Colorado Division of Parks and Wildlife
July 2010–June 2011

WILDLIFE RESEARCH REPORT

State of: Colorado : Division of Parks and Wildlife
Cost Center: 3430 : Mammals Research
Work Package: 0670 : Lynx Conservation
Task No.: N/A : Monitoring Canada Lynx in Colorado Using Occupancy Estimation: Initial Implementation in the Core Lynx Research Area
Federal Aid Project No. N/A

Period Covered: July 1, 2010 – June 30, 2011

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ABSTRACT

In an effort to restore a viable population of federally threatened Canada lynx (*Lynx canadensis*) to the southern portion of their former range, 218 individuals were reintroduced into Colorado from 1999–2006 (Devineau et al. 2010). In 2010, the Colorado Division of Wildlife (now Colorado Parks and Wildlife [CPW]) determined that the reintroduction effort met all benchmarks of success, and that a viable, self-sustaining population of Canada lynx had been established. The purpose of this project was to develop a scientifically rigorous statewide plan to monitor this newly established population. Occupancy estimation, the use of presence/absence data to estimate the proportion of sample units used by a species within a study area, is appropriate for such a program. To evaluate this approach and provide initial estimates of occupancy and detection probability for planning purposes, we conducted a pilot occupancy estimation project in the core reintroduction area in the San Juan Mountains of southwestern Colorado. Lynx habitat in the study area was divided into 75–km^2 sample units (8.66 km x 8.66 km cells), and we stratified the units into those accessible for snow tracking and “inaccessible” units which were sampled via remote cameras. We randomly sampled 30 units from each stratum. Sampling consisted of making multiple visits to each selected unit. We covered 2,178 km during our snow tracking effort (min= 1.4, max = 81.7 per visit) and detected lynx on 12 of the 30 sample units. Estimates of occupancy and detection probability from the top model were 0.62 and 0.37-0.43, respectively. Of the 120 cameras we deployed in late fall to survey the 30 inaccessible units, 113 were still operational when retrieved in early summer; 6 had memory cards that reached capacity in either May or June; 1 was stolen. We obtained 151,191 photos (min = 90, max = 6,948 per camera) from this effort. Work to assign species for each photo is ongoing. These pilot data will be used to conduct simulations and power analyses to determine how many sample units will be required to detect a statewide decline in Canada lynx, assuming that a decline in the actual population will be tied to a decline in the proportion of sample units used by lynx.

WILDLIFE RESEARCH REPORT

MONITORING CANADA LYNX IN COLORADO USING OCCUPANCY ESTIMATION: INITIAL IMPLEMENTATION IN THE CORE LYNX RESEARCH AREA

JACOB S. IVAN

P. N. OBJECTIVE

Assess the use of occupancy estimation as a means of monitoring Canada lynx in Colorado using the Core Research Area in the San Juan Mountains as a test site.

1. Obtain initial estimates of occupancy and detection probability based on pilot work.
2. Conduct power analyses using initial estimates to determine the number of sample units, number of visits, and periodicity of sampling required to detect declines of interest in the statewide lynx population.
3. Develop a standardized, statistically rigorous monitoring protocol for estimating the distribution, stability and persistence of Canada lynx in Colorado.

SEGMENT OBJECTIVES

1. Assess and suggest modifications to survey protocols.
2. Construct database to store and query survey information.
3. Obtain initial estimates of occupancy and detection probability based on pilot work.
4. Determine covariates and covariate structures that will be most useful for modeling occupancy and detection probability in the future.
5. Determine the efficacy of collecting lynx scat during occupancy surveys and whether such collections can be helpful in identification of putative lynx tracks and/or individuals.

INTRODUCTION

The Canada lynx (*Lynx canadensis*) occurs throughout the boreal forests of northern North America. While Canada and Alaska support healthy populations of the species, the lynx is currently listed as threatened under the Endangered Species Act (ESA) of 1973, as amended (16 U. S. C. 1531 et. seq.; U. S. Fish and Wildlife Service 2000) in the conterminous United States. Colorado represents the southern-most historical distribution of naturally occurring lynx, where the species occupied the higher elevation, montane forests in the state (U. S. Fish and Wildlife Service 2000). Lynx were extirpated or reduced to a few animals in Colorado, however, by the late 1970's (U. S. Fish and Wildlife Service 2000), most likely due to multiple human-associated factors, including predator control efforts such as poisoning and trapping (Meaney 2002). Given the isolation of and distance from Colorado to the nearest northern populations of lynx, the Colorado Division of Wildlife (now Colorado Parks and Wildlife [CPW]) considered reintroduction as the best option to reestablish the species in the state. Therefore, a reintroduction effort was begun in 1997, and 218 lynx were released into Colorado from 1999 – 2006 (Devineau et al. 2010). The goal of the Colorado lynx reintroduction program was to establish a self-sustaining, viable population of lynx. Progress toward this goal was tracked via evaluation of critical criteria related to lynx survival, fidelity, and recruitment. Recently, CPW determined that the criteria had been met and a viable Canada lynx population currently exists in Colorado (Shenk and Kahn 2010).

In order to track the distribution, stability, and persistence of this new lynx population, a minimally-invasive, long-term, statewide monitoring program is required. Abundance estimation is not feasible logistically and presents statistical difficulties even when field logistics can be managed. However, occupancy estimation, which uses detection/non-detection survey data to estimate the proportion of area occupied in a study area, is appropriate and feasible. In short, such a monitoring scheme requires multiple visits to a sample of survey units, and on each visit observers record whether a lynx was detected or not. Such information can be used to compute the probability of detecting a lynx given that it is present on a unit, which can in turn be used to estimate the proportion (ψ) of all survey units that are occupied. This metric can be tracked through time and is assumed to be closely tied to the size and extent of the lynx population. That is, if the proportion of survey units occupied by lynx declines through time, we assume this is due to a decline in the lynx population itself. Additionally, occupancy surveys can provide information relative to the distribution of lynx in the state.

CPW initiated work to evaluate detection methods for occupancy estimation in 2009-2010 (Shenk 2009). Three methods of detecting lynx were tested in sample units where lynx were known to occur: snow tracking surveys, remote camera surveillance, and hair snags. The best method for detecting lynx was snow-tracking (daily detection probability = 0.70). Camera surveillance was far less efficient (daily detection probability = 0.085), and hair snares were ineffective (daily detection probability = 0.0; Ivan and Shenk 2010). Snow tracking, however, requires safe and extensive access to a survey unit via truck and/or snowmobile. Therefore, it cannot be used in roadless or wilderness areas, which may provide important lynx habitat. Here we build on this work to test occupancy estimation on a large scale using snow tracking where accessibility permitted it, and remote cameras in areas that were not accessible.

METHODS

Study Area

The study area consisted of the 20,684 km^2 "Lynx Core Research Area" in southwest Colorado. The Core Research Area is defined as areas >2591 m (>8500 ft) in elevation within the area bounded by New Mexico to the south, Taylor Mesa to the west, and Monarch Pass on the north and east (Figure 1). Topography in this area is characterized by wide plateaus, river valleys, and rugged mountains that reach elevations over 4200 m. Engelmann spruce (*Picea engelmanii*) – subalpine fir (*Abies lasiocarpa*) is the most widely distributed coniferous forest type at elevations most typically used by lynx (2591-3353 m, 8500-11,000 ft).

Sampling

The study area was divided into 75 km^2 (8.66 km × 8.66 km) sample units, which reflects the mean annual home range size of reproducing lynx in Colorado (Shenk 2007) and Montana (Squires and Laurion 1999). Sample units that did not meet the following criteria were discarded as they did not represent potential lynx habitat that could be surveyed.

1. ≥ 50 % of the cell contained conifer or montane/alpine habitat, as identified by the SWReGAP LandCover Dataset (http://earth.gis.usu.edu/swgap/swregap_landcover_report.pdf) and
2. ≥ 50 % of the cell was located on public land (tribal, NGO and city and county lands are considered private) as determined by COMaP (Theobald, D.M., G. Wilcox, S.E. Linn, N. Peterson, and M. Lineal. 2008. Colorado Ownership, Management, and Protection v7 database. Human Dimensions of Natural Resources and Natural Resource Ecology Lab, Colorado State University, Fort Collins, CO, www.nrel.colostate.edu/projects/comap).

Each of the remaining sample units was assigned a random number resulting from a spatially balanced sampling scheme (RRQRR; Theobald et al. 2007) and units were stratified by accessibility for snow tracking or camera surveys. The cells with the lowest 30 random numbers for each stratum were selected for sampling during the pilot work. A few cells in both strata were discarded once field work began due to access issues and these were replaced with cells 31, 32, etc.

Snow tracking Surveys

Teams of 2 observers generally searched for lynx tracks within a sample unit using snowmobiles, although portions of some units were surveyed via truck or snowshoe. An effort was made to survey all portions of each unit as access allowed. Each of the 30 units selected for sampling was visited 3 times – roughly once per month from January through March. Occasionally a "visit" actually took place over consecutive days as some units could not be covered completely from a single access point. Once tracks were detected in a unit, that visit was considered complete and no further surveying occurred until the next visit. However, observers forward and back-tracked to find a scat sample. For each visit, observers recorded number of kilometers surveyed, tracking conditions (poor, fair, good, excellent), other species detected, location of lynx tracks, and time/distance to scat discovery.

Camera Surveys

Four remote camera sets (RECONYX RapidFire™ Professional PC85) were placed within each selected "inaccessible" sample unit during September and October. Placement of camera sets was not random within the unit; they were placed strategically on the landscape to maximize coverage of the sample unit and exploit microsites most likely to be used by lynx. Camera sets consisted of 1) a remote camera mounted to a tree using a Master Lock ™ Python™ cable lock, 2) a target tree at which the camera was pointed, generally about 5-10m away, 3) a compact disc strung from a nearby branch to visually attract lynx from a distance, 4) 2 feathers strung up in such a manner as to entice lynx to walk between the camera and the target tree, and 5) wool soaked in commercial scent lure that was packed into the bark of the target tree to hold lynx in front of the camera (Figure 2). Cameras were placed higher than usual, about head-height, and pointed slightly downward at the target tree so photos could be obtained during both snow-free periods and during periods of accumulating snow. Cameras were collected during June and July at which time the number of photos, percent of memory card used, percent battery life remaining, and condition of visual/scent lures was recorded.

Analysis

Assumptions inherent in occupancy estimation are 1) surveyed sites are either occupied or not occupied by the species of interest throughout the duration of the study; no sites change status during the survey period (i.e., the system is closed), 2) the probability of occupancy is constant across sites or can be modeled using covariates, 3) the probability of detection is constant across sites or can be modeled using site-specific covariates, and 4) species detection at a site is assumed to be independent of species detection at other sites (MacKenzie et al. 2006). Sampling mobile carnivores such as lynx presents a clear violation of the first assumption as individuals undoubtedly move into and out of sample units routinely. Fortunately, estimation can proceed, but the quantities estimated are different from traditional occupancy estimation. Rather than estimating the probability that a unit is *occupied* by lynx, we now estimate the probability that a sample unit is *used* by lynx. Also, the estimated detection parameter is not the probability of detection given a site is occupied, it is the product of a) the probability of detection given the species is available for detection, and b) the probability that the species was available. These subtleties aside, the procedure still gives a metric (use) that can be monitored through time to detect trends.

We used the "Occupancy Estimation" data type in Program MARK to produce initial estimates of occupancy (i.e., use, ψ) and detection probability (p) for the snow tracking stratum. We hypothesized that some metric of the number of kilometers surveyed, or number that could be surveyed, would be important in explaining variation in detection probability as it should be an indicator of the amount of access to a unit. Surveys on units with more access should stand a better chance of detecting lynx if they are present. We further hypothesized that tracking conditions during a given visit should have an effect on detection probability. Finally, we did not expect differences among survey teams as both teams were experienced, but we wanted to test that assumption. Therefore, we considered 5 covariates that may explain variation in *p*: 1) total road length available for surveying in each sampled unit, 2) Kilometers surveyed during each visit, 3) maximum number of kilometers surveyed during any visit to a given unit, 4) tracking conditions during each visit, and 5) observer effect. We hypothesized that the proportion of spruce/fir cover in each unit may affect the probability of use, as might proportion of willow (*Salix* spp.), and subalpine/alpine meadow. Thus, we considered those 3 covariates as potentially important for explaining variability in ψ. As this analysis is exploratory, we held ψ constant and built an additive model for each detection covariate (one at a time) to determine the best structure for *p*. Similarly, we held *p* constant and fit additive models using the 3 covariates for ψ. We combined the best structure as determined by AICc (Burnham and Anderson 2002) for each parameter and used results from that single model to produce initial estimates of *p* and ψ. We also ran a model where both *p* and ψ were held constant as a baseline for comparison.

Occupancy estimation for the camera stratum will proceed in a similar fashion as above, but data from the photos is incomplete at this time. Photos will be grouped by month (November to March) for each sample unit such that encounter histories will have 5 "visits" rather than 3. Due to this grouping, there are no meaningful covariates for *p*. Individual cameras recorded moon phase and temperature for each photo, but aggregated over a month, these data are not helpful. Some camera sets used different scent lures than others, but aggregating by unit negates the utility of this information as well. We will consider the same covariates on ψ as listed above.

RESULTS

On average, we covered 24.71 km per visit to each accessible sample unit (min = 1.40 km, max = 81.67 km) for a total of 2,184 km surveyed. We detected 20 lynx tracks in 12 of the 30 units sampled (i.e., tracks were detected on multiple visits to some units; Figure 1). We were able to collect scat from 13 of the 20 tracks, and mean forward/backtracking distance to scat discovery was 0.65 km (min = 0.05, max = 1.60).

According to AICc, the best structures for *p* and ψ were "kilometers surveyed per visit" and "proportion spruce-fir," respectively (Table 1). No other structure for either parameter resulted in improvement over constant *p* and ψ with the exception of modeling ψ as a function of "proportion willow." In fact, this was the AICc top structure, but the parameters could not be estimated so it was dropped from the model set. Estimates (SE) from the model that combined the best structures were ψ = 0.62 (0.25), p_1= 0.37 (0.10), p_2= 0.37 (0.10), and p_3 = 0.43 (0.10) where p_i is the detection probability for visit *I* (i.e., p_1 is the estimated detection probability for January, p_2 = February, p_3 = March) .

As expected, the slope of the spruce-fir effect was highly positive. Probability of use was 0.5 when proportion spruce-fir approached 0.35, and probability of use went to 1.0 when proportion spruce-fir approached 0.6 (Figure 3). The relationships between "proportion meadow" and ψ and "proportion willow" and ψ were also positive, but the relationships were weaker as confidence intervals for these slopes covered zero.

The relationship between *p* and kilometers surveyed was negative. Similarly, the relationship between *p* and visit condition was opposite of our hypothesis (as visit conditions improved, detection probability declined). There was no relationship between "total road length" or "maximum kilometers surveyed" and detection probability. We did not detect differences between teams of observers.

Genetic analysis of scat samples is ongoing. By December 2010, we should be able to assess whether scats were of high enough quality to confirm species and/or individual identification.

Of the 120 cameras deployed during Fall 2010, 113 were still operational when retrieved in Summer 2011 after 234-309 days of deployment. Six had memory cards that reached capacity in either May or June, and one camera was stolen. On average, we obtained 1,260 photos per camera (min = 90, max = 6,948) for a total of 151,191 photos. At the time of retrieval, compact discs were still operational for 46% of camera sets, feathers were operational at 64% of sets, and remnants of scent lure were detected at 55% of sets.

DISCUSSION

Initial results indicate that occupancy (use) can be adequately modeled using data collected via snow tracking. Precision on estimates of ψ and p was relatively poor, but this can be addressed by sampling more units and/or making more visits. Modeling p as a function of the "kilometers surveyed per visit" was a better fit for the data than modeling it as a function of either "total road length within a unit" or "visit conditions." However, we recommend continuing to record "total road length" and "visit conditions" in future surveys as it seems reasonable that these covariates should impact detection probability, and their effects may show through as sample size increases. Similarly, we recommend retaining all covariates on ψ to assess their performance with a larger dataset.

The relationship between p and "kilometers surveyed per visit" was negative, which is likely an artifact of how the units were sampled – when lynx were detected, surveying stopped, so detection probability was higher for visits with few kilometers surveyed. The relationship between p and "visit condition" was opposite of our hypothesis (as visit conditions improved, detection probability declined). Our condition criteria were based largely on the freshness of the snow and degree of melting/crusting where fresh snow was assigned the best condition, and older, crusted snow was assigned the worst. Functionally, this index is an inverse of "time-since-snowfall." Therefore, it is sensible that "poor" condition indices resulted in higher detection probabilities. While the immediate conditions were poor for tracking, significant time had passed in which lynx could move around and leave tracks to be discovered.

We estimated that lynx used approximately 62% of the sample units available in the Core Research Area. However, for this pilot study, lynx habitat was coarsely defined as units with >50% spruce/fir and >50% public land. In several cases, sampled units met these criteria, but field crews that actually made visits indicated these units did not appear to include much lynx habitat. CPW is currently finishing an analysis to produce a map of predicted lynx habitat throughout the state. In the future, we expect to use this map to frame the population of units to sample for lynx monitoring. This more refined population of sample units should reduce time wasted surveying units that do not include good lynx habitat, and will result in an increased estimate of probability of use.

Photos from cameras deployed to sample the inaccessible stratum have not been fully processed, therefore we cannot determine whether that portion of the study worked well enough to be included in any future monitoring effort. Roughly half of the visual attractants we used did not operate through the entirety of the study. These attractants are important for drawing lynx to the set from a distance and their failure diminishes the utility of the cameras for detecting lynx. If cameras are to be used in the future, design changes will be necessary to ensure that most of these visual attractants operate throughout the sampling season.

ACKNOWLEDGMENTS

We thank Britta Schielke, Cate Brown, Wendy Lanier, Joan Meiners, Shane McKenzie, Nick Burgmeier, Doug Clark, Bob Peterson, Tim Hanks, Kei Yasuda, Ashley Bies, Tyler Kelly, Alyssa Winkler, and Carolyn Shores for their efforts in the field. Dale Gomez and Rhandy Ghormley (USFS) graciously coordinated housing for seasonal crews. We thank various personnel from both the Rio Grande and San Juan National Forests for logistical help in the field. Funding was provided by a U.S. Fish and Wildlife Service Section 6 Grant.

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Table 1. Model selection results for estimating occupancy of sample units by Canada Lynx (*Lynx canadensis*) in the Core Research Area, San Juan Mountains, Colorado, Winter 2010-2011.

Model	AICc	ΔAICc	AICc Wt	Num Par
p(KmSurveyPerVisit) ψ(SprFir)	81.25	0.00	0.78	4
p(.) ψ(SprFir)	84.23	2.98	0.17	3
p(KmSurveyPerVisit) ψ(.)	88.60	7.35	0.02	3
p(.) ψ(.)	89.95	8.70	0.01	2
p(TtlRoadLen) ψ(.)	90.29	9.04	0.01	3
p(.) ψ(Meadow)	91.25	9.99	0.01	3
p(Observer) ψ(.)	92.10	10.85	0.00	3
p(MaxKmSurv) ψ(.)	92.42	11.17	0.00	3
p(VisitCond) ψ(.)	97.77	16.52	0.00	5

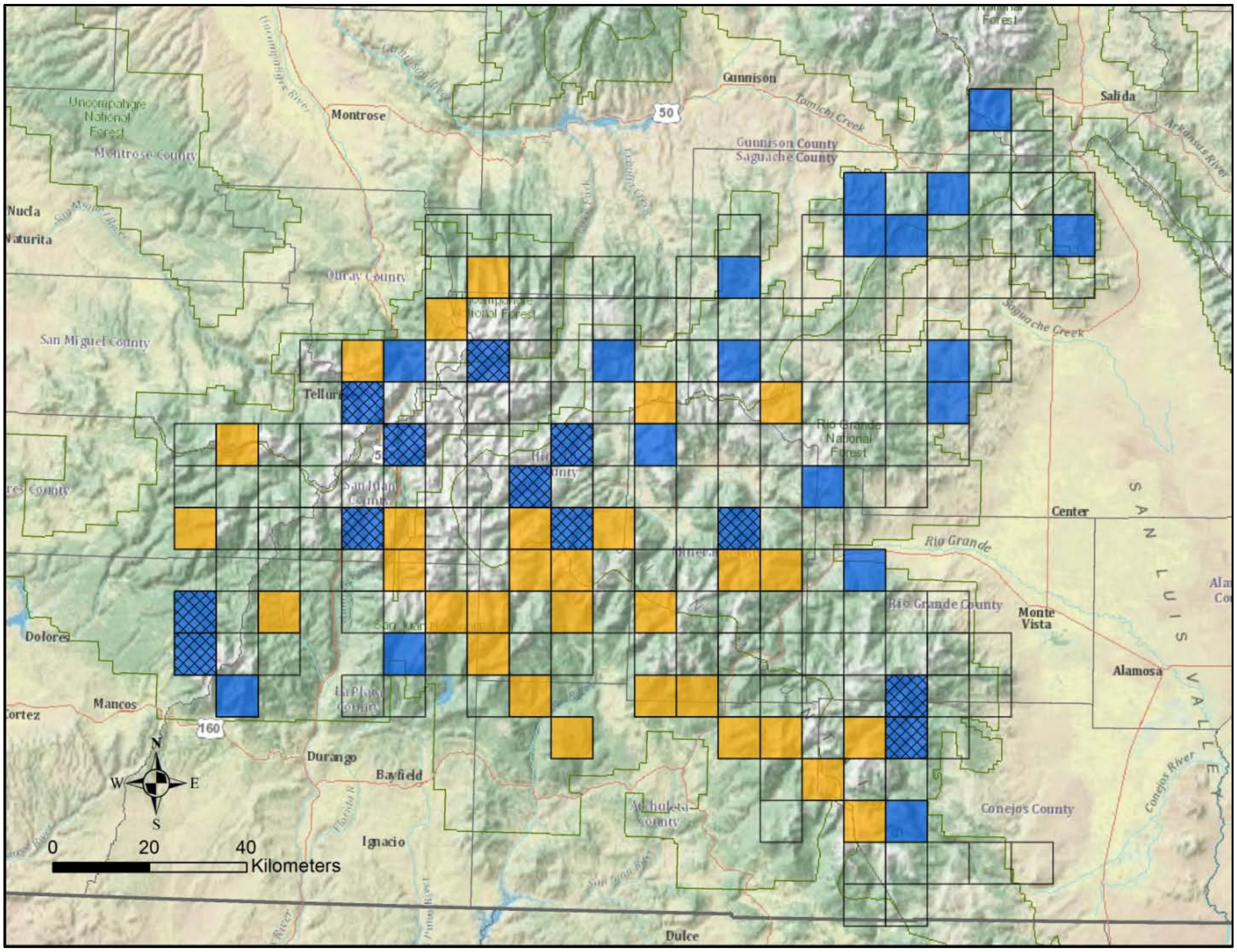

Figure 1. Canada lynx Core Research Area in southwest Colorado. Squares are 75km^2 sample units available for occupancy surveys. Blue represents the sample of 30 "accessible" units selected for snow tracking surveys. Orange are "inaccessible" units selected for surveys using remote cameras. Cross-hatching indicates accessible units where lynx were detected. The data from inaccessible units has not been fully processed and units where lynx were detected are not shown.

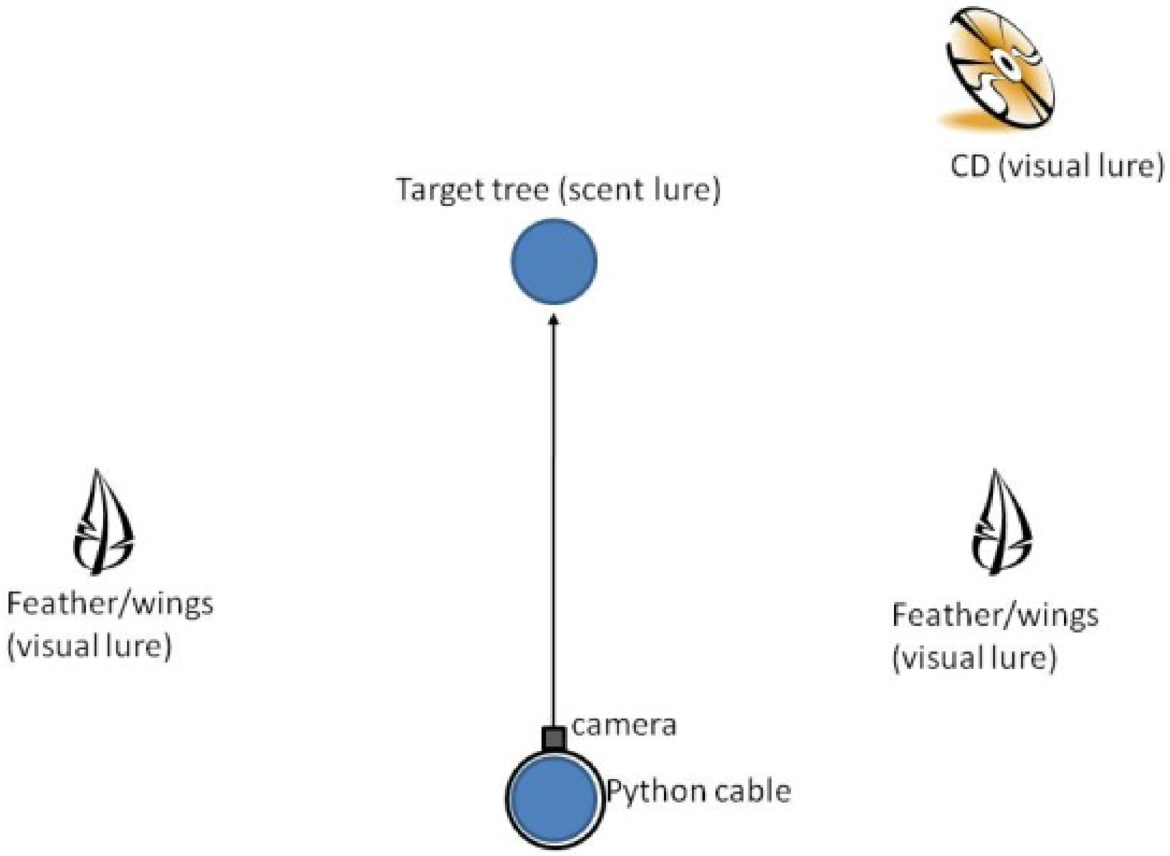

Figure 2. General configuration of remote camera sets for detecting Canada lynx. Four such sets were deployed in each of 30 inaccessible sample units from Fall 2010 to Summer 2011.

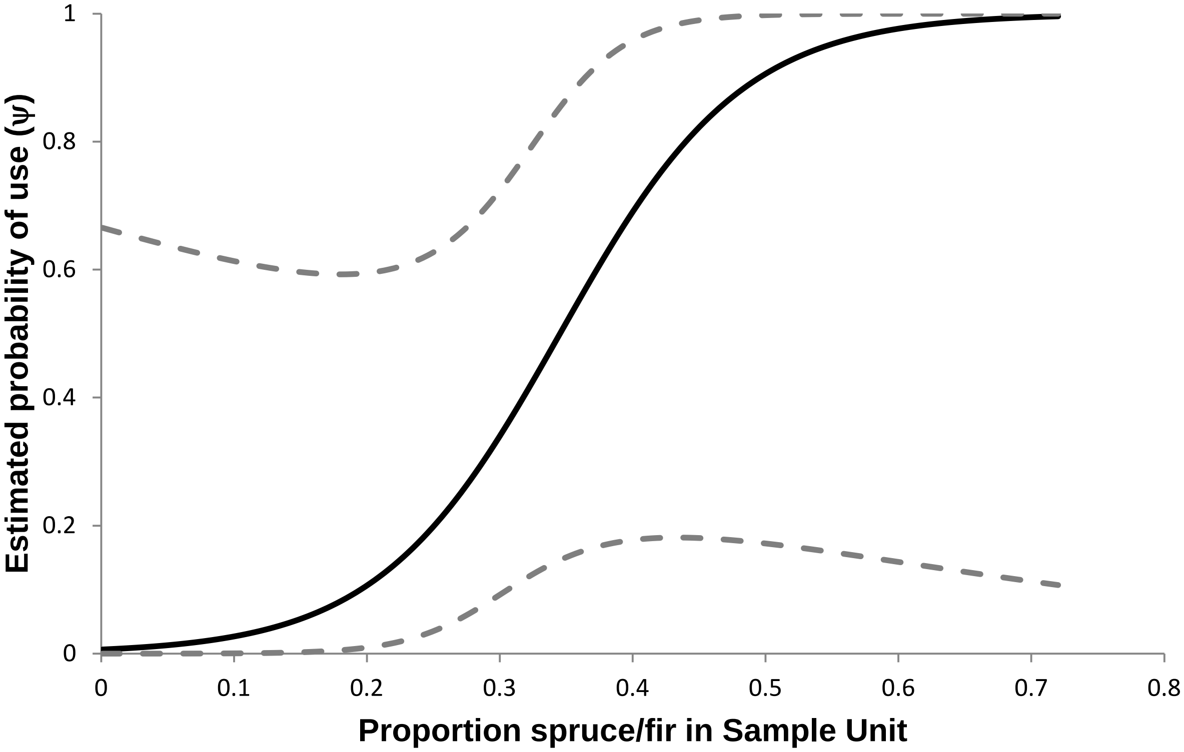

Figure 3. Estimated probability of use (ψ) and 95% confidence intervals plotted against proportion spruce/fir in a sample unit. Relationship is based on snow tracking occupancy surveys completed in southwest Colorado, Winter 2010-2011.

Colorado Division of Parks and Wildlife
July 2010–June 2011

WILDLIFE RESEARCH REPORT

State of:	Colorado	:	Division of Parks and Wildlife
Cost Center:	3430	:	Mammals Research
Work Package:	0638	:	Wolverine Conservation
Task No.:	N/A	:	Assessing the efficacy of monitoring wolverine on a regional scale using occupancy and abundance estimation
Federal Aid Project No.	N/A		

Period Covered: July 1, 2010 – June 30, 2011

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ABSTRACT

The wolverine (*Gulo gulo*) has a circumpolar distribution comprised mostly of tundra and boreal forest. However, its current range extends southward in peninsular fashion to the Cascades and Rocky Mountains of the conterminous United States. Recently the U.S. Fish and Wildlife Service ruled that the North American wolverine in the contiguous U. S. is a candidate species for protection under the Endangered Species Act. Thus, there is considerable interest in identifying monitoring schemes capable of detecting declines in wolverine populations over a large scale. We used spatially explicit simulations in which wolverine were sampled on a virtual landscape to quantify our ability to detect declines using robust-design occupancy estimation. We systematically varied 1) the number of sample units surveyed, 2) the number of visits made to each unit in the sample, and 3) the rate of population decline and computed the power to detect declines under various scenarios. Initial results indicate that occupancy estimation may work well for detecting large declines (50% decline over 10 years), but power to detect less catastrophic declines was low. Approximately 100 sample units would need to be surveyed to have adequate power to detect a 50% decline over 10 years. A census (350 sample unit) would be needed to ensure decent power for detecting smaller declines. Power increases as number of visits to each sample unit increases from 2 to 3 per survey season, but making more than 3 visits does not increase power substantially. If confronted with design tradeoffs that lead to having a better detection probability vs. those that allow for more units to be sampled, it is better to increase detection probability and survey fewer units. Future simulations will address the power to detect increases in population size in addition to declines, and we will attempt to compare power to detect declines using abundance estimation with that obtained using occupancy estimation.

WILDLIFE RESEARCH REPORT

ASSESSING THE EFFICACY OF MONITORING WOLVERINE ON A REGIONAL SCALE USING OCCUPANCY AND ABUNDANCE ESTIMATION.

JACOB S. IVAN

P. N. OBJECTIVE

Assess power for detecting trends in wolverine population growth using occupancy and abundance estimation.

SEGMENT OBJECTIVES

1. Build code to simulate realistic distribution and space use of wolverine on the landscape.
2. Build code to realistically simulate sampling the wolverine population using an occupancy framework.
3. Build code to analyze data “collected” via occupancy surveys.
4. Summarize results of 100s of iterations of randomly generated wolverine distributions and subsequent occupancy surveys; plot power to detect trends against various scenarios intended to reflect the range of conditions expected for both the sampling and process portions of the simulation.

INTRODUCTION

The wolverine (*Gulo gulo*) has a circumpolar distribution comprised mostly of tundra and boreal forest. However, its current range also extends southward in peninsular fashion to the Cascades and Rocky Mountains of the conterminous United States. Recently the U.S. Fish and Wildlife Service ruled that the North American wolverine in the contiguous U. S. was a candidate for protection under the Endangered Species Act (U.S. Fish and Wildlife Service 2010). Therefore, considerable interest exists in identifying monitoring schemes capable of detecting declines in wolverine populations over a large scale. Colorado Parks and Wildlife (CPW) has expressed interest in potentially pursuing a wolverine reintroduction, and monitoring program would be an integral part of such an effort. Additionally, with minor modifications, the simulation approach outlined here could be used to inform current Canada lynx (*Lynx canadensis*) monitoring efforts in Colorado. Thus, the work described here holds benefits for wolverine conservation in general as well as current and future CPW projects.

Estimating abundance or occupancy are 2 means around which a monitoring scheme for wolverines could be constructed. Within these general approaches, there are numerous sampling methods that could be employed in the field. For instance, individual identification necessary for abundance estimation can be obtained from pelage patterns (Royle et al. 2011), scat samples (Flagstad et al. 2004, Ulizio et al. 2006), hair snags (Mulders et al. 2007), or a combination of methods (Magoun et al. 2011). Similarly, occupancy information can be obtained via aerial track surveys (Magoun et al. 2007, Gardner et al. 2010), remote cameras (R. Inman, Wildlife Conservation Society, unpublished data) or any genetic sampling technique. In all cases, the models used to estimate abundance and/or occupancy are the same; field methods only change the probability of detecting (and potentially identifying an individual(s) and the cost of obtaining those detections. Our aim was to use simulation to generically estimate power for detecting population declines of interest in the Northern Rockies. Simulations are spatially explicit, sampling occurs randomly and we are currently using robust design occupancy models to look at power. Here we report only on our initial simulations using occupancy estimation.

METHODS

Simulated landscape and wolverine distribution

All simulations were programmed in R (R Core Development Team 2011), with calls to C++ (Stroustrup 1997), RMARK (Laake and Rexstad 2011), and MARK (White and Burnham 1999) as necessary. The simulation landscape included Idaho, western Montana, and northwest Wyoming (Figure 1). We overlaid this landscape with a raster dataset depicting "persistent spring snow" as this layer adequately captures the bioclimatic niche of wolverines (Copeland et al. 2010). Each 500-m pixel in the raster could take values 1 to 7 depending on the number of years from 2000-2006 that snow was present between April 24 and May 15 in that pixel. At the beginning of each iteration of the simulation, we randomly dispersed home range centers across the landscape subject to the following constraints based on wolverine ecology (Figure 2):

1) Home range centers (points) were required to fall within the spring snow layer.
2) Male home range centers were required to be >12.5 km apart.
3) Female home range centers were required to be >8.5 km apart.
4) Female home range centers could fall within male buffers, and transient males could fall within resident male or female buffers.

Once home range centers were distributed, we temporarily assigned each animal a bivariate normal utilization distribution scaled to match UD estimates from the literature. To impart more realism in these UDs, we multiplied the bivariate normal kernel for each animal by the underlying spring snow layer, then divided each pixel value in the resulting product by the total of all values for that animal to recreate a probability distribution. Functionally this process produces a center-weighted UD in which mass is piled up over pixels with higher values of persistent spring snow. Each animal's UD was different depending on the underlying configuration of spring snow.

We began each simulation with 200 males, 200 females, and 100 transients for a total of 500 wolverines in the Northern Rockies landscape. Our simulated population size was based on available wolverine abundance information and expert opinion. We then simulated a 10%, 20%, or 50% decline in this population over 10 years by randomly removing individuals from the landscape at each time step.

Simulated Sampling

To simulate collection of occupancy data, we overlaid a sampling grid of 225km^2-cells (n = 385 total cells) across the landscape. This cell size corresponds roughly to the home range size of female wolverine. At the beginning of each year, we computed the probability of at least 1 wolverine being available to sample in each cell on any given occasion for each cell in sampling grid:

where *w* = total number of wolverines in the simulation. For each visit within a given year, we drew a random uniform number (i.e., U(0,1)) and compared this number to the product: *p*(≥1 wolverine available)*p*(wolverine detected | available). If the random number was less than this product, wolverine were detected in that cell on that visit (occasion) and we entered a "1" in the encounter history for that cell-occasion. Otherwise, we entered a "0." We proceeded to sample in this manner for each visit to each cell for each year of the simulation. This results in a vector of 0s and 1s (i.e., an encounter history) for each cell that is 10x in length where "x" is the number of visits made during each of 10 years. For each unique landscape and declining wolverine population, we created several different datasets using this general sampling process. We specified detection probability, *p*(wolverine detected | available), to be either 0.2 or 0.8 and specified the number of visit to each cell in a year to be 2, 3, 4, 5, 6, or 7. This results in 2 × 6 = 12 datasets for each simulated population decline. We also considered the situation in which surveys could only be accomplished every other year, which resulted in another 12 datasets in which no data were collected during even years.

Analysis of simulated data

For each simulated dataset we used the R (R Development Core Team 2011) package RMARK (Laake and Rexstad 2011) to construct a robust design occupancy model (MacKenzie et al. 2006, p. 183-224) for fitting in program MARK(White and Burnham 1999). We allowed the occupancy (use) parameter (ψ_t) as well as colonization (γ_t) and extinction (ε_t) to vary through time in an unconstrained manner, but constrained detection probability (*p*) to be constant to reflect how it was simulated. This resulted in 10 estimates of probability of occupancy, or use, from each dataset. We then fit a random effects trend model to these 10 data points (also using the RMARK interface for MARK to account for covariance between estimates; Figure 4), and retained the slope of the trend line along with 95% confidence interval for that slope. When the 95% confidence interval for the slope of the trend line did not include zero, we considered a trend detected, otherwise a trend was not detected. The number of times a trend was detected out of the total simulations is an estimate of the power of the approach to identify the specified declines given the number of visits and detection probability specified.

RESULTS

As expected, initial results indicate that occupancy estimation should work well for detecting large declines (50% decline over 10 years, $\lambda = 0.933$) when detection probability is high ($p = 0.8$). Under these conditions, power was 80% when sampling 50 units, regardless of the number of visits, and approached 100% when sampling 100 units (Figure 5, "continuous sampling" panels). Power declined some, but was still respectable, even when detection probability was low ($p = 0.2$). In that case a power of 0.8 could be achieved with 4-6 visits to 100 sample units. Power to detect a 20% decline over 10 years ($\lambda = 0.977$) was diminished, however, especially when detection probability was low. For instance, in order to achieve 80% power, even with high detection probability, would require surveys in an estimated 300 sample units. There is no realistic chance of detecting minor declines (e.g., 10% over 10 years, $\lambda = 0.989$) using occupancy estimation (Figure 5).

Not surprisingly, power declines when sampling occurs every other year rather than annually (Figure 5, "gap sampling" panels). However, if detection probability is high, adequate power (0.8) can be achieved to detect a 50% decline over 10 years if such a scheme is implemented in a reasonable number of sample units (100), even with as few as 2-3 visits. Ability to detect smaller declines (20% or 10% over 10 years) is poor regardless of detection probability, number of sample units or number of visits (Figure 5, "gap sampling" panels).

Generally, we found that when detection probability is high, power increases as number of visits to each sample unit increases from 2 to 3 per survey season, but making more than 3 visits does not increase power substantially. However, when detection probability is low, gains can be realized by making more visits. This result re-confirms a well-documented phenomenon unique to occupancy estimation (MacKenzie et al. 2006, p. 168). Also, if confronted with design tradeoffs that lead to having a better detection probability vs. those that allow for more units to be sampled, it is always better to increase detection probability and survey fewer units.

DISCUSSION

Our initial simulations suggest that occupancy estimation may work well in a monitoring context if the survey techniques employed have relatively high detection probability and interest lies only in detecting sharp declines in the population. Future work on this project will focus on determining the effects of varying the size of sample units, using alternate starting population sizes, detecting increasing trends rather than decreasing, and making sure that detection and occupancy estimates match well with recently collected pilot data (R. Inman, unpublished data). Additionally, we will incorporate cost functions into the modeling effort and investigate how well occupancy estimation compares to abundance estimation, which can be accomplished by sampling with hare snares or by photographing unique throat patch patterns via remote camera

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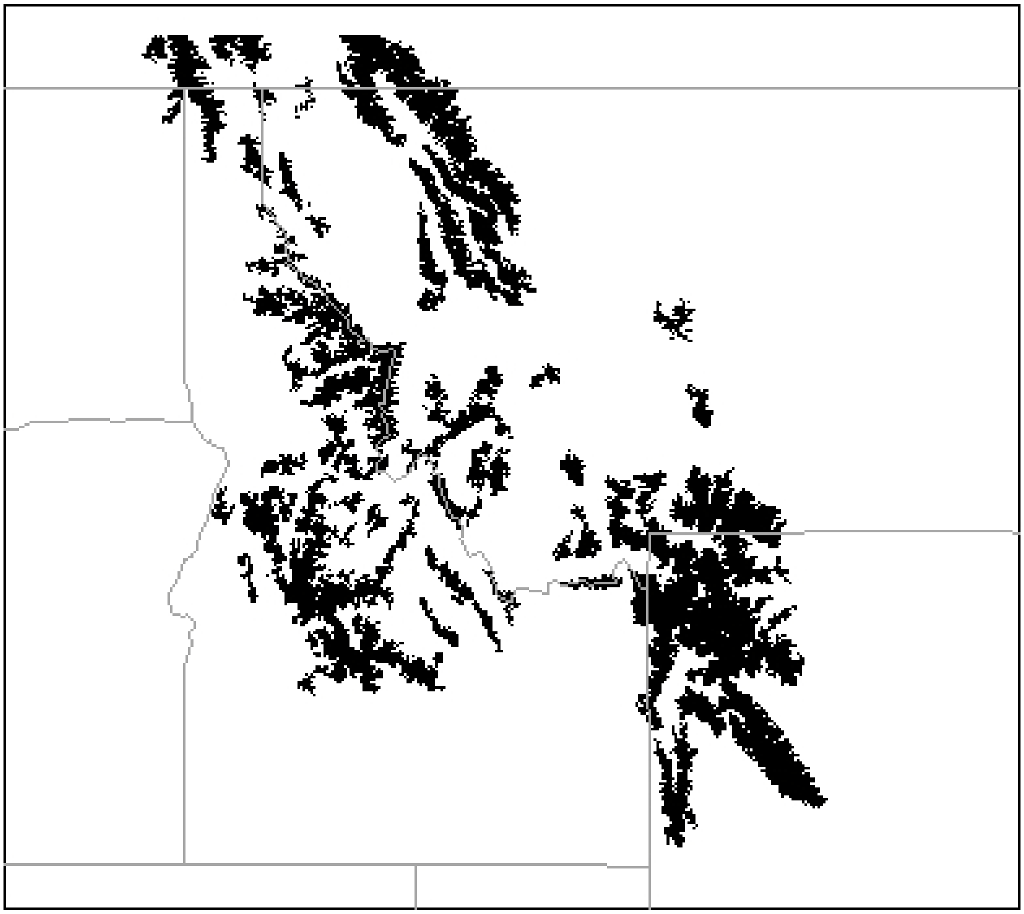

Figure 1. Study area for simulation including montane regions of Idaho, western Montana, and northwest Wyoming. Black polygons indicate primary wolverine habitat defined as areas with snowcover between April 24 and May 15 during at least 1 year from 2000-2006.

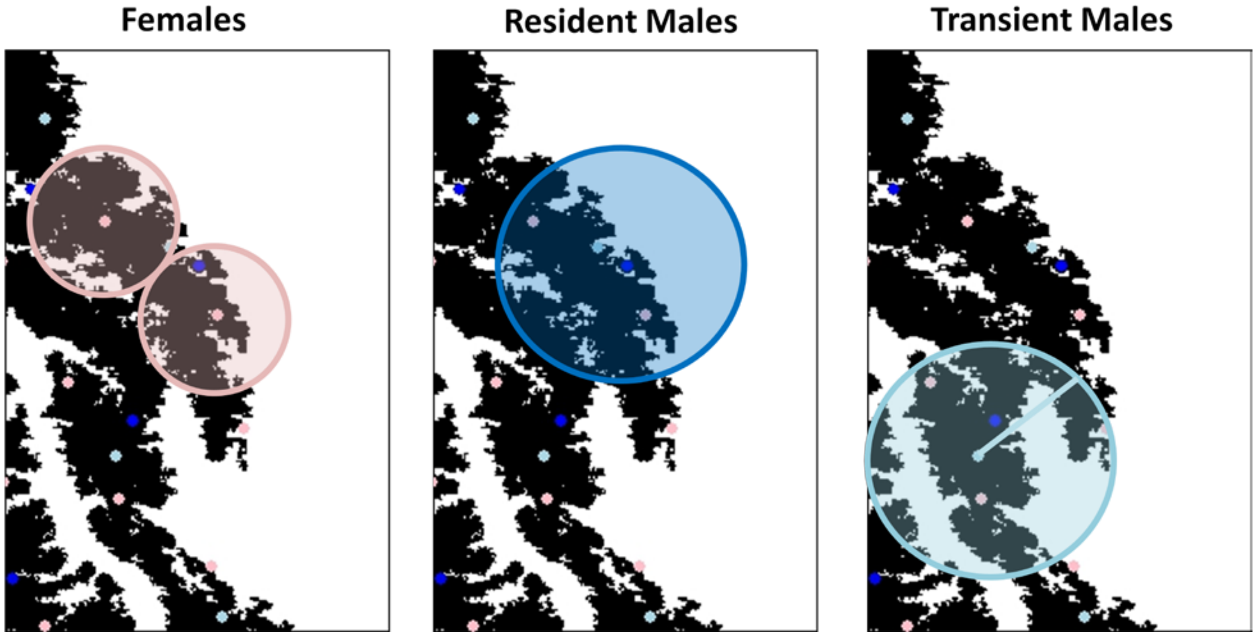

Figure 2. Example distribution of home range centers for male, female, and transient wolverines on the virtual landscape. Home range centers were required to fall within the spring snow layer, and intrasexual territorialty was enforced, except for transient individuals. The buffer around male home range centers was 12.5 km; female buffers were 8.5 km.

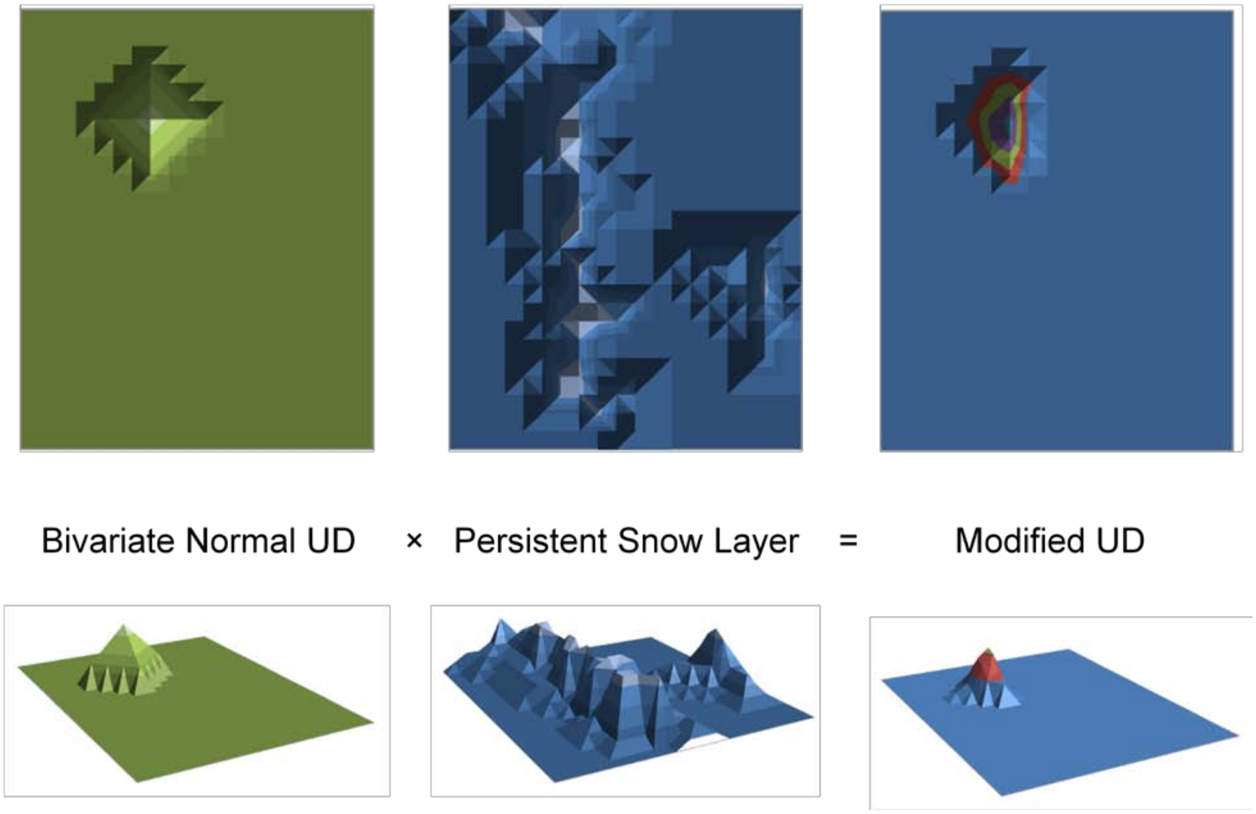

Figure 3. Simulated utilization distributions (UDs) for each individual were created by positioning a bivariate normal UD directly over each home range center (see Figure 2) then multiplying by the underlying persistent snow layer to form a modified, more realistic UD unique to each individual.

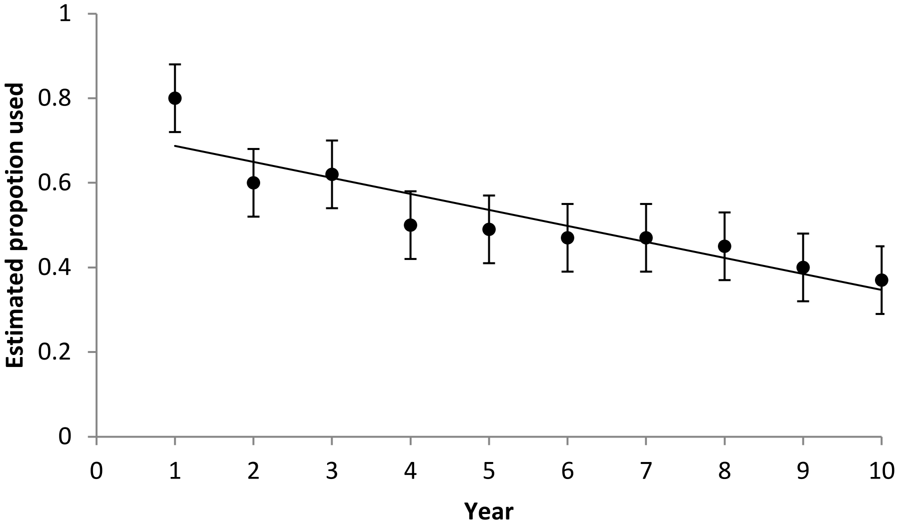

Figure 4. Example output from a single simulation: estimates of occupancy over a 10-year period fitted with a linear random effects model. If the 95% confidence interval on the slope of the linear trend did not include zero, then we concluded that a trend had been detected. The percentage of iterations in which trends were detected out of the total iterations provided a measure of power.

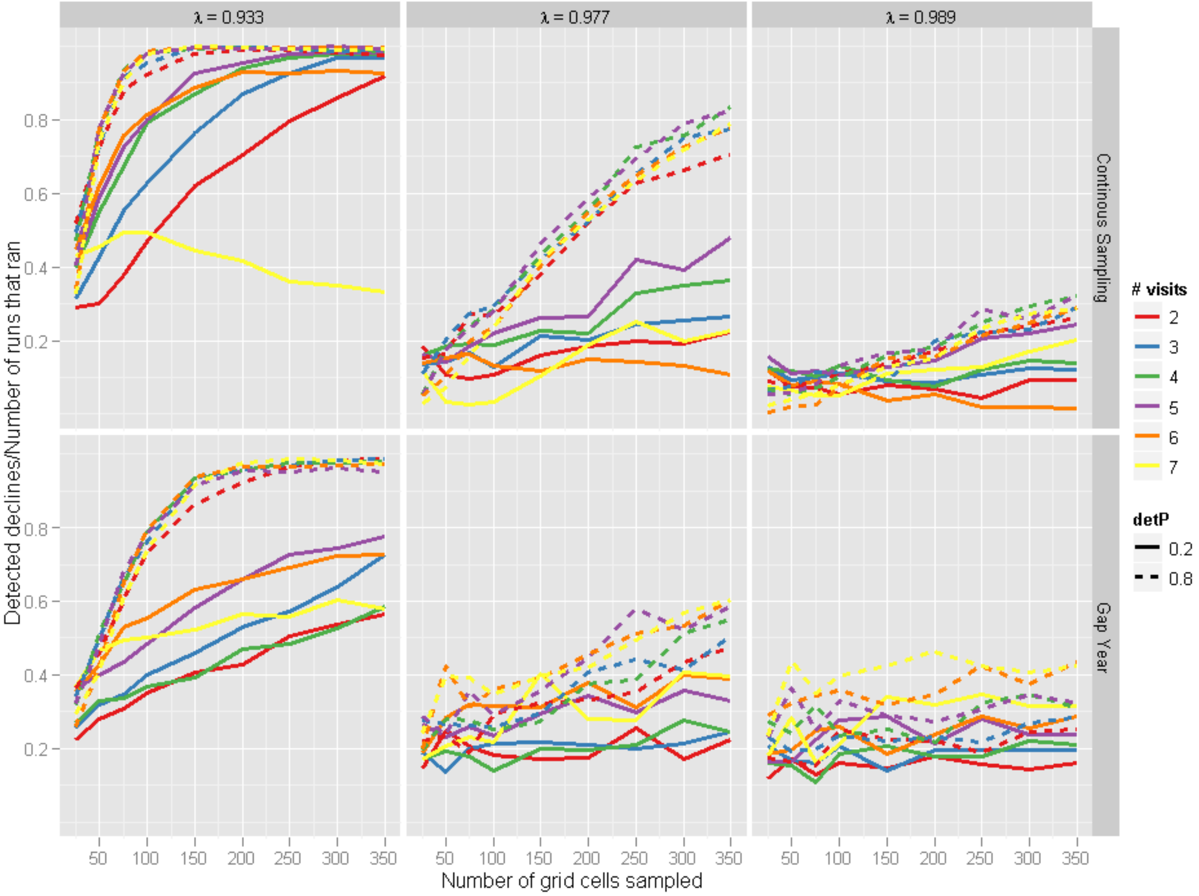

Figure 5. Power to detect population declines of 50% (λ=0.933), 20% (λ=0.977), and 10% (λ=0.989) using occupancy estimation. Curves represent 2 levels of detection probability (0.2 and 0.8) and varying number of visits annually to a sampled unit (2, 3, 4, 5, 6, 7). Top 3 panels depict estimates of power when occupancy surveys occur annually; bottom 3 panels depict power when surveys are conducted biannually. Note that the lowest power to detect a 50% decline with annual sampling is apparently realized with 7 visits to each sampling unit. This result is counterintuitive, and likely due to a coding error. It will be addressed in future simulations.

Colorado Division of Parks and Wildlife
July 2010–June 2011

WILDLIFE RESEARCH REPORT

State of:	Colorado	:	Division of Parks and Wildlife
Cost Center:	3430	:	Mammals Research
Work Package:	0670	:	Lynx Conservation
Task No.:	N/A	:	Predicted lynx habitat in Colorado
Federal Aid Project No.	N/A		

Period Covered: July 1, 2010 – June 30, 2011

Author: J. S. Ivan

Personnel: M. Rice, P. Lukacs, T. Shenk (National Park Service), D. Theobald (Colorado State University), E. Odell

All information in this report is preliminary and subject to further evaluation. Information MAY NOT BE PUBLISHED OR QUOTED without permission of the author. Manipulation of these data beyond that contained in this report is discouraged.

ABSTRACT

In an effort to restore a viable population of federally threatened Canada lynx (*Lynx canadensis*) to the southern portion of their former range, 218 individuals were reintroduced into Colorado from 1999–2006 (Devineau et al. 2010). In 2010, the Colorado Division of Wildlife (now Colorado Parks and Wildlife [CPW]) determined that the reintroduction effort met all benchmarks of success, and that a viable, self-sustaining population of Canada lynx had been established (Shenk and Kahn 2010). The purpose of this project was to develop a statewide predictive map of relative lynx use based upon location data collected during the reintroduction period. To build the map, we divided the state into 1.5 km × 1.5 km cells and tallied the number of locations in each cell. We then fit models to these count data using vegetation, elevation, slope, wetness, and degree of human development in each cell as predictor variables. We produced models for both summer and winter habitat use. We found that regardless of season, lynx were positively associated with spruce/fir (*Picea engelmannii*/*Abies lasiocarpa*), mixed spruce/fir, aspen (*Populus tremuloides*), elevation and slope; they were negatively associated with distance to large forest patches. During summer, lynx use of lodgepole pine (*Pinus contorta*) stands was predicted to increase. Lynx were predicted to avoid montane forest (Douglas-fir [*Pseudotsuga menziesii*], Ponderosa pine [*Pinus ponderosa*]), and areas near high traffic volume road segments, especially during summer. These maps of predicted lynx use should aid land managers in prioritizing areas for conservation, development, and resource extraction with respect to potential impacts to lynx and lynx habitat.

WILDLIFE RESEARCH REPORT

PREDICTED LYNX HABITAT IN COLORADO

JACOB S. IVAN

P. N. OBJECTIVE

Use location data collected during Canada lynx (*Lynx canadensis*) reintroduction to build a model of relative use, then apply this model statewide to produce a predictive map of relative lynx use for Colorado.

SEGMENT OBJECTIVES

1. Compile and filter raw location data to isolate highest quality lynx locations.
2. Compile spatial data for use as covariates for the model (e.g. vegetation type, elevation, etc).
3. Build a series of candidate models to explain variation on locations across the landscape using covariate data layers.
4. Model-average predictions from all candidate models to produce a maps of predicted relative use for Colorado.

INTRODUCTION

In an effort to restore a viable population of federally threatened Canada lynx (*Lynx canadensis*) to the southern portion of their former range, 218 individuals were reintroduced into Colorado from 1999–2006 by the Colorado Division of Wildlife (now Colorado Parks and Wildlife [CPW], Devineau et al. 2010). In 2010, CPW determined that the reintroduction effort met all benchmarks of success, and that a viable, self-sustaining population of Canada lynx had been established (Shenk and Kahn 2010). Attainment of this goal is a conservation success, but it has also created a series of issues for land management agencies to consider as they plan changes to the landscape. These issues require knowledge of the types of landscapes and forest stands important for reproduction, movement, dispersal, and general home range use by lynx.

As a first step toward providing this information, Theobald and Shenk (2011) conducted an analysis to describe the types of areas that were known to be used by re-introduced lynx. Specifically, they used LoCoH (Getz and Wilmers 2004, Getz et al. 2007) methods to create a population-level utilization distribution (UD, a probability surface of lynx occurrence) for lynx in Colorado. They then summarized landscape attributes within the 90% isopleth (i.e., polygon(s) containing 90% of the probability surface) of this UD. This work provides valuable information regarding the types of areas that were *known* to be used by lynx from 1999 to 2010. By nature of the data collection and research focus, most of this “use” information was derived from core areas in the San Juan Mountains of southwest Colorado and Sawatch Range in the central part of the state.

The purpose of the current project is to extend the work of Theobald and Shenk (2011) by producing a map of *predicted* lynx use on a *statewide* scale. Such an exercise will identify areas within Colorado that should contain high quality lynx habitat, regardless of whether or not it was used by the sample of radio-telemetered individuals tracked during reintroduction research. Both works have strengths and weaknesses, but together they provide tools for prioritizing areas for conservation, development, and resource extraction with respect to potential impacts to lynx.

METHODS

Location Data

Location data were collected from reintroduced lynx using 2 types of telemetry devices. All lynx released into Colorado, and those subsequently captured or re-captured, were fitted with a traditional VHF transmitter. VHF data were collected via telemetry from fixed-wing aircraft at approximately weekly intervals when research was ongoing during winter (approximately December – March) and reproductive seasons (May – June), but less often otherwise. Beginning in April 2000, released and captured lynx were outfitted with dual VHF-Argos satellite collars. In addition to sampling via fixed-wing aircraft, the satellite portion of these collars transmitted repeatedly for 12 hours, 1 day per week, year-round. Nearly 40,000 combined locations were collected between VHF and satellite sampling. These data were originally intended for assessing the success of the reintroduction and served CDOW well in estimating survival, productivity, and dispersal. They were not intended for use in constructing a predictive map of habitat use. We used only the best subset of these data following the filters applied by Theobald and Shenk (2011). Specifically, locations obtained during the first 6 months post-release were removed in order to exclude atypical movements made by animals that had not yet settled into home ranges. Next, poor precision satellite data (e.g., Argos location codes A, B, Z, 0 which do not have associated error estimates) were filtered out because they were too unreliable to be informative of lynx habitat use. We minimized dependence among locations (satellite collars transmitted several times per day, and a VHF location could have been obtained during the same day as well) by retaining only the most precise location for each lynx on a given day. When ties occurred, a single location was randomly selected from among the most precise locations. Finally, we discarded all data from lynx that were located fewer than 30 times over the course of the study.

Predictor variables

After filtering the location data, we assembled raw covariate data. We obtained housing density (HDENS, units per 1000 ha), road density (RDENS, km/km^2 – all roads), slope (SLOPE), elevation (ELEV), topographic wetness (TW), distance to high-volume road segments (D10K, annual average daily traffic volume > 10,000 vehicles), and distance to mesic forest patches >50 ha (D50HA) from Theobald and Shenk (2011). We also downloaded vegetation data from the Colorado Vegetation Classification Project (CVCP, Colorado Division of Wildlife, U.S. Department of Interior Bureau of Land Management, U.S. Forest Service. http://ndis.nrel.colostate.edu/coveg/). CVCP is geographically limited to Colorado, but it accurately depicts many vegetation types that may be important to lynx including riparian zones and willow. Other vegetation data sources (i.e., LANDFIRE) have the advantage of a larger spatial extent, but classification of these non-forest vegetation types is not as detailed. We reclassified the 114 vegetation types in CVCP into 17 classes to simplify the number of covariates available for analysis (Appendix 1). Next, we divided the western portion of Colorado into 1.5 km × 1.5 km cells, which corresponds to 1 SD of the error distribution for the most imprecise (satellite) locations retained for analysis, as well as the smallest 90% UD observed for an individual lynx (Theobald and Shenk 2011). We computed the proportion of different vegetation types in each cell as well as mean SLOPE, ELEV, TW, HDENS, RDENS, D10K, and D50HA. We excluded cells with mean elevations <2,438m (8000 ft), assuming such cells do not provide habitat for lynx. This cutoff is consistent with previous literature (McKelvey et al. 2000, Ruediger et al. 2000), and over 99% of locations from our dataset were above 2,438m. We then standardized each covariate using all cells we intended to make predictions for. To maximize precision of parameter estimates and guard against erroneous predictions later on, we computed a correlation matrix between the potential explanatory variables but none were highly correlated (correlation coefficients were all <0.52 for covariates listed here).

Analysis

The response variable of interest for our models was the number of locations per individual in each cell, which we sought to predict using landscape attributes of the cells. We only used cells with ≥1 location for the purpose of constructing models. Excluding cells with no locations (zero counts) results in models that reflect relative use by lynx rather than resource selection. Thus in the generation of the model, we avoided delineation of what was available and suitable to lynx but never used (i.e., we avoided decisions regarding how many zero-count cells to include in the dataset and where they should come from on the landscape), which is a criticism of resource selection approaches. Furthermore, given ~10 years of work including weekly locations on hundreds of animals, we argue that nearly all cells in the Core Study Area that were suitable and available included ≥1 lynx location. This approach does, however, warrant the use of zero-truncated probability models to avoid possibly introducing bias in parameter estimates (Zuur et al. 2009, p. 269). In addition, we expected the data to be over-dispersed (variance of the counts was expected to be larger than the mean), we knew the number of locations collected per animal varied considerably, and we anticipated spatial autocorrelation in the residuals. To evaluate these assertions and determine the best model structure for our data, we successively compared the fits of a basic Poisson generalized linear model (GLM), negative binomial GLM, zero-truncated negative binomial (ZTNB), and ZTNB with an offset. We compared the fit of these alternate structures using Akaike's Information Criterion (AIC, Burnham and Anderson 2002) and found that fitting a basic negative binomial GLM was an improvement over a Poisson (ΔAIC = 700.4), ZTNB was an improvement over the negative binomial (ΔAIC = 6463.0), and ZTNB with an offset provided the best fit (ΔAIC = 53.7). Thus, we used a ZTNB with an offset as the base model structure. We fit all models using the VGAM package (Yee 2010, 2011) in R (R Core Development Team 2011). To assess spatial autocorrelation we computed a variogram using the gstat package (Pebesma 2004) and standardized residuals from a highly parameterized model (including all covariates below; Figure 1). We found minimal autocorrelation, so we proceeded to build ZTNB models absent spatial structure in the error term. Within the general ZTNB model structure, we specified the candidate model set by including combinations of covariates for modeling the mean count for each cell as follows:

1) Lynx are associated with conifer forests and deep snow, and they rely heavily on snowshoe hares. In the Southern Rockies, lynx occur largely in conifer stands within the sub-alpine zone (Aubry et al. 2000). Therefore, we included proportion spruce/fir (SF, *Picea engelmannii*/*Abies lasiocarpa*,), mixed spruce/fir (MIXSF, spruce/fir mixed with Douglas-fir [*Pseudotsuga menziesii*], aspen [*Populus tremuloides*], and/or lodgepole pine [*Pinus contorta*], distance to forest patch >50ha (D50HA), ELEV, and SLOPE in every model. We expected positive associations with each of these covariates except D50HA, which we expected to be negative.

2) Research conducted during the reintroduction of lynx into Colorado focused primarily in the southern portion of the state. Lodgepole pine (LODGE) occurs only in the northern portion of the state, so we know relatively little regarding the importance of this vegetation type with respect to habitat use by lynx. Therefore, we included a LODGE effect in some models, but when LODGE entered as a covariate, we also included a LODGE × latitude (NORTH) interaction to attempt to account for the distribution of this forest type in Colorado. Thus, lodgepole pine was allowed to be an important predictor of lynx use (or not) depending on latitude.

3) Vegetation types other than spruce/fir occur in or adjacent to the subalpine zone. We know relatively little about how lynx use these types but they may be important intermittently and/or as travel corridors. Therefore, we also built models that included combinations of montane forest (MONFOR: Douglas-fir, Ponderosa pine [*Pinus ponderosa*], and mixed Doug-fir/ponderosa pine), aspen (ASPEN), willow (WILLOW), and montane shrub (MONSHB: Gambel oak [*Quercus gambelii*], serviceberry [Amelanchier utahensis], and snowberry [*Symphoricarpos* sp.]).

4) Though lynx are considered a high elevation species, we opted to exclude “alpine” in any model because lynx are forest-dwelling, and there are few opportunities to manage structure of alpine areas, which included both alpine tundra and rock/snow/ice.

5) Lynx are often considered reclusive. Thus, covariates representing human development might be important predictors of habitats used (or not used) by lynx, and we initially considered HDENS, RDENS, and D10K as potential covariates to include in the model set. However, initial model-fitting resulted in HDENS and RDENS having slightly positive effects on lynx locations (but confidence intervals on these slopes were largely centered on zero indicating the effect was negligible), which is probably an artifact of the trapping/collaring effort that often occurred near roads due to logistical considerations. Many cells outside of those used to construct the models had HDENS and RDENS scores that were orders of magnitude above those used to construct the models. Thus, when projected to the entire set of cells covering western Colorado, these models predicted the best lynx habitat in highly developed, urban areas with high road density. Given this implausible result, we excluded HDENS and RDENS from the analysis. We retained D10K because high volume road segments occurred throughout broad areas used by lynx (nearly every state highway has high volume segments) and it did not result in completely implausible results. We expected counts of lynx locations to be positively associated with distance to high traffic volume road segments.

6) TW was excluded from all models after initial model-fitting produced a result similar to HDENS and RDENS. TW was positively associated with lynx locations, which seems reasonable, but when projected to the expanse of western Colorado, the best lynx habitat was predicted in heavily irrigated agricultural areas, residential lawns, and lakes. These features had TW values that were orders of magnitude larger than any forest-dominated cell. Note that this phenomenon, predicting beyond the range of data used to build the model, can be risky, and it may have operated similarly on other variables but went undetected.

7) Lynx often make long-distance movements outside of the winter season, and these movements may include use of many types of vegetation. Therefore, we fit the model set to summer locations (April through October) and then to winter locations (November through March). Seasonal definitions were based on mean daily movement patterns of telemetered lynx (Theobald and Shenk unpublished data). We expected that the association between lynx locations and vegetation types other than SF and MIXSF would vary with season, with more use of these perceived secondary types during summer.

In summary, our model set included all combinations of 5 vegetation types (LODGE, MONFOR, ASPEN, WILLOW, MONSHB) and D10K. Each combination was always paired with the base covariates (SF, MIXSF, ELEV, SLOPE, D50HA) listed in 1) above. This resulted in $2^6 = 64$ models. We used Akaike’s Information Criterion (AIC, Burnham and Anderson 2002) to determine which model structures best explained variation in lynx locations, to assess the importance of each covariate, and to model-average predictions of lynx use for each cell across all models. Predictions were defined as the probability of observing at least 10 locations in a cell over a hypothetical 10-year sampling period, which corresponds to an average of 1 location per year over the time frame of the actual data generating process. We color-coded predictions into 10 quantiles for display such that each color represents 10% of the total (i.e., the darkest red represents the predicted best 10% of cells, dark red plus deep orange represent the predicted best 20% of cells, etc.)

RESULTS

The final winter dataset consisted of 3,915 locations from 68 individuals (min = 30 locations/lynx, max = 113, mean = 57.6). Winter cell counts ranged from 1 to 29 (mean = 2.3). Summer data consisted of 5,464 locations from 74 individuals (min = 30, max = 178, mean = 73.8). Summer cell counts ranged from 1 to 36 total lynx locations (mean = 2.8).

Predicted Winter Use

As expected, relative predicted use by lynx during winter months was negatively associated with D50HA and positively associated with SF, MIXSF, ELEV, and SLOPE (Table 1). Of these associations, SF was strongest (largest magnitude and 95% confidence interval [±2×SE] was well away from zero), followed by ELEV, MIXSF, and D50HA, respectively. The parameter estimate for SLOPE was small and its 95% CI substantially overlapped zero in all models. Thus it was not important in explaining variation in predicted habitat use. Of the covariates that were not included in every model, ASPEN was strongly, positively associated with use and was the only effect in this group that was clearly different from zero. MONSHB was negatively associated with predicted lynx use, but evidence for this effect was weak. WILLOW, MONFOR, and D10K were somewhat positively associated with lynx use, but evidence for these effects was relatively weak as well. LODGE and NORTH did not appear in any of the top models (cumulative AIC weights = 0.12).

The winter predictive map reflects the strong effect of SF. Arbitrarily defining the top 20% of predictions as high quality lynx habitat, there are 1,869,975 ha of such habitat in Colorado. Most of this is predicted to occur in the southern part of the state in the San Juan, Culebra, and Wet Mountain Ranges (Figure 2). In the central portion of the state, high predicted use is expected in the northern Sawatch and West Elk Ranges, along with Grand Mesa. The Park Range and Flat Tops comprise the best predicted winter lynx habitat farther north (Figure 2).

Predicted Summer Use

Associations between relative predicted summer use and SF, MIXSF, ELEV, SLOPE, and D50HA were similar to those observed during winter (Table 2). However, the association with SLOPE was much stronger (larger effect and 95% CI indicated clear separation from zero) during summer, possibly due to den site selection and attendance during this time of year. The association with D50HA was slighter stronger as well. Of the covariates not included in every model, MONFOR and MONSHB were negatively associated with lynx locations; LODGE, NORTH, ASPEN, WILLOW, and D10K were positively associated. The effects of MONFOR, ASPEN, and D10K were substantially different from zero based on 95% CIs. Effects of other covariates were not clearly different from zero.

The summer predictive map reflects more dispersed predicted use by lynx with LODGE, NORTH, and the LODGE × NORTH interaction playing a larger role (Figure 3). The central and southern Sawatch Range in central Colorado is predicted to have more use than during winter, whereas use on Grand Mesa is predicted to decline. In the northern part of the state, lynx use is predicted to shift more toward the Medicine Bow and Front Ranges. Using the same definition as before, we predict 1,791,675 ha of high quality summer habitat in Colorado. The overlap between high quality summer and winter cells (as arbitrarily defined above) is ~95%.

DISCUSSION

The data analyzed here were not collected for the purpose of constructing a predictive map and suffer from at least two shortcomings. First, the locations were not precise. We attempted to account for this imprecision by modeling at a 1.5 km scale, but matching covariates, response variables, and predictions at this scale reduces the clarity of relationships and weakens the modeling process. Second, the bulk of the reintroduction research effort, from which these data originated, was conducted in the southern and central portions of Colorado. Lodgepole pine only occurs in the northern 2/3 of the state, and is dominant there. Thus, predicting lynx habitat use in northern Colorado is difficult because the landscape is very different, yet we have little data available to help model lynx response to that landscape. That is, we are extrapolating beyond the range of covariates used to fit the models, which is tenuous. Caution should be exercised in interpreting results north of I-70.

In addition to issues regarding the location data, we also lack important vegetation data that could be crucial in making accurate predictions. Snowshoe hares (*Lepus americanus*) are tied to forests with dense understory cover throughout their range (Hodges 2000a;b), including Colorado (Dolbeer and Clark 1975, Zahratka and Shenk 2008, Ivan 2011). Given the close tie between hares and lynx, habitat use of the latter should be strongly tied to understory cover as well. However, we have no covariate data for understory. Our models treat all spruce/fir, mixed spruce/fir, and lodgepole forests equally, but the quality of these forests likely varies considerably. Additionally, pine beetle (*Dendroctonus ponderosae*) and spruce beetle (*Dendroctonus rufipennis*) epidemics throughout the state are drastically changing the structure and composition of current and future forests. Our predictions are based on forest composition prior to these outbreaks.

Despite these weaknesses, the predictive maps constructed here also have a distinct strength in that they were constructed objectively from rigorous mathematical models based on empirical data collected from wild lynx. They are the first such maps for Colorado. Results from this effort confirm relationships that were already known (e.g., lynx are strongly associated with high elevation spruce/fir and mixed spruce/fir forests but avoid lower elevation montane forests and montane shrublands), and highlight others that may be of interest. For instance, we found clear evidence that lynx use was positively associated with ASPEN during both summer and winter. It is unclear what the ecological relationship between the two might be and we have no causal evidence for ASPEN driving lynx use. However, this pattern is not a simple artifact of ASPEN occurring near SF or MIXSF – our preliminary vetting of potential covariates indicated that the correlation between ASPEN and SF or MIXSF was small and negative (-0.15 and -0.14, respectively). We also found evidence that lynx use of lodgepole forests may increase during summer, and that they tend to avoid areas near high traffic volume road segments, especially in summer.

The strengths of this analysis and resulting maps merit their inclusion as a tool for making land management decisions. However, inherent weaknesses of the data require the reader to exercise caution when interpreting results. These maps should be viewed as a compliment to expert opinion and existing maps produced by other means. When assessing habitat quality for lynx at a given project site, it is imperative that managers consider current stand characteristics (especially understory) in formulating land use plans or specific management recommendations relative to lynx.

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Table 1. Model selection results (top 10 of 64) and parameter estimates (SE) for zero-truncated negative binomial models fit to cell counts of Canada lynx locations collected during winter (November – March) 1999-2010, southwest and central Colorado, USA.

SF	MIXSF	D50HA	ELEV	SLOPE	LODGE	NORTH	LODGE: NORTH	MONFOR	ASPEN	WILLOW	MONSHB	D10K	AIC	ΔAIC	AIC Wt.	*K*
0.53 (0.07)	0.15 (0.08)	-1.1 (0.69)	0.24 (0.11)	0.07 (0.06)					0.28 (0.08)	0.06 (0.04)			4672.1	0.0	0.15	9
0.48 (0.06)	0.13 (0.07)	-1.09 (0.69)	0.29 (0.11)	0.04 (0.05)					0.26 (0.08)				4672.9	0.8	0.10	8
0.52 (0.07)	0.14 (0.08)	-1.09 (0.69)	0.21 (0.11)	0.07 (0.06)					0.28 (0.08)	0.07 (0.04)	-0.33 (0.38)		4673.2	1.1	0.09	10
0.53 (0.07)	0.17 (0.08)	-1.12 (0.69)	0.25 (0.11)	0.07 (0.06)					0.27 (0.08)	0.06 (0.04)		0.08 (0.09)	4673.2	1.1	0.09	10
0.48 (0.06)	0.15 (0.08)	-1.12 (0.69)	0.3 (0.11)	0.04 (0.05)					0.25 (0.08)			0.09 (0.09)	4673.8	1.7	0.06	9
0.54 (0.07)	0.16 (0.08)	-1.1 (0.69)	0.27 (0.13)	0.07 (0.06)				0.08 (0.22)	0.29 (0.08)	0.06 (0.04)			4673.9	1.9	0.06	10
0.47 (0.07)	0.12 (0.07)	-1.09 (0.69)	0.27 (0.11)	0.04 (0.05)					0.26 (0.08)		-0.29 (0.37)		4674.1	2.1	0.05	9
0.52 (0.07)	0.16 (0.08)	-1.12 (0.69)	0.22 (0.11)	0.07 (0.06)					0.28 (0.08)	0.06 (0.04)	-0.32 (0.38)	0.08 (0.09)	4674.3	2.2	0.05	11
0.49 (0.07)	0.14 (0.08)	-1.1 (0.69)	0.31 (0.13)	0.04 (0.05)				0.05 (0.22)	0.26 (0.08)				4674.8	2.8	0.04	9
0.54 (0.08)	0.18 (0.08)	-1.13 (0.69)	0.27 (0.13)	0.07 (0.06)				0.08 (0.22)	0.28 (0.08)	0.06 (0.04)		0.08 (0.09)	4675.0	3.0	0.03	11

Table 2. Model selection results (top 10 of 64) and parameter estimates (SE) for zero-truncated negative binomial models fit to cell counts of Canada lynx locations collected during summer (April – October) 1999-2010, southwest and central Colorado, USA.

SF	MIXSF	D50HA	ELEV	SLOPE	LODGE	NORTH	LODGE: NORTH	MONFOR	ASPEN	WILLOW	MONSHB	D10K	AIC	ΔAIC	AIC Wt.	*K*
0.47 (0.07)	0.11 (0.07)	-2.74 (0.7)	0.38 (0.12)	0.27 (0.05)	0.13 (0.11)	0.08 (0.1)	0.25 (0.12)	-1.65 (0.39)	0.2 (0.08)			0.2 (0.08)	6684.3	0.0	0.13	13
0.45 (0.07)	0.11 (0.07)	-2.75 (0.7)	0.34 (0.13)	0.26 (0.05)	0.11 (0.11)	0.08 (0.1)	0.24 (0.12)	-1.65 (0.4)	0.2 (0.08)		-0.66 (0.5)	0.2 (0.08)	6684.4	0.1	0.13	14
0.39 (0.06)	0.11 (0.06)	-2.76 (0.67)	0.19 (0.11)	0.24 (0.05)				-1.81 (0.39)	0.14 (0.08)		-0.87 (0.51)	0.15 (0.07)	6684.6	0.3	0.11	11
0.41 (0.06)	0.13 (0.06)	-2.77 (0.67)	0.23 (0.11)	0.25 (0.05)				-1.82 (0.39)	0.13 (0.08)			0.15 (0.07)	6685.9	1.6	0.06	10
0.34 (0.05)	0.07 (0.06)	-2.95 (0.67)	0.09 (0.1)	0.25 (0.05)				-1.84 (0.39)			-0.76 (0.49)	0.16 (0.07)	6686.0	1.7	0.06	10
0.4 (0.06)	0.08 (0.06)	-2.75 (0.67)	0.21 (0.11)	0.25 (0.05)				-1.78 (0.39)	0.15 (0.08)		-0.85 (0.5)		6686.2	1.9	0.05	10
0.47 (0.07)	0.12 (0.07)	-2.74 (0.7)	0.37 (0.12)	0.27 (0.05)	0.13 (0.11)	0.08 (0.1)	0.25 (0.12)	-1.65 (0.39)	0.2 (0.08)	0.01 (0.04)		0.2 (0.08)	6686.3	2.0	0.05	14
0.46 (0.07)	0.11 (0.07)	-2.74 (0.7)	0.33 (0.13)	0.27 (0.05)	0.11 (0.11)	0.07 (0.1)	0.24 (0.12)	-1.65 (0.4)	0.2 (0.08)	0.01 (0.04)	-0.67 (0.5)	0.19 (0.08)	6686.3	2.0	0.05	15
0.39 (0.06)	0.11 (0.06)	-2.77 (0.67)	0.2 (0.11)	0.24 (0.05)				-1.81 (0.39)	0.14 (0.08)	0 (0.04)	-0.86 (0.51)	0.15 (0.07)	6686.6	2.3	0.04	12
0.36 (0.05)	0.09 (0.06)	-2.94 (0.67)	0.13 (0.09)	0.25 (0.05)				-1.86 (0.38)				0.16 (0.07)	6686.8	2.4	0.04	9

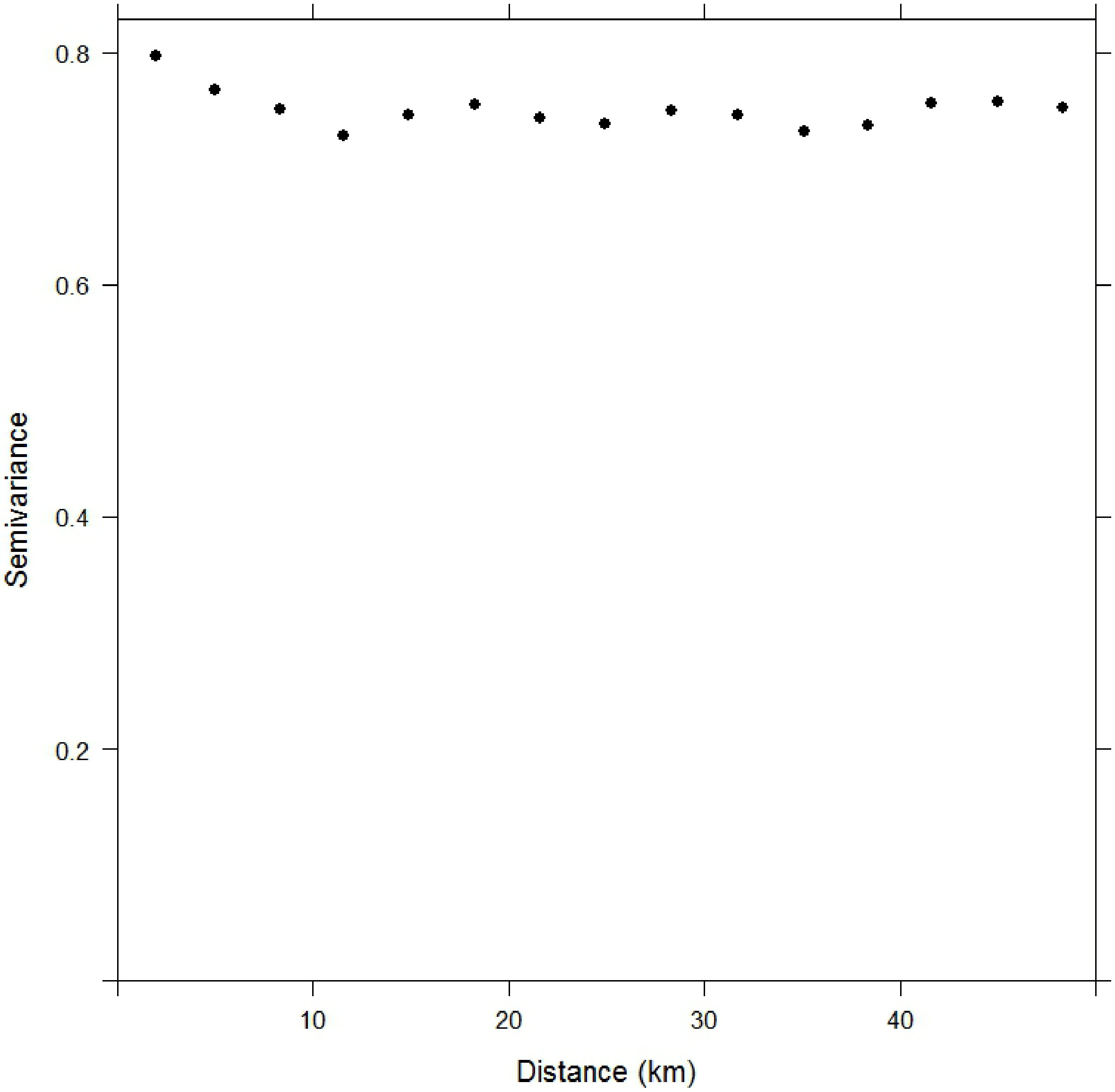

Figure 1. Variogram contructured using standardizied residuals from a highly parameterized model fit to count data of lynx locations within 1.5km × 1.5km cells, 1999-2011, southwestern and central Colorado. Variance among pairs of points is similar regardless of the distance separating them, indicative of a lack of residual spatial autocorrelation after fitting important covariate effects. Strong evidence of spatial autocorrelation in residuals would result in a graph with small variance between pairs points that are near to each other, and larger variance at greater distances (i.e., a monotonically increasing pattern).

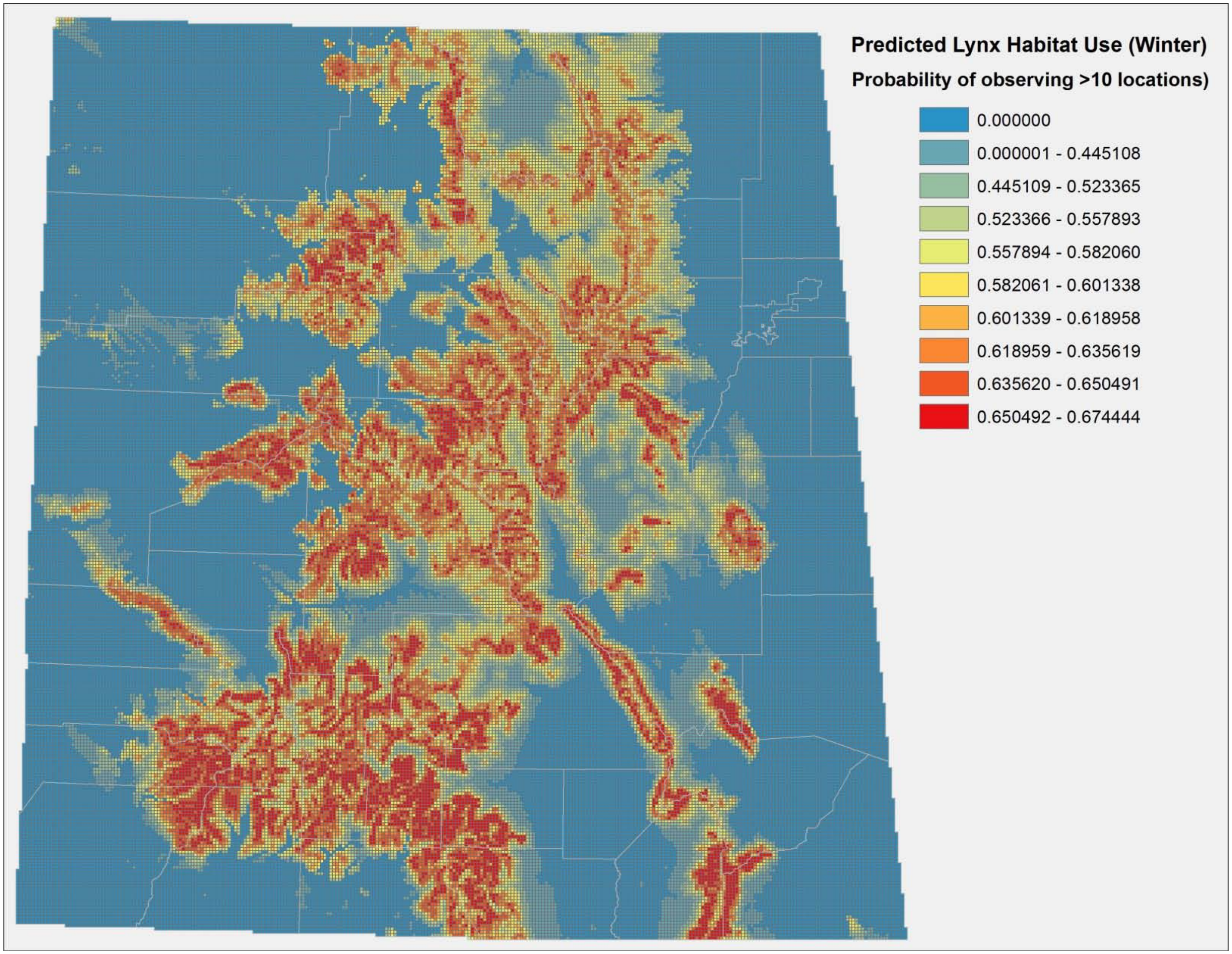

Figure 2. Predicted winter habitat use by Canada lynx in western Colorado. Predictions are probabilities of observing at least 10 locations within a 1.5 × 1.5km cell over a hypothetical 10-year sampling period. Predictions were averaged across 64 models constructed using all combinations of covariates of interest.

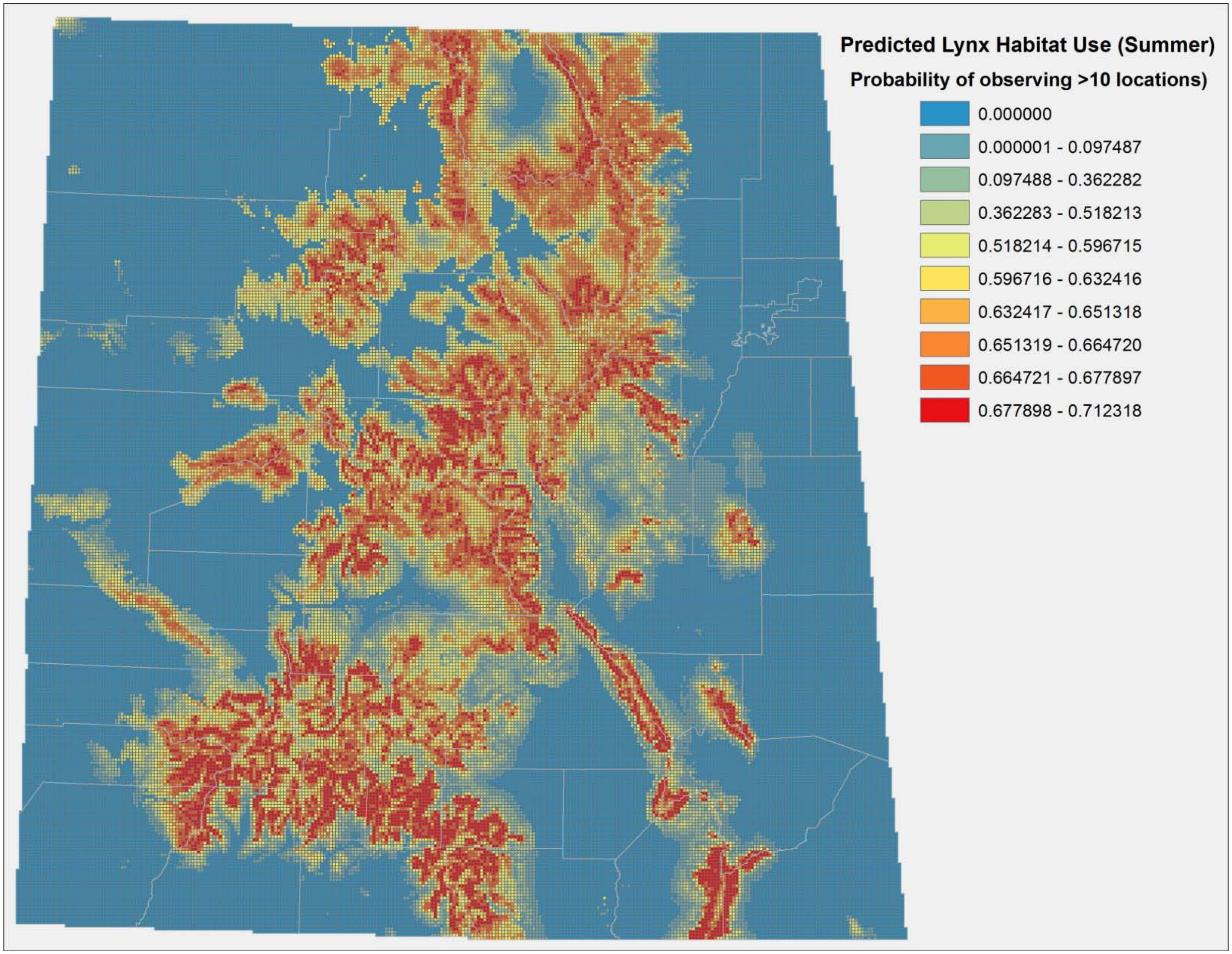

Figure 3. Predicted summer habitat use by Canada lynx in western Colorado. Predictions are probabilities of observing at least 10 locations within a 1.5 × 1.5km cell over a hypothetical 10-year sampling period. Predictions were averaged across 64 models constructed using all combinations of covariates of interest.

Appendix 1. Raster reclassification of CVCP dataset for use in lynx predictive map analysis.

Lynx Reclass	CVCP Value	Description
Null	0	Unclassified
2	1	Urban/Built Up
2	2	Residential
2	3	Commercial
1	4	Agriculture Land
1	5	Dryland Ag
1	6	Irrigated Ag
1	7	Orchard
4	8	Rangeland
4	9	Grass/Forb Rangeland
8.2	10	Snakeweed/Shrub Mix
4	11	Grass Dominated
4	12	Forb Dominated
4	13	Grass/Forb Mix
4	15	Mid-grass Prairie
4	16	Short-grass Prairie
14	17	Sand Dune Complex
4	18	Foothill and Mountain Grasses
4	19	Disturbed Rangeland
4	20	Sparse Grass (Blowouts)
8.2	21	Shrub/Brush Rangeland
8.2	22	Sagebrush Community
8.2	23	Saltbush Community
8.2	24	Greasewood
8.2	25	Sagebrush/Gambel Oak Mix
8.2	26	Snakeweed
8.1	27	Snowberry
8.1	28	Snowberry/Shrub Mix
8.2	29	Bitterbrush Community
8.2	30	Salt Desert Shrub Community
8.2	31	Sagebrush/Greasewood
8.2	32	Shrub/Grass/Forb Mix
8.2	33	Sagebrush/Grass Mix
4	34	Rabbitbrush/Grass Mix
8.2	35	Sagebrush/Mesic Mtn Shrub Mix
4	36	Grass/Misc. Cactus Mix
4	37	Winterfat/Grass Mix
4	38	Bitterbrush/Grass Mix
4	39	Grass/Yucca Mix
8.2	40	Sagebrush/Rabbitbrush Mix
10	43	Pinon-Juniper
10	44	Juniper
8.1	46	Gambel Oak
8.2	47	Xeric Mountain Shrub Mix
8.1	48	Mesic Mountain Shrub Mix
8.1	49	Serviceberry/Shrub Mix
3.1	50	Upland Willow/Shrub Mix

8.2	51	Manzanita
10	53	PJ-Oak Mix
10	54	PJ-Sagebrush Mix
10	55	PJ-Mtn Shrub Mix
10	56	Sparse PJ/Shrub/Rock Mix
10	57	Sparse Juniper/Shrub/Rock Mix
10	58	Juniper/Sagebrush Mix
10	59	Juniper/Mtn Shrub Mix
11	62	Aspen
8.1	63	Aspen/Mesic Mountain Shrub Mix
13	65	Ponderosa Pine
9.1	66	Englemann Spruce/Fir Mix
13	67	Douglas Fir
12	68	Lodgepole Pine
9.1	69	Sub-Alpine Fir
9.1	70	Spruce/Fir Regeneration
9.2	71	Spruce/Lodgepole Pine Mix
13	72	Bristlecone Pine
13	73	Ponderosa Pine/Douglas Fir Mix
13	75	Limber Pine
9.2	77	Lodgepole/Spruce/Fir Mix
9.2	78	Fir/Lodgepole Pine Mix
9.2	79	Douglas Fir/Englemann Spruce Mix
13	80	Mixed Forest Land
9.1	81	Spruce/Fir/Aspen Mix
13	82	P. Pine/Gambel Oak Mix
13	83	Ponderosa Pine/Aspen Mix
13	84	Douglas Fir/Aspen Mix
13	85	P. Pine/Aspen/Gamble Oak Mix
12	86	Lodgepole Pine/Aspen Mix
9.2	87	Spruce/Fir/Lodgepole/Aspen Mix
13	88	Ponderosa Pine/Mesic Mtn. Shrub
13	89	Ponderosa Pine/Aspen/Mesic Mtn.
14	90	Barren Land
6	91	Rock
6	92	Talus Slopes & Rock Outcrops
1	93	Soil
2	94	Disturbed Soil
7	96	Alpine Meadow
7	97	Alpine Forb Dominated
7	98	Alpine Grass Dominated
7	99	Alpine Grass/Forb Mix
7	100	SubAlpine Shrub Community
6	101	Snow
7	102	Subalpine Meadow
7	103	Subalpine Grass/Forb Mix
3.2	104	Riparian
3.2	105	Forested Riparian
3.2	106	Cottonwood
3.1	108	Conifer Riparian
3.2	109	Shrub Riparian

3.1	110	Willow
3.2	111	Exotic Riparian Shrubs
3.2	112	Herbaceous Riparian
3.2	113	Sedge
5	114	Water