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Colorado Division of Parks and Wildlife
July 2011–June 2012

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

Period Covered: July 1, 2011 – June 30, 2012

Author: J. S. Ivan*

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*(J. S. Ivan was the sole Colorado Parks and Wildlife contributor for this work and is thus listed as “author.” However, the draft manuscript included here was a collaborative effort and all personnel listed are co-authors on the manuscript. M. Ellis is the first author.)

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ABSTRACT

Conservation biologists and resource managers are often faced with the task of designing monitoring programs for species that are rare, diffuse, or patchily distributed across large landscapes. These efforts are frequently very expensive and seldom can be conducted by one entity. It is essential that a power analysis is undertaken to ensure stated goals are feasible. We developed a spatial-based simulation, which accounts for natural history, habitat use, and sampling scheme, to investigate power for monitoring wolverines in two areas of the U.S. Rocky Mountains. The first area is a well-established metapopulation of wolverine in the northern Rocky Mountain states of Montana, Idaho, and Wyoming, where the current population is approximately 350 individuals and there are concerns of population decline. Based on current population size estimates and detection probabilities in the northern U.S. Rockies, most sampling schemes are likely to only detect large declines in population sizes (i.e. 50% decline over 10 years). In general, increasing the number of grids sampled or the per visit detection probability had a much greater effect on power than increasing the number of visits per year. For small populations, we found very low power to detect declines. The second analysis was a forecast of the effort required to monitor an increasing population in the southern U.S. Rockies, given recolonization or reintroduction. Occupancy-based methods can only produce enough power to detect population trends if populations are increasing dramatically (i.e. doubling or tripling in 10 years), regardless of the sampling effort. In sum, our approach provides a spatially based framework to evaluate monitoring protocols and objectives by explicitly incorporating the link between changes in population size and estimated occupancy, all while accounting for natural history of the species in question. These analyses were specific to wolverines, but our approach could easily be adapted to other species.
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.

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 1000s 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.
5. Prepare manuscript for publication

INTRODUCTION

Wildlife populations worldwide have faced major population reductions in abundance and geographic range due to both natural and anthropogenic causes (Butchart et al. 2010, Hoffmann et al. 2010, Rands et al. 2010, Inman et al. 2011). Currently, many populations are facing multiple threats including habitat fragmentation and loss, climate change, direct and indirect exploitation, disease, invasive species, and the interaction among these threats (Primack 2006, Laurance et al. 2008, Povilitis and Suckling 2010). Responding to these major threats to wildlife and fish populations worldwide, many countries have adopted legislations aimed at affording protection to species of conservation concern (Hutchins et al. In Press, Waples et al. In Review). Two of the more powerful pieces of legislation are Canada’s Species at Risk Act (SARA) and the United States’ Endangered Species Act (ESA). These acts not only identify species at risk and aim to protect them from additional harm, but also stipulate and provide mechanisms for recovery. For example, in the United States approximately half of the annual budget spent on threatened and endangered species is designated for recovery (GAO 2005, Male and Bean 2005). However, determining when a species of concern is declining or subsequently recovering requires information about trend.

The majority of studies that have examined trends in fish and wildlife were historically based in assessments of population abundance (Dennis et al. 1991, Bart et al. 2007, Foster et al. 2009, Broms et al. 2010). While estimates of abundance are important, other measures such as changes in genetic or demographic parameters or changes in geographic range size have been used to infer trend (Gaston 1991, Schwartz et al. 2007, Marucco et al. 2009, Broms et al. 2010). Recently, more attention has been placed on estimating changes in occupancy of a species geographic range (Joseph et al. 2006, MacKenzie et al. 2006). Occupancy estimation generally requires multiple surveys to a set of sample units, noting on each survey whether the species of interest was detected or not. Subsequently, these repeat-visit data are used to estimate the probability of detecting the species of interest if it was present, and then adjusting the raw presence-absence data in light of this probability to estimate the proportion of area occupied (MacKenzie et al. 2006).
et al. 2006). If occupancy estimation is conducted over multiple time intervals, trend in occupancy is obtained (Field et al. 2005, MacKenzie 2005, Marsh and Trenham 2008).

Before launching an occupancy study, power analysis should be conducted to allocate monitoring effort efficiently (Field et al. 2005, MacKenzie 2005, Rhodes et al. 2006). Most studies base power analyses for occupancy estimation on detecting declines in occupancy over time; however, these simulations rarely consider spatial dynamics. Also, monitoring trends in occupancy is often used as a surrogate for trends in abundance, but this link is rarely evaluated (e.g. Field et al. 2005, Finley et al. 2005, Otto and Roloff 2011). Rhodes et al. (2006) and Rhodes and Jonzén (2011) modeled spatial and temporal correlations in population dynamics to account for spatial structure in populations and provide allocation recommendations in occupancy studies. They find, when spatial correlation is low and temporal correlation is high, it is most efficient to sample many sites infrequently. In the opposite situation, when spatial correlation among population dynamics is high and temporal correlation is low, they recommend sampling few sites often. Finally, when there is a decoupling of abundance and space, they suggest maximizing spatial replication (Rhodes and Jonzén 2011). Furthermore, if interest is in detecting declines in occupancy, they suggest sampling high quality habitats, whereas if the objective is to detect an increase, sampling intermediate-quality habitats is the best strategy. We extended their work by building a species-specific model of a population changing over time. We then sampled from this population using a multi-season occupancy framework to determine power to detect population trends under various scenarios. This approach allows us to optimally allocate scarce monitoring resources for designing an occupancy-based monitoring effort.

Our model was designed to optimize sampling allocation for a large-scale wolverine monitoring effort. Wolverines are a Holarctic carnivore species known for their large home ranges, low densities, and occasional long distance movements (Lofroth and Krebs 2007, Squires et al. 2007, Inman et al. 2012). The species is currently under consideration for listing under the ESA (USFWS 2010) largely due to the fact that their numbers were greatly reduced (possibly eliminated) in the contiguous United States in the early 20th century. Wolverine populations have recolonized Idaho, Montana, Washington, and Wyoming and single male wolverines have recently dispersed to California and Colorado (Aubry et al. 2007, Moriarty et al. 2009). Yet, they are still absent from significant portions of their historical range and their current abundance in the contiguous United States is still likely to be at most 500 individuals.

Recent research by Aubry et al. (2007) and Copeland et al. (2011) has shown that the historical distribution of wolverine was consistent with the distribution of persistent spring snow. Copeland et al. (2011) characterized persistent spring snow cover in the entire northern hemisphere based on a 21-day composite (24 April–15 May) of images from 2000-2006 at a 0.5km² resolution using moderate resolution imaging spectroradiometer (MODIS) satellite images (Hall et al. 2006). They found that >99% of wolverine den sites and >89% year-round telemetry locations were located within areas that were classified as having persistent spring snow in at least one of the seven years for which data were available. Schwartz et al. (2009) demonstrated that wolverine gene flow was facilitated by areas with persistent spring snow compared to areas that were snow free.

In this paper we use habitat (i.e., persistent spring snow), movement, and home range data to build a spatially based model for assessing the power for monitoring wolverine in their current range and in areas where they may eventually recolonize either naturally or through reintroduction.

METHODS

**Study area**

There are two study areas for this project. The primary study area consists of the U.S. Rocky Mountains in northern and central Idaho, western Montana, and northwest Wyoming ("Northern
Rockies”, Figure 1). The area is composed of individual mountain ranges each characterized by high alpine areas (maximum elevation 3900 m) and surrounded by wide areas of semiarid grasslands and irrigated agriculture (elevation ~1400 m). This area is known to be occupied by wolverines, with current population estimates ranging from 200-500 individuals (USFWS 2010). We removed from our analyses mountain ranges on the edge of this range, including the Wallowa Mountains of Eastern Oregon, the Bighorn Mountains of Eastern Montana and Wyoming, and the Bear River Range on the Idaho/Utah border; all three of which have no historical records of wolverines (Aubry et al. 2007) and do not contain continuous patches of persistent spring snow cover (Schwartz et al. 2009, Copeland et al. 2011). We allowed areas ‘used’ by simulated wolverines to extend up to 50 km into Alberta and British Columbia, Canada to account for continuous wolverine populations in the Northern Rockies, but excluded these areas from occupancy analyses.

The second study area is the mountainous region of the Southern U.S. Rockies (“Southern Rockies”). This area is characterized by high, steep mountains (max elevation 4,400 m). As a result, there are strong gradients in physical attributes of the landscape, which lead to heavily dissected vegetation types. In the Southern Rockies, alpine and subalpine zones can be relatively narrow and give way to montane forests, montane shrublands, and semiarid grassland or sagebrush communities over relatively short distances. This area does not currently have a population of wolverines, although wolverines are thought to have occurred there historically (Aubry et al. 2007), and there seems to be adequate habitat, including persistent spring snow (Aubry et al. 2007, McKelvey et al. 2011). Areas of persistent spring snow are more patchily distributed in the Southern Rockies landscape, and separated from areas of persistent spring snow in the Northern U.S. Rockies by >200km. Most mountain ranges in this study area occur in Colorado, but we included the Medicine Bow and Sierra Madre ranges in southern Wyoming, as well as the southern San Juan Mountains in northern New Mexico.

Individual Utilization Distributions

We randomly selected points within areas of persistent spring snow (using Copeland et al. 2010) for the center of individual home ranges for adult female, adult male, and transient male wolverines. Among these three groups, locations were chosen independently to allow for overlapping home ranges (Copeland 1996, Inman et al. 2011); however, within each group, selection of home range centers was constrained to reflect territoriality. The buffer distances required between home ranges centers were at least 16 km for adult females, reflecting a 225 km² home range, and at least 25.2 km for adult and transient males, reflecting 500 km² home ranges (Banci 1994, Krebs et al. 2007, Schwartz et al. 2009). We also required that all home range centers were located in snow patches large enough to support at least one resident female wolverine (Krebs et al. 2007). Within each group (adult females, adult/resident males, adult/transient males), locations for home range centers were randomly selected in an iterative fashion until no additional individuals could be placed in the landscape or until the desired number of individuals was met.

Once home range centers were established for a given simulated landscape, we assigned a bivariate normal utilization distribution for each individual. For resident females, we assumed that an individual spends 90% of her time within their 225 km² home range (radius = 8.5 km). For resident males, we assumed individuals spend 90% of their time within their 12.6 km home range radius, but we allowed for larger sizes and greater overlap among transient male home ranges by assuming individuals only spend 70% of their time in the original 500 km² home range. Each of these distributions produced a surface with decreasing probability of use with increasing distance from the home range center. To make these bivariate normal utilization distributions more realistic, we overlaid them on the persistent spring snow layer and multiplied the layers together. In the persistent spring snow layer, areas of non-snow were weighted as having 1/20 the probability of use compared to snow areas, based on resistance values found for models of genetic least cost paths (Schwartz et al. 2009). We standardized the product of the
two layers to transform it back into a probability density. Thus, each individual utilization distribution takes a unique shape based on availability of snow.

In this approach, it is possible for individuals to make short term, long distance movements during a given study period. The tails of the bivariate normal utilization distribution allow for a very small, but non-zero, probability of reaching any point on the landscape. In preliminary analyses, we tested for the effect of excluding these long distance movement events by cutting off the tails of the bivariate normal, such that the probability of an individual being more than 1-2 standard deviations away from its home range center was set to 0, compared to a situation with no limit on movement. Although allowing short-term, long-distance movements did affect the estimated occupancy of the landscape, the effect on power was minor. Occasional long-distance movements are possible in wolverine ecology, especially by males and transients (Moriarty et al. 2009). For territorial males and females, we would expect these movements to be less likely over the course of the relatively short survey period. Thus we based our power analyses on a ‘mixed’ scenario in which long distance movements were possible for transient males (i.e. no limit), resident males were allowed some larger movement events (limited to within 2 s.d. of home range center), and movements of females, which may have dens, were limited 1 sd from their home range center.

Following the rules state above, our program, SPACE (Spatially-based Power Analyses for Conservation and Ecology), created 1000 surfaces for N=500 or N=200 individuals on the Northern Rockies landscape, reflecting high and low estimates of wolverine population size in the study area. We then simulated 10%, 20%, or 50% declines in our simulated populations over a decade (\( \lambda = 0.989, 0.977, 0.933 \)) by randomly removing an appropriate number of individuals at each time step. We also simulated scenarios (\( n_{sim} = 1000 \)) for a hypothetical reintroduced or recolonizing population in the Southern Rockies. These populations were started with N=30 individuals then allowed to increase by 50%, 100%, or 200% over a decade (\( \lambda = 1.041, 1.072, 1.0116 \)). We initiated all populations with a 2:1:2 ratio of females:resident males:transient males.

**Sampling**

To estimate occupancy, we sampled from our simulated landscapes during each time step or “year” of the simulation. We divided the study area into 225 km² sample units (cells), matching home range sizes for resident females, a strategy widely used for monitoring carnivores (e.g., Zielinski and Stauffer 1996). We excluded cells that did not overlap the persistent snow layer by ≥50%. This resulted in 388 cells for the main Northern Rockies study region, and 128 cells for the Southern Rockies. For each cell, the probability of at least one wolverine being present (hereafter, ‘probability of presence’ was Eqn 3):

\[
P(# \text{wolverines} \geq 1)_j = 1 - P(\text{wolverines absent})_j = 1 - \prod_{i=1}^{N} \left( 1 - \int_{(x,y) \in \Omega_j} f_i(x, y) \, dx \, dy \right)
\]

where N is the number of wolverines in the simulated study area, \( f(x,y) \) is the probability density function (i.e., utilization distribution) describing the use surface for the \( i \)-th wolverine, and \( \Omega_j \) represents the area included in the \( j \)-th grid. We approximated integral values by summing pixel values in the raster, assuming equal pixel areas.

To construct a simulated encounter history (i.e., the data necessary for occupancy estimation) for cell \( j \) in year \( k \), we assigned a 1 (present) or 0 (absent) for each visit by comparing a random draw from Uniform (0,1) with the probability of presence for that cell (draws less than the probability of presence resulted in a detection, and a 1 in the encounter history for that visit). Thus, a cell with simulated encounter history “010” indicates that 3 visits were made to the cell in a given year, and wolverines were
detected on the second visit only. After initial construction, we used progressively reduced versions of
the encounter histories to explore the effect of changes in parameters associated with sampling on power
to detect population changes. For example, we omitted data from even numbered years (i.e., inserted “,”
for each “0” or “1” of the omitted years) to examine the effect of sampling every other year; we tested the
effects of smaller sample sizes by reducing the number of cells or visits included in the encounter
histories; and we reduced the number of detections to simulate imperfect detection (See Table 1). To
create encounter histories with lower detection probability, we randomly removed an appropriate
proportion of 1s from each encounter history. Thus, to go from a detection probability of 1.0 to 0.8, we
retained 0.8/1.0 = 80% of the 1s; for each 1 (wolverine detected) in a given encounter history, we
conducted a random draw from uniform (0,1) and compared this draw against 0.8. We retained the 1 if
the draw was ≤0.8, and changed it to a 0 (wolverine not detected) otherwise. Similarly, to go from
encounter histories reflecting detection probability = 0.8 to detection probability = 0.2, we evaluated each
1 in a given history, retaining it if the random draw was ≤0.25 (0.2/0.8), changing it to 0 otherwise.

We used these encounter histories to obtain annual estimates of occupancy and detection
probability for each simulated landscape and parameter set. Note that the subject of our simulations is a
mobile carnivore capable of moving freely between sample cells, and our simulation setup reflected this
reality. Therefore, interpretation of estimated occupancy parameters was different than the usual context
in which the status (occupied or not) of a given cell is assumed static over the course of a survey.
Specifically, the estimate of occupancy (Ψ) generated under this context is the probability that any given
cell is used rather than occupied, and any reference to Ψ or “occupancy” from here forward refers to
probability of use. Furthermore, the estimate of detection probability generated in this context is actually
the product of true detection probability (i.e., probability of detection given that the species of interest is
present; this quantity is specified directly for any given simulation) and a landscape-wide probability that
an individual is present and available for detection (i.e., probability of presence; see above). We refer to
the detection probability estimated by the model aspest, and the actual detection probability specified for
the simulations aspsim, such that pest = psim × probability of presence.

We used the R (R Development Core Team 2011) package RMark to input the encounter
histories and construct models to fit in Program MARK (White and Burnham 1999). Specifically, we
employed the ‘Robust Design Occupancy’ data type (MacKenzie et al. 2006) in which colonization (γ)
could vary through time but was constrained to be the complement of extinction (ε; i.e., changes in
occupancy were considered random rather than Markovian or static) and detection probability (p)
varied with time. This model structure is appropriate because: 1) we were interested primarily in the occupancy
estimates themselves; we had no interest in modeling occupancy dynamics (colonization, extinction)
explicitly, 2) the simulation specifications allowed “movement” in and out of adjacent cells, thus
mimicking random changes in occupancy, and 3) “movement” between adjacent cells forced pest to be a
function of probability of presence, which changed through time depending on the simulated landscape
and birth/death of individuals. Thus, pest should have varied through time as well.
We extracted the 10 occupancy estimates and the variance-covariance matrix for these estimates from
each simulation, then used the variance components procedure in RMark to fit a linear random effects
trend model to the estimates. A trend was ‘detected’ if the 95% confidence interval of the trend
parameter (on the logit scale) from the random effects model excluded zero and was in the correct
direction (e.g., <0 for declining trends; Tallmon et al. 2010). Thus, we computed the statistical power
produced by a sampling scenario, i.e. the probability that we detect a significant trend given that there is a
trend in the underlying data, as the percentage of simulations in which a trend was detected.

For datasets in which we simulated sampling every other year, we fit models in which we fixed
γ1 = γ2, γ3 = γ4, etc. such that the product of these parameters were estimated, and we bridged years in which
no data were collected to produce valid estimates of occupancy for those years where data were collected.
In these scenarios, only 5 occupancy estimates were generated, and we fit random effects models to those 5 estimates.

We repeated these analyses for each combination of population growth or decline, simulated detection probability ($p_{sim}$), number of visits, cell size, number of cells sampled, and annual or alternating year sampling schemes that were applied to the 1000 simulated landscapes of $N = 30, 200, or 500$ (Table 1). Where applicable, all sampling was cumulative to facilitate the most meaningful contrasts between levels of a parameter; for example, a sample of $n = 50$ cells would include the same cells as an $n = 25$ sample with 25 additional cells included. Similarly, an encounter history with 4 visits would include the same string of 0s and 1s as a 3-visit history, with one additional visit included. Our simulations were designed to be generalizations in that we do not attempt to define when a sampling season might begin, what the sampling mechanism was, or what constitutes a visit. Thus, these simulations could represent flying over selected cells in the study area to search for tracks in the snow, in which case a ‘visit’ is a single flight (Gardner et al. 2010), or they could reflect the use of hair snag devices in which a ‘visit’ is 1 month of continuous sampling (Magoun et al. 2011). We bracketed the sampling parameters (cell size, detection probability, visits) based on previous efforts described in the literature (Magoun et al. 2007, Gardner et al. 2010, Magoun et al. 2011).

RESULTS

Effects of home range parameters

Due to the spacing rules among individuals that we used to reflect wolverine territoriality, the Northern Rockies landscape becomes saturated with approximately 850 individuals (420 ± 6 females, 219 ± 4 resident males, 219 ± 4 transient males; mean ± s.d. across 100 simulated landscapes). For $N=800$, the median probability of at least one wolverine per cell across the landscape was 0.47. This value reflects the availability of individuals on the landscape, yielding on average 280.4 cells in which wolverine were available for detection per sampling occasion across the 388 cells in the grid. As the population size decreased, the average probability of at least one wolverine per cell fell to 0.74 (212.4 detections per occasion) for $N=500$ and 0.05 (18.9 detections per occasion) for $N=30$ across simulations. With perfect detection associated with sampling ($p_{sim} = 1$), these cell-based probabilities for use translate to an estimated occupancy ($\Psi$) of 0.99±0.01 for the entire landscape for populations with $N = 500$ individuals and 0.06±0.01 for $N = 30$.

Effects of population size and trend

We investigated the upper limits of power with occupancy estimation by examining the ability to detect trends when the simulated detection probability was perfect ($p_{sim} = 1$) and with a large number of visits (5) to each unit. We focused these analyses on the U.S. Northern Rockies landscape and a quickly declining population ($\lambda = 0.933$). Even with perfect detection and intense sampling, detecting a large decline (50% over 10 years) in a large starting population ($N = 500$) with adequate power (>80% chance of detecting the trend) required a sample of 50 out of 388 cells (Figure 2). As the population size decreased, the amount of sampling needed to detect a 50% decline even under this ‘best case’ scenario with perfect detection increased dramatically. For example, when $N=200$, achieving 80% power required sampling approximately 75 to 150 cells. Detecting trends in small populations ($N=30$) was difficult; even if we included the entire grid (388 cells) in the sample and assumed perfect detection, we had less than 70% power to detect a trend.

Regardless of the starting sample size, power to detect trends was lower for increasing populations compared to the decreasing scenarios described above. For example, to detect a 50% increase ($\lambda = 1.041$) with >80% confidence, the amount of the total sampling grid that would need to be included in the sample increased to ~25% of the grid ($n_{cells} \approx 60$) for $N=500$ or ~ 50% ($n_{cells} \approx 125$) for
N=200. For N=30, sampling the entire grid, assuming perfect detection probability, and with an intense sampling effort (5 visits), we were able to detect a 50% increase in <40% of the simulations.

With current population sizes (N=500) in the Northern Rockies, the ability to detect declines fell dramatically as the strength of the decline decreased (Figure 3). We found a reasonable chance (≥80%) of detecting a 50% decline in population size over a 10-year period, depending on the combination of sample size and detection probability. However, for a 10% decline in population size over the 10 year period, no amount of sampling could yield enough power to detect the trend. Similarly, even with a large sample size and high detection probability, a 20% decline was detected in <60% of the simulations (Figure 3). With either population increases or declines, sampling every other year substantially increased the number of cells and visits that would need to be sampled.

Trade-offs in sampling methodology

After the strength of the population decline or increase, the parameter that most influences power to detect change was the simulation detection probability ($p_{sim}$). In nearly all scenarios relatively large gains in power were realized when $p_{sim}$ increased from 0.2 to 0.8. For instance, a monitoring scheme that called for 2 visits to each of 100 sample units would have ~25% chance of detecting a 50% decline over 10 years when $p_{sim} = 0.2$. Power for detecting that same decline under the same sampling regime increased to 80% when $p_{sim} = 0.8$ (Figure 3, upper left panel). By comparison, an increase in sample size from $n_{cells} = 50$ to $n_{cells} = 300$ resulted in only a doubling in power (25% to ~50%). In fact, when $p_{sim} = 0.2$, 80% power cannot be achieved even if the entire grid is sampled. Similar gains in power relative to simulation detection probability and sample were realized in other scenarios we simulated. The exceptions to this result were when the goal was to detect a 10% decline over 10 years or to detect a 20% decline when sampling was only conducted every other year. Both scenarios yield very low power and negligible improvement with increased $p_{sim}$ or sample size (Figure 3, middle panels).

The number of visits to each sample unit influenced power as well, although generally to a lesser degree than magnitude of population change, simulation detection probability, and sample size. Even with perfect simulation detection probability ($p_{sim} = 1$), the power to detect a trend increased with the number of visits at each grid cell due to the number of opportunities for an individual to be present. When simulation detection probability is high but imperfect (i.e., $p_{sim} = 0.8$), some gain in power could be realized by visiting each sampled cell 3 times vs. visiting them only twice (Figure 3, separation between the two lightest dotted lines). However, the gain realized for making 4 visits rather than 3 is small, and there is no appreciable difference in power for 4, 5, 6, or 7 visits under the scenarios we simulated. When simulated detection probability was low (i.e., $p_{sim} = 0.2$), potentially greater gains in power could be realized by making more visits, but it depends on the scenario (Figure 3, in some cases there is a moderate amount of separation in the solid lines, in other cases there is not). Note that at low detection probabilities ($p_{sim} = 0.2$), it is often inadvisable to make more visits to each sampled cell because such an approach actually decreases power (See discussion).

Effect of Cell Size

In order to achieve the threshold of 80% power to detect a 50% population decline, changing cell sizes in the grid had implications for both the number of cells and the total area that would need to be sampled. (Figure 5). Grids of 100km$^2$ and 225km$^2$ cells yielded similar power in terms of the percent of the grid that would need to be included in the sample, although the smaller cell size requires sampling more cells (i.e., the total grids were comprised of 887 100km$^2$ cells versus 388 225km$^2$ cells). Assuming 3 visits and high detection, getting 80% power for detecting a 50% decline required 120 cells (12,000km$^2$) from the small grid versus 70 cells (15,750km$^2$) for the medium sized grid. As the size of the grid increased, the power to detect trends in occupancy decreased. The 1000km$^2$ grid produced very low power to detect population trends. In this case, the grid in the Northern Rockies comprised only 76 cells. Including every cell in the sample, with seven visits and high detection probability, we detected a 50%
population decline in <20% of the runs. The phenomenon in which power is actually reduced with a high number of visits occurs for the 225km² cell size at low \( p_{\text{sim}} \), and for the 500km² and 1000km² size at high \( p_{\text{sim}} \).

**Power to detect increases in small populations**

For small populations (\( N=30 \)), power for detecting population trends was limited except for situations with large population increases and high detection probability (Figure 4). For the purposes of comparison, there was greater power for detecting trends in the Southern Rockies landscape than in the Northern Rockies, although the total sampling area in the Southern Rockies landscape is approximately only a third of the Northern Rockies. For both landscapes, a doubling of the population over ten years (\( \lambda = 1.072 \)) could be detected with >80% power in scenarios where a large proportion of the landscape was included with relatively high capture probability. If simulation detection probability is low, then adequate power can only be achieved via sampling a large portion of the available landscape, and making a large number (\( \geq 5 \)) of visits to each sampled cell.

**DISCUSSION**

Monitoring population trends over time is one of the most common goals for management of endangered species. Using a spatially explicit simulation for wolverine in the U.S. Rocky Mountains, we were able to test the ability of occupancy-based approaches to detect trends in population size under a range of monitoring scenarios. Even for large changes in population size (e.g. 50% declines over 10 years), we found that detecting population trends required large-scale, intensive sampling. In many scenarios, no amount of sampling could produce sufficient power to achieve monitoring goals. Our results highlight the importance of analyzing the statistical power of monitoring schemes and using approaches that incorporate the effect of sampling and power over the course of multiple steps in a monitoring protocol.

In the case of the wolverine, work has commenced to evaluate the effectiveness of various approaches for detecting presence. These range from using fix-winged aircraft to find tracks in 100-km² (Magoun et al. 2007) or 1000-km² (Gardner et al. 2010) sampling cells, to using cameras at bait stations (Mulders et al. 2007, Magoun et al. 2011), to the use of non-invasive genetic sampling (Ulizio et al. 2006, Schwartz and Monfort 2008, Magoun et al. 2011). These efforts produce varying detection probabilities from 0.2 to 0.8 as bracketed in our simulations.

However, matching estimates from field studies to our results, is not straightforward. It is important to note that detection probability estimated from pilot analyses is not the same as the \( p_{\text{sim}} \) input in our analyses. Due to the ‘mobile animal’ phenomenon, animals are capable of moving freely between sample cells and therefore can be detected in multiple cells during one sampling occasion. As a result, occupancy models cannot separate the effects of true detection probability (\( p_{\text{sim}} \)) and probability of presence (See Methods). Consequently, \( p_{\text{est}} \) returned from pilot studies will be smaller than the detection probabilities used in our simulations (\( p_{\text{sim}} \)). For example, if pilot work indicates that \( p_{\text{est}} = 0.2 \), power can be assumed to be slightly better than the curves shown for \( p_{\text{sim}} = 0.2 \) in our figures. The exact correspondence between \( p_{\text{est}} \) and \( p_{\text{sim}} \) is dependent on cell size, population size, and home range size of the species in question. Thus, no rule of thumb holds for converting between the two. However, matching \( p_{\text{est}} \) derived from pilot work to curves for \( p_{\text{sim}} \) can still be useful as it will result in conservative estimates of power, which would be a prudent way to design monitoring schemes.

In the case of wolverines, pilot work specific to occupancy monitoring in the Northern Rockies has been carried out using camera stations (B. Inman, Wildlife Conservation Society, unpublished data) and hair snags (J. Waller, Glacier National Park, unpublished data) in 100-km² sample units. Initial results from this work suggest \( p_{\text{est}} \) is approximately 0.25 – 0.3, which in our simulations corresponded to
\(p_{\text{sim}} \approx 0.8\) (i.e., \(p_{\text{est}} = p_{\text{sim}} \times\) probability of presence, where our mean probability of presence was 0.33; thus 0.25/0.33 \(\approx 0.8\)). It’s important to note that the mean probability of presence depends on assumptions about the number of animals, the landscape, and home range configurations. Based on this estimate, and assuming 3-4 visits to each sample unit (sampling occurred during 3-4 months over winter for each pilot study), our research suggests that roughly 100-150 100-km\(^2\) cells would need to be sampled per year to attain an 80% probability of detecting a 50% decline in the Northern Rockies population (Figure 5). Thus, intensive sampling over a small area is unlikely to be a viable solution for detecting population trends. To accomplish anything meaningful, monitoring will require well-coordinated surveys across multiple entities and jurisdictions. Anything less than a large-scale, coordinated effort will likely be of limited or no value.

The spatially explicit nature of our approach is especially important in linking changes in occupancy to population trends. Our results demonstrate that the underlying landscape can influence power to detect population changes. Specifically, in the comparison of power for populations with N=30 in the Northern versus Southern Rockies, power to detect trends in occupancy was similar in terms of percent of the total study area included in the sample, but very different in terms of the absolute area that needs to be sampled. For example, to detect a 3x increase of the N=30 populations with a 225km\(^2\) grid and \(>80\%\) power required sampling \(\sim 20\%\) of either landscape, which translates to sampling 16000km\(^2\) in the northern landscape versus 6000km\(^2\) in the south. Note, however, that the scenarios in this comparison, populations of N=30 in the Northern versus Southern U.S. Rockies, are intended to illustrate the effect of underlying landscape for a fixed population size. In reality, changing the size of a study area would generally also change the size of the population included, which we found to substantially affect power to detect trends.

Previous recommendations for selecting cell sizes have been ad hoc. In some cases, our results indicate a relatively straightforward relationship between cell size and the number of cells needed or the total area sampled to achieve a given power threshold. Between a 100km\(^2\) grid and a 225km\(^2\) grid, with high detection probability, 80% power can be obtained either by sampling many small cells or fewer of the larger cells. However, by the time cell sizes reach 1000km\(^2\) for wolverine, the home ranges for multiple individuals are included in the cell, such that occupancy-based methods alone will only pick up changes once a much larger population decline has occurred. The point at which this switch occurs will likely depend on an interaction of the population size, landscape, home range sizes, and cell size.

We also discovered a counterintuitive anomaly when computing power under scenarios in which cell size is equal to home range size, as is often advised for occupancy surveys of mobile carnivores. Specifically, we noted that when detection probability is low, power generally increases with increasing visits to each sample unit, but there is a point at which conducting more visits actually decreases power. We offer the following explanation for this phenomenon: When the cell size is equal to the home range size, the interplay between \(p_{\text{sim}}\) (i.e., 0.2) and availability is such that the \(p_{\text{est}}\) is fairly low and makes a substantial upward adjustment on the count of cells \(c\) in which wolverines were actually detected. As we make more visits we detect wolverine use in cells that are seldom used, so \(c\) increases, but \(p_{\text{est}}\) from the model does not (only the precision on \(p_{\text{est}}\) improves). After about 6 or 7 visits \(c\) increases enough that the occupancy estimates resulting from upward adjustments on \(c\) approach 1.0. If estimates for all years are at or near 1.0, then there is no trend and we have no power to detect declines. This does not occur when cell sizes are small, because \(c\) will also be small, and any upward adjustments will not approach 1.0. A similar phenomenon occurs if cells are large and \(p_{\text{sim}}\) is high. In that case, most cells are used, and \(c\) will be large, especially with a large number of visits. Thus, even a small upward adjustment on \(c\) pushes the estimates to close to 1.0, which again makes detecting trends difficult. Thus, if maximizing power is a goal, increasing visits beyond a certain threshold may not be helpful depending on cell size, availability of animals, and the probability of detecting them given their presence.
Our simulations currently do not include cost functions, so trade-offs between cell size, number of cells to sample, number of visits at each cell, and detection probability have been conducted absent an important real-world consideration. For instance, in a given situation, it may be easy to complete more visits to a site (e.g., leave camera sets out 1 more month), but extremely costly to improve capture probability (e.g., purchase an entire set of new cameras with improved functionality). Therefore, managers may opt to make more visits to improve power even though intensifying effort (visits) by a given percent may be inferior to improving detection probability by a similar percentage. Future simulation work should include cost as a factor in weighing the importance of the design factors we considered here.

Most studies base power analyses for occupancy estimation solely on detecting various simulated declines in occupancy. Here, we employed a more mechanistic, spatially-based approach in which we simulated animals on a landscape, accounted for their natural history (territoriality, difference between sexes), tied their space use to key habitat features (persistent spring snow), and forced declines or increases in the real parameter of interest (abundance) to determine whether occupancy estimation could detect those changes. Thus, our approach is a direct test of the link between occupancy and abundance, providing a more meaningful examination of whether real-world changes of interest in population size can actually be detected using occupancy estimation. It also sets the stage for direct comparisons between occupancy and estimation of other metrics (e.g., abundance) that could potentially be used to monitor populations. That is, we have established the machinery necessary to simulate ‘truth’ (the configuration of animals on the landscape and changes in that configuration and/or number) and can then sample from that true population in various ways to simulate data gathering under different monitoring approaches. While results from this analysis can be used directly to guide the monitoring of wolverine or similar species, the largest contribution is the framework which can be used for making decisions about the design of a large scale monitoring effort provided information on movement and habitat use is available. Our goals were to establish this framework to encourage cost-effective decisions in designing monitoring programs and to inspire well-coordinated surveys across multiple entities and jurisdictions. Without such coordination our analyses convincingly show that most efforts for species like wolverine will be wasted.

ACKNOWLEDGMENTS

We thank Paul Lukacs, Gary White, and Larissa Bailey for providing invaluable technical advice, and Jeff Laake for implementing the “random occupancy dynamics” model into RMark so it could be used in this analysis. We thank the RMRS and a PECASE award to MKS for providing the initial funding for this effort.

LITERATURE CITED


USFWS. 2010. Endangered and threatened wildlife and plants; 12-month finding on a petition to list the North American wolverine as endangered or threatened.


Prepared by ___________________________

Jacob S. Ivan
Table 1. A summary of variables and ranges of those variables tested in our simulations using program SPACE.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Values tested</th>
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<tr>
<td>Population size</td>
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<tr>
<td>Population growth rates</td>
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<tr>
<td>Limit on movement</td>
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<td>Simulated detection probability</td>
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<tr>
<td>Number of cells sampled</td>
<td>10 - 90% of grid</td>
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<tr>
<td>Number of visits</td>
<td>2 - 7</td>
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<tr>
<td>Cell size</td>
<td>100, 225, 500, 1000 km²</td>
</tr>
<tr>
<td>Sampling</td>
<td>Annual or alternating years (every other year)</td>
</tr>
</tbody>
</table>
Figure 1. Map of study area. Distribution of persistent spring snow in the U.S. Rocky Mountains. Two separate landscapes were included in this study: one corresponding to fairly continuous habitat in the U.S. Northern Rockies, which is currently occupied by wolverines, and a second area in the Southern Rockies, where wolverines may recolonize or be reintroduced.
Figure 2. Effect of population size. Effect of population size on power to detect trends in the Northern U.S. Rockies. Assumes perfect detection associated with sampling for a 50% decline ($\lambda = 0.933$) or a 50% increase ($\lambda = 1.041$) from initial population sizes of 30, 200, and 500 individuals in the Northern Rockies. Simulated populations were sampled using a grid of 225km$^2$ cells overlaid on the landscape.
Figure 3. Power for detecting trends in the U.S. Northern Rockies. Results from a power analysis for assessing the feasibility of using occupancy to monitor trend in the population of wolverines in the U.S. Northern Rockies, assuming N=500 individuals and a cells size of 225km². Results are parsed by population growth rate ($\lambda = 0.933, 0.977, 0.989, 1.041$ corresponding to 50%, 20%, and 10% declines over 10 years or a 50% increase), sampling effort (whether sampling occurred annually or every other year), detection probability for sampling, number of visits per year, and number of grid cells sampled from a total of 388. Power is based on number of detected trends in 1,000 simulated populations.
Figure 4. Comparison of N=30 populations in Northern and Southern Rockies. Power to detect population trends for populations of 30 wolverines in U.S. Northern Rockies compared to the same population size in the Southern Rockies landscape. Ability to detect a population decline depends on population growth rate ($\lambda = 0.933, 1.041, 1.072, 1.116$ corresponding to a 50% decline over 10 years or 50%, 2-fold, or 3-fold increases in population size over 10 years) and sampling effort (detection probability for sampling, number of visits per year, number of grid cells sampled from a total of 388 for the Northern Rockies or 128 for Colorado). Power is based on number of detected trends from 1,000 simulated populations.
Figure 5. Effect of cell size on power. Effect of grid size on power to detect population trends in the wolverine population (N=500) in the Northern Rockies using occupancy. As grid size changes, the total number of grid cells on the landscape also changes from 887 for a 100km$^2$ grid, 388 for a 225 km$^2$ grid, to 76 for a 1000km$^2$ grid.
**ABSTRACT**

In an effort to restore a viable population of 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-km² 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. A summary of snow tracking results can be found in Ivan (2011). 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. We determined species for each photo and checked our work using multiple observers. Average agreement between observers was 96%. We estimated that approximately 25% of inaccessible cells were used by lynx. Detection probability was 0.43. These pilot data are currently being used to conduct simulations and power analyses to determine how many sample units will be required to detect population changes of interest in Colorado.
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.

SEGMENT OBJECTIVES

1. Obtain initial estimates of occupancy and detection probability from units where remote cameras were the primary detection method.
2. Determine covariates and covariate structures that will be most useful for modeling occupancy and detection probability for camera surveys.
3. Combine these results with those obtained via previous work (snow tracking) to inform simulation work aimed at determining the number of sample units, and visits to each unit, required to detect changes of interest in the lynx population in Colorado.

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 km² “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 engelmannii) - 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 km² (8.66 km × 8.66 km) sample units, which reflects the mean annual home range size of reproductively active female 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, city, and county lands were 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

A detailed discussion of the methods and results associated with snow tracking surveys appears in Ivan (2011). We do not repeat that discussion here. Instead we focus on methods and results from the remote cameras, as those data were unavailable for the 2011 report.

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. All photo attributes were imported into a database and species was assessed for each photo based on review by at least 2 observers.

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, \( \psi \)) and detection probability (\( p \)) for the camera stratum. Photos were grouped by month (November to March) for each sample unit such that encounter histories included 5 “visits.” Due to this grouping, there were no meaningful covariates for \( p \). Individual cameras recorded moon phase and temperature for each photo, but aggregated over a month, these data were not helpful. Some camera sets used different scent lures than others, but aggregating by unit negates the utility of this information as well.

We hypothesized that the proportion of spruce/fir and/or willow (\( Salix \) spp.) cover in each unit may affect the probability of use and/or probability of detection. Thus, we considered these covariates as potentially important for explaining variability in \( \psi \) and \( p \). We held \( \psi \) constant and built an additive model for each detection covariate (one at a time) to determine the best structure for \( p \). We then held \( p \) at the best structure as determined by AICc (Burnham and Anderson 2002) and fit additive models using the
covariates for $\psi$. We also ran a model where both $p$ and $\psi$ were held constant as a baseline for comparison. We report estimates of $p$ and $\psi$ from the AICc top model.

**RESULTS**

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. We obtained 445 photos of lynx and detected them in 7 of the 30 units sampled (Figure 1). Average agreement between photo reviewers was 96%.

Of the model structures we fit, none was clearly better than the others as AICc weight was distributed fairly evenly (Table 1). Beta estimates for fitted models suggested that $\psi$ was positively associated with both percent spruce/fir and percent willow in a given unit. Spruce/fir was also positively associated with detection probability, whereas willow was negative associated with detection probability. However none of these models were as well supported by the data as the null model in which $\psi$ and $p$ were considered constant across cells. Thus, results generally followed our expectations, but the null model came out on top likely due to sparse data and small samples in this pilot study. Model-averaged estimates for $\psi$ and $p$ were 0.25 and 0.42, respectively. Detection probability using cameras was about the same as for snowtracking (Ivan 2011), but estimated probability of use for inaccessible sampling units was about half that estimated for accessible cells sampled via snow tracking.

**DISCUSSION**

Initial results indicate that occupancy (use) can be adequately modeled using data collected via snow tracking. Precision on estimates of $\psi$ and $p$ was relatively poor, but this can be addressed by sampling more units and/or making more visits. Modeling $p$ and $\psi$ as functions of the covariates (spruce/fir and willow) was not as well supported as specifying them to be constant across units. However, we recommend continuing to record and use these covariates and others in future surveys as it seems reasonable that these covariates should impact detection probability and/or use, and their effects may be important as sample size increases.

We estimated that lynx used approximately 25% of the sample units available in the Core Research Area. However, for this pilot study, lynx habitat was coarsely defined as units with >50% conifer and/or montane cover 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 recently finished 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. Indeed, re-running the analysis using only those cells (n = 24) within the top 40% of predicted lynx habitat in the state increased the occupancy estimate to 0.31.

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. We suggest that attractants be attached via wire rather than fishing line. We also suggest that auditory
attractants may be helpful. In a recent study on cougars (*Puma concolor*) in the Front Range of Colorado, visitation rates at camera sites increased dramatically when auditory attractants were used in addition to scent lures and visual attractants (Kirstie Yeager, personal communication).

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.

LITERATURE CITED


Prepared by ___________________________

Jacob S. Ivan
Table 1. Model selection results for estimating lynx occupancy of sample units surveyed via remote camera in the Core Research Area, San Juan Mountains, Colorado, Winter 2010–2011.

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<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>ΔAICc Wt</th>
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</tr>
<tr>
<td>( \psi(\text{willow}) \rho(.) )</td>
<td>85.92</td>
<td>1.38</td>
<td>0.14</td>
<td>3</td>
</tr>
</tbody>
</table>

Figure 1. Canada lynx Core Research Area in southwest Colorado. Squares are 75km² 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 units where lynx were detected.
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.
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, 2011 – June 30, 2012

Author: J. S. Ivan

Personnel: M. Rice, P. Lukaes, 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. Prepare manuscript for submission to *Journal of Wildlife Management*.

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

While this worked was completed in January 2012, the final report was included in revisions to the previous annual report and is not repeated here. We refer the reader to Ivan (2011) for details regarding methods and results from this work. Our intent is to work this report into a manuscript submission to *Journal of Wildlife Management* by Fall 2012.
SUMMARY

As expected, relative predicted use by lynx during winter months was negatively associated with distance to large patches of conifer (D50HA) and positively associated with spruce/fir (SF), mixed spruce/fir (MIXSF), elevation (ELEV) and slope. Of these associations, the relationship with spruce/fir was strongest. Predicted use was also positively associated with topographic wetness and aspen cover. We projected these associations (and other more minor associations included in competing models) onto a map of the state and arbitrarily defined the top 20% of predictions as high quality lynx habitat. There are 1,869,975 ha of such habitat in Colorado. Most of this high quality habitat was predicted to occur in the southern part of the state in the San Juan, Culebra, and Wet Mountain Ranges. 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 comprised the best predicted winter lynx habitat farther north.

Associations between relative predicted summer use and SF, MIXSF, ELEV, slope, and D50HA were similar to those observed during winter. However, the associations with D50HA and slope were stronger during summer. We also found positive associations between lodgepole pine, aspen, and distance to high volume road segments. The summer predictive map reflects more dispersed predicted use by lynx with the lodgepole playing a larger role, especially farther north. 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 was predicted to shift more toward the Medicine Bow and Front Ranges.

LITERATURE CITED

ABSTRACT

To improve understanding of snowshoe hare ecology in the southern portion of their range, and enhance the ability of agency personnel to manage subalpine landscapes for snowshoe hares (Lepus americanus) and lynx (Lynx canadensis) in Colorado, we estimated snowshoe hare density, survival, recruitment, and movement in west-central Colorado, USA from July 2006–March 2009. We sampled 3 types of forest stands that purportedly provide good habitat for hares: 1) mature Engelmann spruce (Picea engelmannii)/subalpine fir (Abies lasiocarpa), 2) early seral, even-aged lodgepole pine (Pinus contorta), and 3) mid-seral, even-aged lodgepole pine that had been pre-commercially thinned. In all stand types and all seasons, snowshoe hare densities were <1.0 hares/ha. During summer, hare densities [±SE] were highest in early seral lodgepole pine (0.20 [0.01] to 0.66 [0.07] hares/ha), lowest in mid-seral lodgepole pine (0.01 [0.04] to 0.03 [0.03] hares/ha), and intermediate in mature spruce-fir (0.01 [0.002] to 0.26 [0.08] hares/ha). During winter, densities were similar among the 3 stand types. Annual survival of hares was highest in mature spruce-fir (0.14 [0.05] to 0.20 [0.07]) and similar between the 2 lodgepole stand types (0.10 [0.03] to 0.16 [0.06]). Stand attributes indicative of dense cover were positively correlated with density estimates and explain relatively more process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival. Both density and survival of hares in early seral lodgepole stands were positively correlated with the occurrence of similar stands in the surrounding landscape. Recruitment of juvenile hares occurred during all 3 summers in early seral lodgepole stands, 2 of 3 summers in mature spruce-fir stands, and in only 1 of 3 summers in mid-seral lodgepole. Within-season movements of hares were larger during winter than during summer and tended to be larger in early seral lodgepole stands. Hares in both early and mid-seral lodgepole stands tended to make larger movements between seasons than hares in spruce-fir stands, possibly reflecting the variable value of these stands as mediated by snow depth. Based on stand-specific estimates of density, demography, and movement, we conclude that thinned, mid-seral lodgepole stands are less important than mature spruce-fir and small lodgepole stand types. Management for snowshoe hares (and lynx) in central
Colorado should focus on maintaining the latter. Given the more persistent nature of spruce-fir compared to early seral lodgepole, and the fact that such stands cover considerably more area, mature spruce-fir may be the most valuable stand type for snowshoe hares in the region.

We used simulation to compare relative performance of the method we developed to estimate density for this project (TELEM) to other contemporary methods that are widely used (i.e., spatially explicit capture-recapture (SECR), and mean maximum distance moved (MMDM)). We evaluated performance (percent error) under all combinations of 3 levels of detection probability (0.2, 0.4, 0.6), 3 levels of occasions (5, 7, 10), and 3 levels of abundance (10, 20, 40 animals). We also tested each estimator using 5 different models for animal home ranges. TELEM performed best across most combinations of capture probabilities, sampling occasions, true densities, and home range configurations, and performance was unaffected by home range shape. SECR outperformed MMDM estimators in nearly all comparisons and may be preferable to TELEM at low capture probabilities, but performance varied with home range configuration. MMDM estimators exhibited substantial positive bias for most simulations, but performance improved for elongated or infinite home ranges.
Assess the relative value of 3 stand types (mature spruce/fir, early seral lodgepole pine, and thinned, mid-seral lodgepole pine) that purportedly provide high quality hare habitat by estimating density, survival, recruitment, and movements of hares in such stands during summer and winter.

SEGMENT OBJECTIVES

1. Publish manuscripts in peer-reviewed scientific journals.

INTRODUCTION

Snowshoe hares (*Lepus americanus*), their famous 10-year population cycle, and close association with Canada lynx (*Lynx canadensis*) have been well-studied in boreal Canada for decades. Snowshoe hare range, however, extends south into the Sierra Nevada, Southern Rockies, upper Lake States, and Appalachian Mountains. Ecology of snowshoe hares in these more southerly regions is not as well understood, though hare research in the U.S. Rocky Mountains has accelerated over the past decade. Through this recent work, biologists have identified stands of young, densely-stocked conifers and those of mature, uneven-aged conifers as primary hare habitat in the region. Both stand types are characterized by dense understorey vegetation that provides both browse and protection from elements and predators.

From 1999 to 2006, Canada lynx were reintroduced into Colorado in an effort to restore a viable population to the southern portion of their former range. Snow tracking of released individuals and their progeny indicated that the majority of lynx winter diet in Colorado was comprised of snowshoe hares. Thus, long-term success of the lynx reintroduction effort hinges, at least partly, on maintaining adequate and widespread populations of snowshoe hares in the state. To improve our understanding of snowshoe hare ecology in the southern portion of their range, and enhance the ability of agency personnel to manage subalpine landscapes for snowshoe hares and lynx in Colorado, we conducted an observational study to evaluate purported primary hare habitat in the state. Specifically, we estimated snowshoe hare density, survival, recruitment, and movement indices in mature, uneven-aged spruce/fir (*Picea engelmannii/Abies lasiocarpa*) and 2 classes of young, even-aged lodgepole pine: 1) “small” lodgepole pine (*Pinus contorta*) stands, which were clear cut 20–25 years prior to this study and had regenerated into densely stocked stands with trees 2.54–12.69 cm in diameter, and 2) “medium” lodgepole pine stands (tree diameter = 12.70–22.85 cm) which were clear cut 40-60 years prior to this study and pre-commercially thinned ~20 years prior.

Animal density is one of the most common and fundamental parameters in wildlife ecology and was the first metric we used to evaluate the stand types. However, density can be difficult to estimate from mark-recapture data because animals move on and off of a trapping grid during a sampling session (i.e., lack of geographic closure). Thus, we first developed a density estimator that uses ancillary radio telemetry locations, in addition to mark-recapture information, to account for lack of geographic closure resulting in relatively unbiased estimates of density. We also completed a series of simulations to test the performance of this “telemetry” estimator over a range of sampling parameters (i.e., capture probabilities, sampling occasions, densities, and home range configurations) likely to be encountered in the field, and
compared its performance to two other commonly used, contemporary estimators: spatially explicit capture-recapture (SECR), and mean maximum distance moved (MMDM).

**STUDY AREA**

The study area encompassed roughly 1200 km² around Taylor Park and Pitkin, Colorado, USA (39°50'N, 106°34'W; Figure 1), and included a portion of the “Core Reintroduction Area” occupied by reintroduced Canada lynx (Shenk 2009). Open sagebrush (*Artemisia tridentata*) parks dissected by narrow riparian zones of willow (*Salix* spp.) and potentilla (*Potentilla* spp.) dominated the relatively low elevation (~2800–3000 m) parts of the study area. Extensive stands of lodgepole pine occupied low and mid-elevation slopes (~3000–3300 m), giving way to narrow bands of Engelmann spruce/subalpine fir in the sub-alpine zone (~3200–3600 m). Alpine tundra topped the highest parts of the study area (~3300–4200 m). Moist spruce-fir forests also occurred on north-facing slopes at mid-elevations.

Climate was typical of continental, high-elevation zones with relatively short, mild summers and long, harsh winters. Mean July temperature was 14 °C; mean January temperature was −11 °C (Ivan 2011). Maximum snow depth on the study area averaged 80 cm but ranged from 22–163 cm depending on year, elevation, and aspect (Ivan 2011). Snowpack generally persisted from November through May (low elevations) or June (high elevations and north-facing slopes).

Some human habitation occurred in the study area, mostly in the form of seasonal residences. Considerable recreational use occurred during summer in the form of dispersed camping and off-highway vehicle traffic. A suite of native predators were present within the study area including lynx, cougar (*Puma concolor*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), pine marten (*Martes Americana*), Great Horned Owl (*Bubo virginianus*) and Northern Goshawk (*Accipiter gentilis*).

**METHODS**

Refer to Ivan (2011) for methods associated with fieldwork conducted during 2006–2009 and subsequent statistical analyses. During fiscal year 2011–2012 we completed work on 2 manuscripts submitted as a pair to the journal *Ecology*. The first of these manuscripts lays out an approach to estimating animal density using auxiliary telemetry information to improve estimates. The second manuscript uses simulation to compare performance of this new estimator to other contemporary estimators. We have just completed what we believe to be final revisions to these papers. Additionally, we spent much of year combining the demography and movement chapters of the primary author’s dissertation into a single, comprehensive treatment of snowshoe hare ecology in central Colorado that includes analyses on hare density, survival, recruitment, and movement. This manuscript was recently submitted to the *Journal of Wildlife Management* for consideration as either a research article or monograph.

**RESULTS AND DISCUSSION**

A comprehensive treatment of the results is widely available in dissertation form (Ivan 2011), so we do not repeat that here. We are currently in the process of publishing results in the peer-reviewed literature. Below is list of manuscripts that have been submitted for publication (abstracts are provided in Appendix I):


SUMMARY

In all stand types and all seasons, snowshoe hare densities were <1.0 hares/ha. During summer, hare densities [±SE] were highest in early seral lodgepole pine (0.20 [0.01] to 0.66 [0.07] hares/ha), lowest in mid-seral lodgepole pine (0.01 [0.04] to 0.03 [0.03] hares/ha), and intermediate in mature spruce-fir (0.01 [0.002] to 0.26 [0.08] hares/ha). During winter, densities were similar among the 3 stand types. Annual survival of hares was highest in mature spruce-fir (0.14 [0.05] to 0.20 [0.07]) and similar between the 2 lodgepole stand types (0.10 [0.03] to 0.16 [0.06]). Stand attributes indicative of dense cover were positively correlated with density estimates and explain relatively more process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival. Both density and survival of hares in early seral lodgepole stands were positively correlated with the occurrence of similar stands in the surrounding landscape. Recruitment of juvenile hares occurred during all 3 summers in early seral lodgepole stands, 2 of 3 summers in mature spruce-fir stands, and in only 1 of 3 summers in mid-seral lodgepole. Within-season movements of hares were larger during winter than during summer and tended to be larger in early seral lodgepole stands. Hares in both early and mid-seral lodgepole stands tended to make larger movements between seasons than hares in spruce-fir stands, possibly reflecting the variable value of these stands as mediated by snow depth. Based on stand-specific estimates of density, demography, and movement, we conclude that thinned, mid-seral lodgepole stands are less important than mature spruce-fir and small lodgepole stand types. Management for snowshoe hares (and lynx) in central Colorado should focus on maintaining the latter. Given the more persistent nature of spruce-fir compared to early seral lodgepole, and the fact that such stands cover considerably more area, mature spruce-fir may be the most valuable stand type for snowshoe hares in the region.

The estimator we developed is based on a modified Huggins closed capture estimator. It directly accounts for lack of geographic closure (animals moving on and off of the sampling grid during the sampling period) using telemetry data, and this auxiliary information is used to compute estimates of density. Contrary to other approaches, this method is free from assumptions regarding the distribution of animals on the landscape, the stationarity of their home ranges, and biases induced by abnormal movements in response to baited detectors. The estimator is freely available in Program MARK. We found that our approach performed best across most combinations of capture probabilities, sampling occasions, true densities, and home range configurations, and performance was unaffected by home range shape. Spatially explicit capture-recapture methods outperformed “mean maximum distance moved” (MMDM) estimators in nearly all comparisons and may be preferable to our telemetry estimator at low capture probabilities, but performance varied with home range configuration. MMDM estimators exhibited substantial positive bias for most simulations, but performance improved for elongated or infinite home ranges.

LITERATURE CITED


Prepared by ___________________________
Jacob S. Ivan
Figure 1. Study area near Taylor Park and Pitkin, central Colorado. We estimated snowshoe density, demography, and movement in 3 late-seral Engelmann spruce/subalpine fir stands (circles), 3 mid-seral lodgepole stands (squares), and 6 early-seral lodgepole stands (triangles) from summer 2006 through winter 2009.
APPENDIX I

PROJECT PAPERS

The following manuscript (referenced here by abstract) is currently in review at the journal *Ecology*.

**USING AUXILIARY TELEMETRY INFORMATION TO ESTIMATE ANIMAL DENSITY FROM CAPTURE-RECAPTURE DATA**

JACOB S. IVAN, GARY C. WHITE, AND TANYA M. SHENK

**ABSTRACT**

Estimation of animal density is fundamental to ecology, and ecologists often pursue density estimates using grids of detectors (e.g., cameras, traps, hair snags) to sample animals. However, under such a framework, reliable estimates can be difficult to obtain because animals move on and off of the study site during the sampling session (i.e., the site is not closed geographically). Generally, practitioners address lack of geographic closure by a) inflating the area sampled by the detectors based on the mean distance individuals moved between trapping events, or b) invoking hierarchical models in which animal density is assumed to be a spatial point process, and detection is modeled as a declining function of distance to a detector. We provide an alternative in which lack of geographic closure is sampled directly using telemetry, and this auxiliary information is used to compute estimates of density based on a modified Huggins closed capture estimator. Contrary to other approaches, this method is free from assumptions regarding the distribution of animals on the landscape, the stationarity of their home ranges, and biases induced by abnormal movements in response to baited detectors. The estimator is freely available in Program MARK.

The following manuscript (referenced here by abstract) is currently in review at the journal *Ecology*.

**USING SIMULATION TO COMPARE METHODS FOR ESTIMATING DENSITY FROM CAPTURE-RECAPTURE DATA**

JACOB S. IVAN, GARY C. WHITE, TANYA M. SHENK

Estimation of animal density is fundamental to wildlife research and management, but estimation is often complicated by lack of geographic closure of sampling grids. Contemporary methods for estimating density using mark–recapture data include: 1) approximating the effective area sampled by an array of detectors based on the mean maximum distance moved (MMDM) by animals during the sampling session, 2) spatially explicit capture–recapture (SECR) methods that formulate the problem hierarchically with a process model for animal density and an observation model in which detection probability declines with distance from a detector, and 3) a telemetry estimator (TELEM) that uses auxiliary telemetry information to estimate the proportion of animals on the study site. We used simulation to compare relative performance (percent error) of these methods under all combinations of 3 levels of detection probability (0.2, 0.4, 0.6), 3 levels of occasions (5, 7, 10), and 3 levels of abundance (10, 20, 40 animals). We also tested each estimator using 5 different models for animal home ranges. TELEM performed best across most combinations of capture probabilities, sampling occasions, true densities, and home range configurations, and performance was unaffected by home range shape. SECR outperformed MMDM estimators in nearly all comparisons and may be preferable to TELEM at low capture probabilities, but performance varied with home range configuration. MMDM estimators
exhibited substantial positive bias for most simulations, but performance improved for elongated or infinite home ranges.

The following manuscript (referenced here by abstract) is currently in review at the Journal of Wildlife Management.

Density, Demography, and Seasonal Movements of Snowshoe Hares in Central Colorado

JACOB S. IVAN, GARY C. WHITE, TANYA M. SHENK

ABSTRACT

To improve understanding of snowshoe hare ecology in the southern portion of their range, and enhance the ability of agency personnel to manage subalpine landscapes for snowshoe hares (Lepus americanus) and lynx (Lynx canadensis) in Colorado, we estimated snowshoe hare density, survival, recruitment, and movement in west-central Colorado, USA from July 2006–March 2009. We sampled 3 types of forest stands that purportedly provide good habitat for hares: 1) mature Engelmann spruce (Picea engelmannii)/subalpine fir (Abies lasiocarpa), 2) early seral, even-aged lodgepole pine (Pinus contorta), and 3) mid-seral, even-aged lodgepole pine that had been pre-commercially thinned. In all stand types and all seasons, snowshoe hare densities were <1.0 hares/ha. During summer, hare densities [±SE] were highest in early seral lodgepole pine (0.20 [0.01] to 0.66 [0.07] hares/ha), lowest in mid-seral lodgepole pine (0.01 [0.04] to 0.03 [0.03] hares/ha), and intermediate in mature spruce-fir (0.01 [0.002] to 0.26 [0.08] hares/ha). During winter, densities were similar among the 3 stand types. Annual survival of hares was highest in mature spruce-fir (0.14 [0.05] to 0.20 [0.07]) and similar between the 2 lodgepole stand types (0.10 [0.03] to 0.16 [0.06]). Stand attributes indicative of dense cover were positively correlated with density estimates and explain relatively more process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival. Both density and survival of hares in early seral lodgepole stands were positively correlated with the occurrence of similar stands in the surrounding landscape. Recruitment of juvenile hares occurred during all 3 summers in early seral lodgepole stands, 2 of 3 summers in mature spruce-fir stands, and in only 1 of 3 summers in mid-seral lodgepole. Within-season movements of hares were larger during winter than during summer and tended to be larger in early seral lodgepole stands. Hares in both early and mid-seral lodgepole stands tended to make larger movements between seasons than hares in spruce-fir stands, possibly reflecting the variable value of these stands as mediated by snow depth. Based on stand-specific estimates of density, demography, and movement, we conclude that thinned, mid-seral lodgepole stands are less important than mature spruce-fir and small lodgepole stand types. Management for snowshoe hares (and lynx) in central Colorado should focus on maintaining the latter. Given the more persistent nature of spruce-fir compared to early seral lodgepole, and the fact that such stands cover considerably more area, mature spruce-fir may be the most valuable stand type for snowshoe hares in the region.