpolated the AADT information to calculate the mean probability that a bobcat would be struck by a vehicle while moving through the landscape. The moving window was 3.3 km and represented the radius of average annual home ranges of female bobcats in the region (Litvaitis et al. 2006). Estimated collision probabilities were an average for a single road crossing. Because bobcats are wide ranging, we expect that individuals in this portion of the state will likely make multiple crossings. Estimates of annual collision mortality (d_{road}) require the number of crossings (n) a bobcat would make, where

$$d_{\text{road}} = 1 - (1 - p_{\text{killed}})^{n_{\text{crossings}}}.$$

Effect of Roads on Habitat Suitability and as Barriers to Bobcat Movements

We gathered information on bobcat habitat associations, including responses to roads, using two different approaches. First, incidental observations (December 2007–January 2013) by citizens throughout the state were reported to a project web site. These locations were biased toward areas where bobcats were easily detected (e.g., roadsides, developments, and agricultural fields; Broman et al. 2014). As a result, observation-based locations were only used to model second-order habitat selection (Johnson 1980) or placement of individual home ranges with respect to average snowfall because this feature is known to affect the distribution of bobcats (Reed 2013) but is less likely to be affected by observer bias because it varies at a relatively large spatial scale. The distribution of New Hampshire bobcats in relation to regional patterns of snowfall revealed by observation-based locations was corroborated by camera-trap detections (Sirén 2015).

Third-order habitat selection (use of specific features and resources within individual homes; Johnson 1980) was based on telemetry locations obtained from adult bobcats that were trapped and equipped with GPS-capable collars during the winters of 2009–2010 and 2010–2011 in southwestern and southeastern portions of the state, respectively (Fig. 1). All study animals were handled in accordance with the University of New Hampshire Institutional Animal Care and Use Committee (Protocol #081201). Telemetry-based locations were screened to evaluate precision and variation in detection rates among different vegetation communities (Reed 2013). The resulting pool of locations was then used to model selection with respect to ten candidate variables including National Land Cover Database 2006 (Fry et al. 2011), distance to forest edge (km), distance to stream (km), elevation (m), slope, aspect, a vector ruggedness measurement (VRM, Sappington et al. 2007), distance to road (km), road density (km/km^2), and traffic density (unit/km^2). Additional details on development of the habitat suitability model are provided by Reed (2013).

Resource selection probability functions (RSPF) were developed for both second and third order of habitat selection. Individual RSPF models were fit using the package Resource Selection (Lele et al. 2013) in the statistical program R (R Core Team 2012). Models of second- and third-order selection were combined by multiplying them together using Raster Calculator in ArcMap 10.0 (Johnson et al. 2004), and the resulting map served as a *conductance* layer in connectivity modeling using program Circuitscape (McRae and Shah 2009), with the assumption that areas of higher suitability would have greater conductance than areas of lower suitability. Functionally, the conductance layer was the inverse of a resistance layer.

Circuit theory, in the context of program Circuitscape (McRae and Shah 2009), displays the relative cost of moving through a landscape. McRae and Beier (2007) applied this approach to gene flow and found that it performed better than isolation by distance and least-cost-path methods. We suspected that this approach could also identify potential *pinch points* of movement through high-cost areas (i.e., low habitat suitability).

After model validation at the home-range scale, models were extrapolated to the rest of New Hampshire. Due to differences in spatial extent of some layers (i.e., being constrained to either New Hampshire or the continental United States), the RSPF layer was buffered by random pixels with scores between 0 and 1 (Koen et al. 2010). This assured that the sources and ground points did not bias the connectivity model (Koen et al. 2010). Circuitscape was run to and from each cardinal direction, and resulting model scores were averaged. Connectivity scores were then extracted to major roads and divided into degrees of connectivity. Road segments that could limit connectivity were identified [see Reed (2013) for additional details of these procedures].

Effects of Roads on Bobcat Population Structure

Because bobcats have the ability to disperse great distances and state borders do not necessarily represent ecological boundaries, we took a broader regional approach in assessing the genetic consequences of roads. We collected spatially referenced tissue samples from 237 bobcats in New Hampshire, Vermont, and Massachusetts between 2008 and 2014. Tongue samples from Vermont and Massachusetts were collected from bobcats harvested by licensed hunters and trappers. Samples from New Hampshire came from road mortalities and animals captured for our telemetry study.

Genomic DNA was extracted using the DNeasy blood and tissue kit (Qiagen Inc., Valencia, CA). Each sample was genotyped at 13 known felid microsatellite loci (Menotti-Raymond et al. 1999, 2005; Carmichael et al. 2000; Faircloth et al. 2005). These data were used to assess common population genetic parameters (e.g., heterozygosity and inbreeding coefficients) and to evaluate subpopulation structure. We also calculated pairwise genetic distances between individuals (Rousset 2000). The values were correlated (Mantel 1967) to Euclidean distance between locations to assess the relative influence of geographic distance on gene flow.

We first used the program Micro-checker (van Oosterhout et al. 2004) to test for genotyping errors (e.g., null alleles). We tested for Hardy–Weinberg and linkage equilibrium and calculated F-statistics, diversity, and heterozygosity using the web-based version of the program Genepop (Raymond and Rousset 1995). The programs Structure (Pritchard et al. 2000) and Geneland (Guillot et al. 2005) were used to examine the population structure of bobcats in the region. Both programs use Bayesian methods to infer the optimal number of subpopulations from genetic data and assign membership to individuals in a population. The inferred structure was mapped in relation to potential natural and anthropogenic barriers to gene flow. Analysis in Geneland used spatial coordinates for each sample and assumed a correlated allele frequency model with 100,000 iterations and a number of populations between 1 and 15. Structure was run using the admixture and correlated allele frequency models with a burn-in period of 10,000 and 20,000 Markov chain Monte Carlo repetitions for 1–10 populations.

Results

Roads as a Risk Factor

During 2008–2013, 98 bobcat-vehicle collisions were reported from 73 of the 259 townships in the state (Fig. 2). Collision rates (collisions/100 km^2 of township area) were moderately correlated with density (km/km^2) of all roads within the township ($r_{\text{Spearman}} = 0.31$, $P = 0.007$). That relationship improved when we restricted the comparison

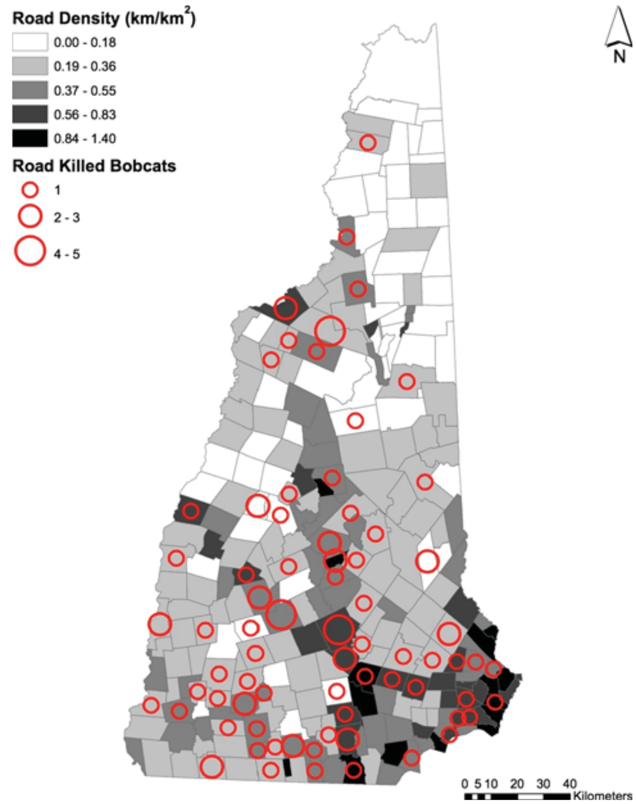

Fig. 2 Distribution of bobcat-vehicle collisions (2008–2013) in relation to density of state/interstate highways (Class 1) and primary roads (Class 2) within townships of New Hampshire

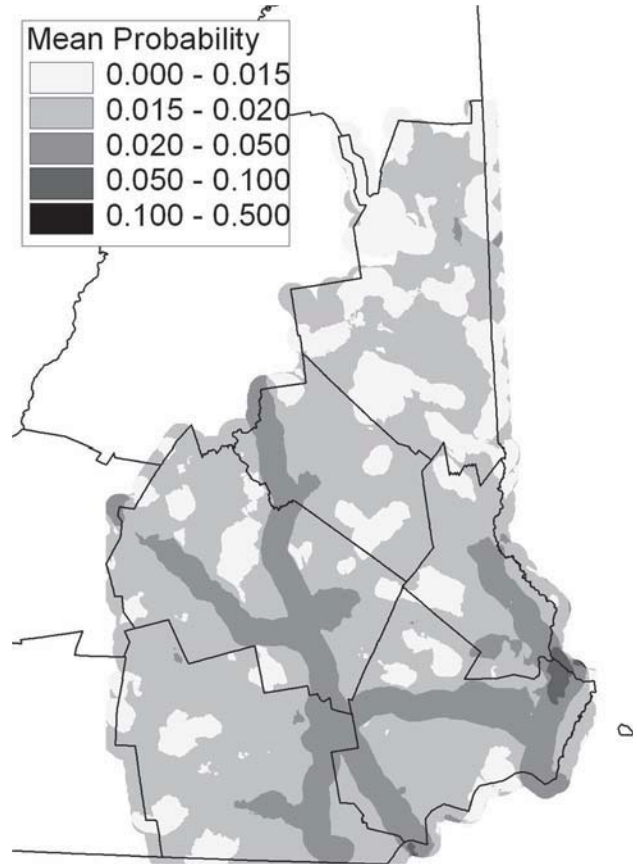

Fig. 3 Probability of a bobcat being struck by a vehicle during a single road crossing in six counties of southeast New Hampshire. Modified from Litvaitis and Tash (2008)

to collision rates versus density of high-traffic volume roads ($r_{\mathrm{Spearman}} = 0.42$, $P < 0.001$).

The probability of being struck by a vehicle during a single road crossing was ≤10 % for most of southeastern New Hampshire (Fig. 3). However, if an individual bobcat occupied a landscape where the average collision probability was 10 %, but if it crossed roads ten times during the year, the annual probability of a collision would increase to 65 %. As expected, risk of mortality was greatest along the state and interstate highways where AADT can exceed 50,000 vehicles. Our estimates of collision were based on traffic volume during 1800–0600 hours, the period we considered bobcats to be most active. That period included only 24 % of the daily number of vehicles (Litvaitis and Tash 2008).

Effect of Roads on Habitat Suitability and as Barriers to Bobcat Movements

We received 729 sightings between December 2007 and January 2013. After screening, 665 sightings were assigned geographic coordinates, and these locations were buffered with the largest home-range radius of our telemetry-marked bobcats (9.6 km). The resulting model of second-order habitat selection (placement of home ranges) indicated that average monthly mean snow depths of >20 cm reduced suitability of habitats, especially in the White Mountains and extreme northern townships (Reed 2013).

Eighteen adult bobcats (13 M:5 F) in our two study areas provided 89–884 usable locations per individual. Habitat suitability was modeled at third-order selection (resource selection within home ranges) and bobcats selected forests, shrub/scrub, and wetlands, and avoided developed areas, agricultural areas, and open water relative to availability. They also showed avoidance of areas with high road densities and selected areas closer to forest edges. Bobcats preferred more rugged and steeper sloped areas, with southern facing slopes. Finally, there was selection for areas closer to streams. Additional details of model development are summarized by Reed (2013).

Habitat suitability was high in southern areas or regions with low elevations (Fig. 4). On the other hand, areas with deep snow (White Mountains and northern townships) had low suitability (Fig. 4). Likewise, intensively developed areas (south central and southeastern townships) were ranked as poor habitat, especially along interstate highway

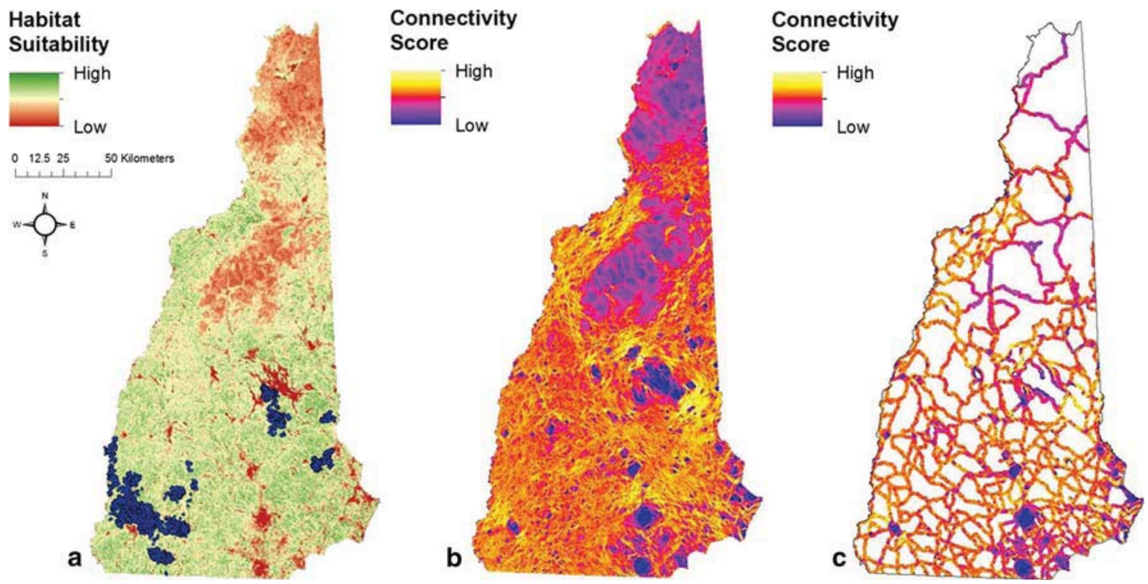

Fig. 4 **a** Habitat suitability for bobcats in New Hampshire based on locations from transmitter-equipped bobcats (*blue dots*) and incidental observations (*left*). **b** Relative connectivity of bobcat habitat based on habitat suitability and resistance to movement (*middle*). **c** Relative barrier effects to movement imposed by major roads (*right*)

corridors. Outside of these areas, much of the state was considered moderate to good bobcat habitat (Fig. 4).

Circuitscape analysis using the RSPF model showed relatively high connectivity throughout the state, with the exception of the White Mountains and the northern portion of the state. Pinch points of potential movement were seen between major urban areas (e.g., Merrimack Valley) and near major geographic features such as the western edge of the White Mountains and between Lake Winnipesaukee and the White Mountains (Fig. 4). Additionally, potential movement by bobcats was limited in response to high-traffic volume roads in much of the southeastern portion of the state (Fig. 4).

Effects of Roads on Bobcat Population Structure

To date, 237 samples have been successfully genotyped at 13 loci. Micro-checker revealed null alleles at 6 loci; as a consequence, they were omitted from further analysis. All remaining loci were in Hardy–Weinberg and linkage equilibrium, as was the sample population as a whole. The number of alleles per locus ranged from 5 to 11 ($\bar{x} = 8.7$). Observed heterozygosity was slightly lower than expected at six of the seven retained loci, which is indicative of population subdivision.

Comparing pairwise genetic distance to Euclidean distance using the Mantel test can help determine what amount of genetic differentiation is due to distance alone (isolation by distance, IBD; Wright 1943). We tested for a signature of IBD in both the New Hampshire population and the regional population. There was no significant signature of IBD in the New Hampshire population. There was a significant but modest effect of IBD in the regional population ($P = 0.001$). While IBD is expected to increase as the spatial extent of the study area increases, the lack of a strong correlation indicates that landscape factors such as land use, elevation, and climate may be the driving forces affecting bobcat dispersal.

Based on the results of the Geneland analysis, the optimal number of populations was determined to be four (Fig. 5). Genetic structuring was more apparent in New Hampshire, as all four subpopulations are represented in the state and three exist exclusively within state borders. By contrast, all bobcats sampled from Vermont represent a single subpopulation, suggesting a relatively high degree of gene flow. This corresponds with a markedly lower density of high-volume roadways in Vermont as compared to New Hampshire (Fig. 5). All eight samples from western Massachusetts were members of the Vermont population. All subpopulations had major roadways delineating all or part of their boundaries. Within New Hampshire, interstate highways 89, 91, 93, and state highway 101 seem to be effective barriers to gene flow (Fig. 5).

Inbreeding coefficients for the subpopulations showed apparent heterozygote deficiency in the eastern and southwestern New Hampshire subpopulations (Table 1). Central New Hampshire showed a slight excess of heterozygotes, and the Vermont/Massachusetts subpopulation had the expected level of heterozygosity. The greatest degree of genetic differentiation occurred in the eastern New

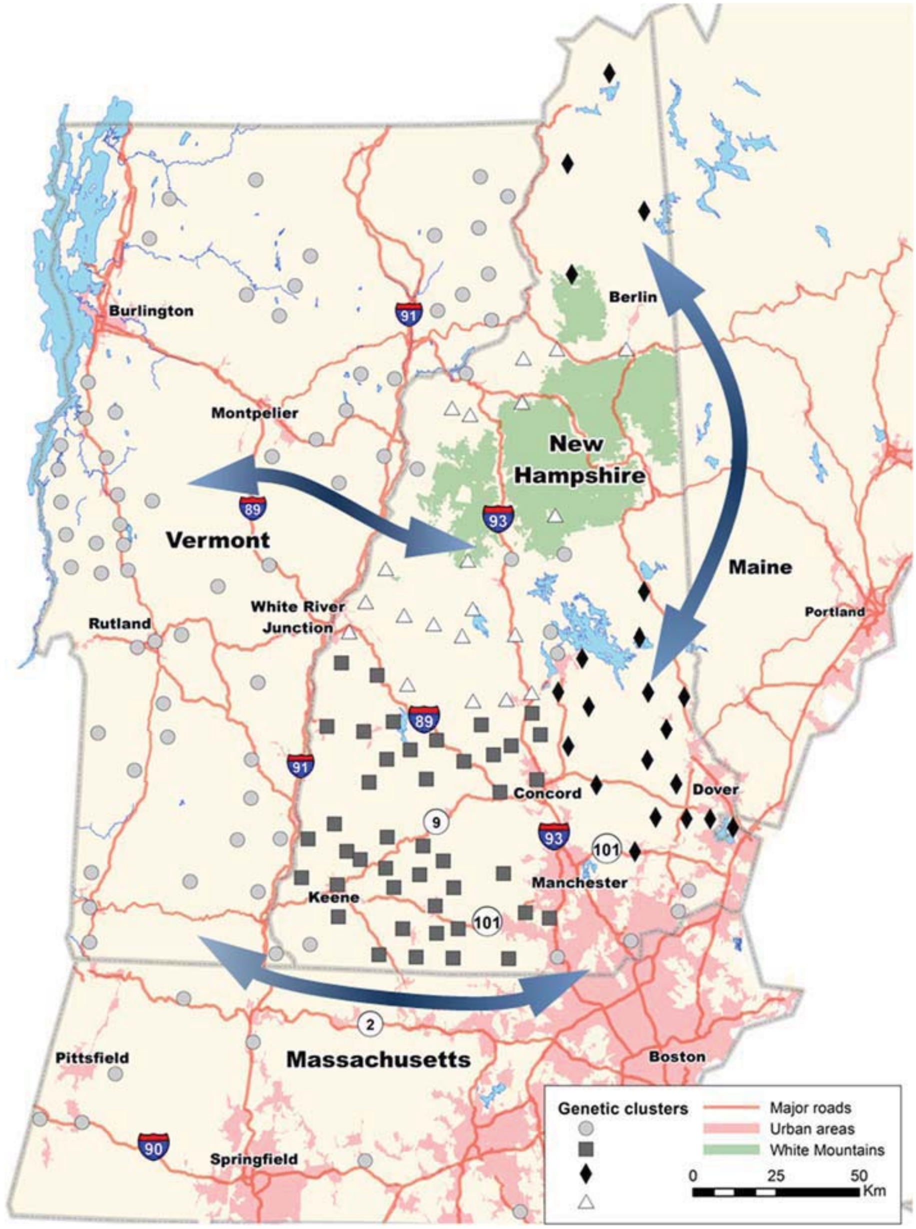

Fig. 5 Genetic structure of bobcats in the study area. Programs Geneland and Structure both indicated the optimal number of populations to be four: Vermont/Massachusetts (*circle*), Southwestern New Hampshire (*black square*), Eastern New Hampshire (*black diamond*), and Central New Hampshire (*white triangle*). Spatial structure of the demes implies potentially dispersal routes (indicated by the *arrows*)

Hampshire and southwestern New Hampshire subpopulations (Table 2), which span the highest density of roads and development in the state. Again, central New Hampshire had the least divergence of all the subpopulations.

Discussion

Our investigation has demonstrated that bobcats are responding to the detrimental effects caused by roads (Fahrig 2002): habitat loss, road mortalities, barrier effect, and subsequent population fragmentation. The obvious

Table 1 Bobcat genetic diversity across seven microsatellite loci (n = number of individuals, A = allelic diversity per locus, H_o = observed heterozygosity, H_e = expected heterozygosity, and F_{IS} = inbreeding coefficient)

Region/population cluster	n	A	H_o	H_e	F_{IS}
Vermont/Massachusetts	115	6.9	0.71	0.71	−0.024
Southwestern New Hampshire	65	7.0	0.67	0.72	0.010
Eastern New Hampshire	31	6.0	0.68	0.73	0.066
Central New Hampshire	26	6.7	0.75	0.74	−0.014
Overall	237	6.6	0.70	0.72	−0.002

Table 2 Pairwise population differentiation (F_{ST}) for four subpopulations of bobcats in the northeastern United States as identified by GENELAND

	Vermont/Massachusetts	Southwestern New Hampshire	Eastern New Hampshire
Southwestern New Hampshire	0.010		
Eastern New Hampshire	0.024	0.019	
Central New Hampshire	0.008	0.014	0.020

reduction of suitable habitats in the immediate proximity of roads is a consequence of the *foot print* of the paved corridor that eliminated vegetation. More subtle are the apparent spillover or road-zone effects that extend beyond the immediate corridor (Forman et al. 2003). Transmitter-equipped bobcats showed an avoidance of areas in proximity to roads based on use-versus-availability analysis (Reed 2013) .That avoidance could be a consequence of limited prey in these areas or a response to a perceived risk factor (e.g., traffic noise). We suspect that perceived risk is a more likely explanation because roadsides are often characterized by brushy edges that may be suitable habitat for potential prey (Bissonette and Rosa 2009; Fahrig and Rytwinski 2009). This may be especially relevant to some multi-lane highways in our study area that support relatively dense populations of lagomorphs (J. Litvaitis, personal observations; Fenderson et al. 2014).

Although vehicle collisions are an obvious mortality factor, the effect of these deaths on bobcat abundance may not be as obvious. Previously, Litvaitis et al. (2006) speculated on the potential demographic responses of several vertebrates to road mortalities by comparing species-specific traits (e.g., age at first reproduction, and other known mortality factors). Bobcats were considered to have an intermediate resilience to vehicle-caused mortalities (Litvaitis et al. 2006). If recorded road mortalities (~20/year) are an accurate approximation of all bobcats killed on roads in New Hampshire (it is illegal for citizens to posses carcasses of bobcats in New Hampshire), then comparing that rate of loss to Reed's (2013) estimate of the statewide bobcat population (~1400, based on area requirements and the abundance of suitable habitats) suggests that road deaths are relatively modest and likely a compensatory factor that has little influence on statewide populations. Our assessment of the compensatory versus additive nature of these mortalities is in the context that trapping and hunting seasons are currently closed in New Hampshire. At the local or township scale, the influence of road mortalities on bobcat abundance is not known.

Related to this, our collision models suggest that bobcats occupying areas with suitable but highly fragmented habitat would be vulnerable to elevated mortality rates that potentially limit survival. If frequent road crossings result in elevated mortality rates, we might expect that areas with abundant roads are functioning as demographic sinks, where dispersing juveniles encounter suitable habitats but do not survive long enough to reproduce. However, the recent expansion of bobcats into southeastern New Hampshire reported by Broman et al. (2014) may challenge that expectation. Two possible explanations may resolve this conflict. Bobcats may substantially reduce mortality risks associated with road crossings by simply moving along underpasses (Cain et al. 2003) that are abundant in the region given the prevalence of large wetlands and riparian corridors (Broman 2012). Four of our transmitter-equipped female bobcats occupied home ranges that were fragmented by state highways. All individuals regularly crossed highways, and one was killed while doing so. Unfortunately, telemetry locations of these bobcats were not collected at a frequency that would enable us to identify actual crossing points and determine if bobcats passed through culverts or underpasses rather than on the highway surface.

Incidental observations may also provide an explanation for a reduction in the lethal effects of roads, especially in southeastern New Hampshire. A number of residents in this region observed and photographed bobcats capturing prey in backyards, especially gray squirrels (*Sciurus carolinensis*) and wild turkeys (*Meleagris gallopavo*) that were attracted to bird feeders (Broman et al. 2014). In addition to enhancing winter survival of bobcats that have difficulty capturing prey during periods of deep snow (Litvaitis et al. 1986), the concentrated prey associated with suburban settlements in winter may result in less frequent road crossings by bobcats. Supporting this speculation, one resident reported that a juvenile bobcat spent several weeks underneath a porch from which it made regular forays to attack squirrels foraging at a nearby bird feeder. Thus, the availability of such prey may at least partially ameliorate the negative effects associated with an abundance of roads in developed areas.

Legacy Effects

The lack of a pattern of genetic isolation by distance within New Hampshire and the presence of a distance effect at the regional scale confirm that our study area represents an appropriate scale for studying bobcat dispersal. Because Euclidean distance accounted for such a small portion of the genetic variation among bobcats, it is likely that landscape variables play a major role in determining dispersal ability and direction for bobcats in the region. The population structure revealed by GENELAND and STRUCTURE lends support to the consequences of the barriers imposed by roads and urban development on genetic exchange among bobcats. This is evident in portions of New Hampshire where sharp divisions exist in highly developed areas that contain otherwise optimal bobcat habitat. As Riley et al. (2006) noted, the barrier effects of major transportation corridors can affect bobcat population structure in a relatively short time. The interstate highways in our study region were constructed in the 1960s and 1970s, approximately 40–50 years before our investigation. Yet, major roadways do not consistently structure bobcat populations. For example, there was no subdivision between populations north and south of Interstate 89 in Vermont. This suggests that the magnitude of road effects may depend not only on time since construction, but also on other local landscape and environmental factors (including traffic volume). As we obtain additional tissue samples, we plan a hierarchical analysis (Balkenhol et al. 2014) to examine such interactions.

The spatial structuring of bobcat populations also revealed potential dispersal routes (Fig. 5). Most notably, the western portion of the White Mountains in central New Hampshire seems to be a corridor for gene flow in east–west and north–south directions. Furthermore, central New Hampshire may be acting as a reservoir for genetic diversity of bobcats in the region. Four of seven loci had alleles that were found only in New Hampshire. No private alleles were found in Vermont or Massachusetts. Despite having the smallest number of individuals, the central New Hampshire deme had the highest heterozygosity and strong allelic diversity. It also showed the least divergence, and hence the greatest connectivity with other populations in the study area.

Bobcats as a Focal or Umbrella Species for Landscape Connectivity

A common assumption of most efforts to maintain or restore landscape connectivity is that it is not possible to evaluate the movement patterns and dispersal needs of all species of concern (e.g., Lambeck 1997). Consequently, the use of a small group of "focal species" that exemplify the needs of a much larger assemblage seems a pragmatic tactic. With a focal species approach, conservationists rely on empirical information or expert opinion on the habitat associations and dispersal patterns of members of the focal group to identify potential linkages (habitat corridors) that may sustain community or ecosystem-wide connectivity (Beier et al. 2007, 2008). Related to the focal species approach is the "umbrella species" concept, where one or a few species with large home ranges serve as a management model, and it is assumed that the needs of species with smaller area requirements are contained within the lands maintained for the umbrella species (Roberge and Angelstam 2004; Breckheimer et al. 2014). Because of their wide-ranging movements, carnivores are often selected as focal or umbrella species (Carroll et al. 2001; Bani et al. 2002; Singleton et al. 2002; Sergio et al. 2005). However, recent evaluations indicate that the general habitat affinities of some carnivores may not include the requirements of other at-risk taxa (Thorne et al. 2006; Cushman and Landguth 2012).

Although carnivores alone may not capture the range of conditions needed in a comprehensive plan for maintaining landscape connectivity, our study has demonstrated that bobcats are responding to landscape fragmentation caused by expanding human populations. Using a combination of telemetry-based information on individual movement patterns and genetic-based information on population structure, we have identified obstacles and potential pathways for continued large-scale movements by bobcats. Additional work will determine to what extent other species utilize the dispersal pathways we identified. We contend that the patterns revealed by bobcats make it a suitable member of a group of focal species to guide efforts to maintain habitat connectivity in our region. Recently, the Nature Conservancy did indeed include bobcats as a focal species for their "Staying Connected" initiative, an effort to sustain landscape connections across the northern Appalachians, including New Hampshire (The Nature Conservancy 2013). In that application, expert opinion rather than empirical information was used to develop cost-surface maps for bobcats and several other wide-ranging forest mammals.

In conclusion, we have shown the utility of using bobcats as a model organism to understand the variety of threats that roads pose to a wide-ranging species. Such information should be useful in developing approaches to maintain existing connectivity or mitigate the negative effects of roads.

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References

Aresco MJ (2005) Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. J Wildl Manag 69:549–560

Balkenhol N, Holbrook JD, Onorato D, Zager P, White C, Waits LP (2014) A multi-method approach for analyzing hierarchical genetic structures: a case study with cougars *Puma concolor*. Ecography 37:552–563

Bani L, Baietto M, Bottoni L, Massa R (2002) The use of focal species in designing a habitat network for a lowland area of Lombardy, Italy. Conserv Biol 16:826–831

Beckman JP, Clevenger AP, Huijser MP, Hilty JA (eds) (2010) Safe passages – highways, wildlife, and habitat connectivity. Island Press, Washington, DC

Beier P, Majka D, Bayless T (2007) Linkage designs for Arizona. Corridor Design. http://www.corridordesign.org/linkages/arizona. Accessed 15 Oct 2014

Beier P, Majka DR, Spencer WB (2008) Forks in the road: choices in procedures for designing wildland linkages. Conserv Biol 22:836–851

Bissonette JA, Rosa SA (2009) Road zone effects in small-mammal communities. Ecol Soc 14:27. http://www.ecologyandsociety.org/vol14/iss1/art27/. Accessed 15 Oct 2014

Breckheimer I, Haddad NM, Morris WF, Trainor AM, Fields WR, Jobe RT, Hudgens BR, Moody A, Walters JR (2014) Defining and evaluating the umbrella species concept for conserving and restoring landscape connectivity. Conserv Biol 28:In press

Broman DJA (2012) A comparison of bobcat habitat suitability models derived from radio telemetry and incidental observations. M. S. Thesis, University of New Hampshire, Durham

Broman DJA, Litvaitis JA, Ellingwood M, Tate P, Reed G (2014) Modeling bobcat distributions using incidental observations and telemetry locations: are the results comparable? Wildl Biol 20:229–237

Cain AT, Tuovila VR, Hewitt DG, Tewes ME (2003) Effects of a highway and mitigation projects on bobcats in Southern Texas. Biol Conserv 114:189–197

Carmichael LE, Clark W, Strobeck C (2000) Development and characterization of microsatellite loci from lynx (*Lynx canadensis*), and their use in other felids. Mol Ecol 9:2155–2234

Carroll C, Noss RF, Paquet PC (2001) Carnivores as focal species for conservation planning in the rocky mountain region. Ecol Appl 11:961–980

Crooks KR (2002) Relative sensitivities of mammalian carnivores to habitat fragmentation. Conserv Biol 16:488–502

Crooks KR, Sanjayan MA (eds) (2006) Connectivity conservation. Cambridge University Press, Cambridge

Cushman SA, Landguth EL (2012) Multi-taxa population connectivity in the Northern Rocky Mountains. Ecol Model 231:101–112

Fahrig L (2002) Animal populations and roads. In: Evink GL, Garret P, Zeigler D (eds) Proceedings of the International Conference on Ecology and Transportation and the Environment. The Center for Transportation and the Environment at North Carolina State University, Raleigh, pp 9–11

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14: 21. http://www.ecologyandsociety.org/vol14/iss1/art21/. Accessed 15 October 2014

Faircloth BC, Reid A, Valentine T, Eo SH, Terhune TM, Glenn TC, Palmer WE, Nairn CJ, Carroll JP (2005) Tetranucleotide, trinucleotide, and dinucleotide loci from the bobcat (*Lynx rufus*). Mol Ecol Notes 5:387–389

Fenderson LE, Kovach AI, Litvaitis JA, O'Brien K, Boland K, Jakubas W (2014) Genetic structure and connectivity of the New England cottontail (*Sylvilagus transitionalis*) in a highly-fragmented landscape. Ecol Evol 4:1853–1875

Forman RTT, Reineking B, Hersperger AM (2002) Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environ Manag 29:782–800

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshal CC, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson WJ, Turrentine T, Winter TC (2003) Road ecology: science and solutions. Island Press, Washington, DC

Fry J, Xian G, Jin S, Dewitz J, Homer C, Yang L, Barnes C, Herold N, Wickham J (2011) Completion of the 2006 National Land Cover Database for the conterminous United States. Photo Eng Remote Sens 77:858–864

Gibbs JP, Shriver G (2002) Estimating the effects of road mortality on turtle populations. Conserv Biol 16:1647–1652

Guillot G, Mortier F, Estoup A (2005) GENELAND: a computer package for landscape genetics. Mol Ecol Notes 5:712–715

Hels T, Buchwald E (2001) The effects of road kills on amphibian populations. Biol Conserv 99:331–340

Jansen D, Sherwood K, Fleming E (2010) The I-75 project: lessons from the Florida panther. In: Beckman JP, Clevenger AP, Huijser MP, Hilty JA (eds) Safe passages – highways, wildlife, and habitat connectivity. Island Press, Washington, DC, pp 205–222

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. J Appl Ecol 41:238–251

Justice D, Deely A, Rubin F (2002) New Hampshire land cover assessment. Complex Systems Research Center, Durham

Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. PloS One 5:e11785

Lambeck RJ (1997) Focal species: a multi-species umbrella for nature conservation. Conserv Biol 11:849–856

Lele SR, Keim JL, Solymos P (2013) ResourceSelection: Resource selection (probability) functions for use-availability data. R package version 0.2-2. http://CRAN.R-project.org/package=ResourceSelection. Accessed 1 Oct 2013

Litvaitis JA (1993) Response of early successional vertebrates to historic changes in land use. Conserv Biol 7:866–873

Litvaitis JA, Tash JP (2008) An approach towards understanding wildlife-vehicle collisions. Environ Manag 42:688–697

Litvaitis JA, Clark AG, Hunt JH (1986) Prey selection and fat deposits of bobcats (*Felis rufus*) during autumn and winter in Maine. J Mammal 67:389–392

Litvaitis JA, Tash JP, Stevens CL (2006) The rise and fall of bobcat populations in New Hampshire: relevance of historical harvests to understanding current patterns of abundance and distribution. Biol Conserv 128:517–528

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer Res 27:209–220

McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Natl Acad Sci 104:19885–19890

McRae BH, Shah VB (2009) CIRCUITSCAPE user's guide. University of California, Santa Barbara

Menotti-Raymond M, David VA, Lyons LA, Schaffer AA, Tomlin JF, Hutton MK, O'Brien SJ (1999) A genetic linkage map of microsatellites in the domestic cat *(Felis catus)*. Genomics 57:9–23

Menotti-Raymond MA, David VA, Wachter LL, Butler JM, O'Brien SJ (2005) An STR forensic typing system for genetic individualization of domestic cat *(Felis catus)* samples. J Forensic Sci 50:1061–1070

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959

R Core Team. (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J Hered 86:248–249

Reed GC (2013) Bobcats in New Hampshire: understanding the relationships between habitat suitability, connectivity and abundance in a changing landscape. MS Thesis, University of New Hampshire, Durham

Riley SPD, Pollinger JP, Sauvajot RM, York EC, Bromley C, Fuller TK, Wayne RK (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores. Mol Ecol 15:1733–1741

Roberge J, Angelstam P (2004) Usefulness of the umbrella species concept as a conservation tool. Conserv Biol 18:76–85

Roberts NM, Crimmins SM (2010) Bobcat population status and management in North America: evidence of large-scale population increase. J Fish Wildl Manag 1:169–174

Rousset F (2000) Genetic differentiation between individuals. J Environ Biol 13:58–62

Sappington JM, Longshore KM, Thompson DB (2007) Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. J Wildl Manag 71:1419–1426

Sergio F, Newton I, Marches L (2005) Top predators and biodiversity. Nature 436:192

Simmons JM, Sunnucks P, Taylor AC, van der Ree R (2010) Beyond roadkill, radiotracking, recapture and *FST*—a review of some genetic methods to improve understanding of the influence of roads on wildlife. Ecol Society 15(1): 9. http://www.ecologyandsociety.org/vol15/iss1/art9/. Accessed 15 Oct 2014

Singleton PH, Gaines WL, Lehmkuhl JF (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. Research Paper PNW-RP-549. US Forest Service Pacific Northwest Research Station, Portland, Oregon

Sirén APK (2015) A comparison of snow track and camera surveys for detecting Canada lynx (*Lynx canadensis*) and sympatric carnivores in north-central New England. Final Report, New Hampshire Fish and Game Department, Concord

Sundquist D, Hewes J (2010) Population growth and land use change in the Granite State. The Society for the Protection of New Hampshire Forests. Concord, New Hampshire. Web. http://www.forestsociety.org/. Accessed 25 Feb 2012.

The Nature Conservancy (2013) Staying connected in the northern Appalachians: mitigating fragmentation and climate change impacts on wildlife through functional habitat linkages. Final report submitted to the New Hampshire Fish and Game Department and the United States Fish and Wildlife Service. http://stayingconnectedinitiative.org/assets/SCI-CSWG-Final-Report-Summary-5-17-13. Accessed 15 Oct 2014

Thorne JH, Cameron D, Quinn JF (2006) A conservation design for the central coast of California and the evaluation of mountain lion as an umbrella species. Nat Areas J 26:137–148

van Langevelde F, Jaarsma CF (2004) Using traffic flow theory to model traffic mortality in mammals. Landsc Ecol 19:895–907

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Wright S (1943) Isolation by distance. Genetics 31:114–138