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WILDLIFE RESEARCH REPORT

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		:	Reintroduced to Colorado
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ABSTRACT

In an effort to establish a viable population of Canada lynx (*Lynx canadensis*) in Colorado, the Colorado Division of Wildlife (CDOW) initiated a reintroduction effort in 1997 with the first lynx released in February 1999. From 1999-2007, 218 wild-caught lynx from Canada and Alaska were released in Colorado. We documented survival, movement patterns, reproduction, and landscape habitat-use through aerial (n = 10,935) and satellite (n = 26,082) tracking. Most lynx remained near the core release area in southwestern Colorado. From 1999-August 2008, there were 112 mortalities of released adult lynx. Approximately 30.4% were either human-induced or likely human-induced through either collisions with vehicles or gunshot. Starvation and disease/illness accounted for 18.8% of the deaths while 36.6% of the deaths were from unknown causes. Of these mortalities, 26.8% occurred outside of Colorado. Monthly mortality rate was lower inside the study area than outside, and slightly higher for male than for female lynx, although 95% confidence intervals for sexes overlapped. Mortality was higher immediately after release (first month = 0.0368 [SE = 0.0140] inside the study area, and 0.1012 [SE = 0.0359] outside the study area), and then decreased according to a quadratic trend over time. Reproductive females had the smallest 90% utilization distribution home ranges ($\bar{x}$ = 75.2 km^2, SE = 15.9 km^2), followed by attending males ($\bar{x}$ = 102.5 km^2, SE = 39.7 km^2) and non-reproductive animals ($\bar{x}$ = 653.8 km^2, SE = 145.4 km^2). Reproduction was first documented in 2003 with subsequent successful reproduction in 2004, 2005 and 2006. No dens were documented in 2007 or 2008. From snow-tracking, the primary winter prey species (n = 548 kills) were snowshoe hare (*Lepus americanus*, annual $\bar{x}$ = 73.3%, SE = 4.7, n = 10) and red squirrel (*Tamiasciurus hudsonicus*, annual $\bar{x}$ = 18.2%, SE = 4.2, n = 10); other mammals and birds formed a minor part of the winter diet. Lynx use-density surfaces were generated to illustrate relative use of areas throughout Colorado. Within the areas of high use in southwestern Colorado, site-scale habitat use, documented through snow-tracking, supports mature

Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest stands with 42-65% canopy cover and 15-20% conifer understory cover as the most commonly used areas in southwestern Colorado. Little difference in aspect (slight preference for north-facing slopes), slope ($\bar{x}$ = 15.7°) or elevation ($\bar{x}$ = 3173 m) were detected for long beds, travel and kill sites (*n* = 1841). Den sites (*n* = 37) however, were located at higher elevations ($\bar{x}$ = 3354 m, SE = 31 m) on steeper ($\bar{x}$ = 30°, SE = 2°) and more commonly north-facing slopes with a dense understory of coarse woody debris. Two years of a study to evaluate snowshoe hare densities, demography and seasonal movement patterns among small and medium tree-sized lodgepole pine stands and mature spruce/fir stands have been completed in 2006-2008 and will continue through 2009 (see Appendix I of this report). Results to date have demonstrated that CDOW has developed lynx release protocols that ensure high initial post-release survival followed by high long-term survival, site fidelity, reproduction and recruitment of Colorado-born lynx into the Colorado breeding population. What is yet to be demonstrated is whether Colorado can support sufficient recruitment to offset annual mortality for a viable lynx population over time. Monitoring continues in an effort to document such viability.

WILDLIFE RESEARCH REPORT

POST RELEASE MONITORING OF LYNX (*LYNX CANADENSIS*) REINTRODUCED TO COLORADO

TANYA M. SHENK

P. N. OBJECTIVE

The initial post-release monitoring of Canada lynx (*Lynx canadensis*) reintroduced into Colorado will emphasize 5 primary objectives:

1. Assess and modify release protocols to ensure the highest probability of survival for each lynx released.
2. Obtain regular locations of released lynx to describe general movement patterns and habitats used by lynx.
3. Determine causes of mortality in reintroduced lynx.
4. Estimate survival of lynx reintroduced to Colorado.
5. Estimate reproduction of lynx reintroduced to Colorado.

Three additional objectives will be emphasized after lynx display site fidelity to an area:

6. Refine descriptions of habitats used by reintroduced lynx.
7. Refine descriptions of daily and overall movement patterns of reintroduced lynx.
8. Describe hunting habits and prey of reintroduced lynx.

Information gained to achieve these objectives will form a basis for the development of lynx conservation strategies in the southern Rocky Mountains.

SEGMENT OBJECTIVES

1. Complete winter 2007-08 field data collection on lynx habitat use at the landscape scale, hunting behavior, diet, mortalities, and movement patterns.
2. Complete winter 2007-08 lynx trapping field season to collar Colorado born lynx and re-collar adult lynx.
3. Complete spring 2008 field data on lynx reproduction.
4. Summarize and analyze data and publish information as Progress Reports, peer-reviewed manuscripts for appropriate scientific journals, or CDOW technical publications.
5. Complete the second year of field work to evaluate snowshoe hare (*Lepus americanus*) densities, demography and seasonal movement patterns among small and medium tree-sized lodgepole pine stands and mature spruce/fir stands (see Appendix I).

INTRODUCTION

The Canada lynx occurs throughout the boreal forests of northern North America. Colorado represents the southern-most historical distribution of lynx, where the species occupied the higher elevation, montane forests in the state. Little was known about the population dynamics or habitat use of this species in their southern distribution. Lynx were extirpated or reduced to a few animals in the state by the late 1970's due, most likely, to predator control efforts such as poisoning and trapping. Given the isolation of Colorado to the nearest northern populations, the CDOW considered reintroduction as the only option to attempt to reestablish the species in the state.

A reintroduction effort was begun in 1997, with the first lynx released in Colorado in 1999. To date, 218 wild-caught lynx from Alaska and Canada have been released in southwestern Colorado. The goal of the Colorado lynx reintroduction program is to establish a self-sustaining, viable population of lynx in this state. Evaluation of incremental achievements necessary for establishing viable populations is an interim method of assessing if the reintroduction effort is progressing towards success. There are 7 critical criteria for achieving a viable population: 1) development of release protocols that lead to a high initial post-release survival of reintroduced animals, 2) long-term survival of lynx in Colorado, 3) development of site fidelity by the lynx to areas supporting good habitat in densities sufficient to breed, 4) reintroduced lynx must breed, 5) breeding must lead to reproduction of surviving kittens 6) lynx born in Colorado must reach breeding age and reproduce successfully, and 7) recruitment must equal or be greater than mortality over an extended period of time.

The post-release monitoring program for the reintroduced lynx has 2 primary goals. The first goal is to determine how many lynx remain in Colorado and their locations relative to each other. Given this information and knowing the sex of each individual, we can assess whether these lynx can form a breeding core from which a viable population might be established. From these data we can also describe general movement patterns and habitat use. The second primary goal of the monitoring program is to estimate survival of the reintroduced lynx and, where possible, determine causes of mortality for reintroduced lynx. Such information will help in assessing and modifying release protocols and management of lynx once they have been released to ensure their highest probability of survival.

Additional goals of the post-release monitoring program for lynx reintroduced to the southern Rocky Mountains included refining descriptions of habitat use and movement patterns and describing successful hunting habitat once lynx established home ranges that encompassed their preferred habitat. Specific objectives for the site-scale habitat data collection include: 1) describe and quantify site-scale habitat use by lynx reintroduced to Colorado, 2) compare site-scale habitat use among types of sites (e.g., kills vs. long-duration beds), and 3) compare habitat features at successful and unsuccessful snowshoe hare chases.

Documenting reproduction is critical to the success of the program and lynx are monitored intensively to document breeding, births, survival and recruitment of lynx born in Colorado. Site-scale habitat descriptions of den sites are also collected and compared to other sites used by lynx.

The program will also investigate the ecology of snowshoe hare in Colorado. A study comparing snowshoe hare densities among mature stands of Engelmann spruce (*Picea engelmannii*)/subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*) and Ponderosa pine (*Pinus ponderosa*) was completed in 2004 with highest hare densities found in Engelmann spruce/subalpine fir stands and no hares found in Ponderosa pine stands. A study to evaluate the importance of young, regenerating lodgepole pine and mature Engelmann spruce/subalpine fir stands in Colorado by examining density and demography of snowshoe hares that reside in each was initiated in 2005 and will continue through 2009 (see Appendix I).

Lynx is 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). Colorado is included in the federal listing as lynx habitat. Thus, an additional objective of the post-release monitoring program is to develop conservation strategies relevant to lynx in Colorado. To develop these conservation strategies, information specific to the ecology of the lynx in its southern Rocky Mountain range, such as habitat use, movement patterns, mortality factors, survival, and reproduction in Colorado is needed.

STUDY AREA

Byrne (1998) evaluated five areas within Colorado as potential lynx habitat based on (1) relative snowshoe hare densities (Bartmann and Byrne 2001), (2) road density, (3) size of area, (4) juxtaposition of habitats within the area, (5) historical records of lynx observations, and (6) public issues. Based on results from this analysis, the San Juan Mountains of southwestern Colorado were selected as the core reintroduction area, and where all lynx were reintroduced. Wild Canada lynx captured in Alaska, British Columbia, Manitoba, Quebec and Yukon were transported to Colorado and held at The Frisco Creek Wildlife Rehabilitation Center located within the reintroduction area prior to release.

Post-release monitoring efforts were focused in a 20,684 km^2 study area which included the core reintroduction area, release sites and surrounding high elevation sites (> 2,591 m). The area encompassed the southwest quadrant of Colorado and was bounded on the south by New Mexico, on the west by Utah, on the north by interstate highway 70, and on the east by the Sangre de Cristo Mountains (Figure 1). Southwestern Colorado is characterized by wide plateaus, river valleys, and rugged mountains that reach elevations over 4,200 m. Engelmann spruce/subalpine fir is the most widely distributed coniferous forest type within the study area. The lynx-established core area is roughly bounded by areas used by lynx in the Taylor Park/Collegiate Peak areas in central Colorado and includes areas of continuous use by lynx, including areas used during breeding and denning (Figure 1).

METHODS

REINTRODUCTION

Effort

Wild Canada lynx were captured in Alaska, British Columbia, Manitoba, Quebec and Yukon and transported to Colorado where they were held at the Frisco Creek Wildlife Rehabilitation Center prior to release. All lynx releases were conducted under the protocols found to maximize survival (see Shenk 2001). Estimated age, sex and body condition were ascertained and recorded for each lynx prior to release (see Wild 1999). Lynx were transported from the rehabilitation facility to their release site in individual cages. Specific release site locations were recorded in Universal Transverse Mercator (UTM) coordinates and identification of all lynx released at the same location, on the same day, was recorded. Behavior of the lynx on release and movement away from the release site were documented.

Movement, Distribution and Relative Use of Areas by Lynx

To monitor lynx movements and thus determine distribution and relative use of areas all released lynx were fitted with radio collars. All lynx released in 1999 were fitted with Telonics™ radio-collars. All lynx released since 1999, with the exception of 5 males released in spring 2000, were fitted with Sirtrack™ dual satellite/VHF radio-collars. These collars have a mortality indicator switch that operated on both the satellite and VHF mode. The satellite component of each collar was programmed to be active for 12 hours per week. The 12-hour active periods for individual collars were staggered throughout the week. Signals from the collars allowed for locations of the animals to be made via Argos, NASA, and NOAA satellites. The location information was processed by ServiceArgos and distributed to the CDOW through e-mail messages.

Datasets.-- To determine recent (post-reintroduction) movement and distribution of lynx reintroduced, born or initially trapped in Colorado and relative use of areas by these lynx, regular locations of lynx were collected through a combination of aerial and satellite tracking. Locations were recorded and general habitat descriptions for each aerial location was recorded. The first dataset of lynx locations included all locations obtained from daytime flights conducted with a Cessna 185 or similar aircraft to locate lynx by their VHF collar transmitters (hereafter aerial locations). VHF transmitters have been used on lynx since the first lynx were released in February 1999. The second type of lynx location data was collected via satellite from the satellite collar transmitters placed on the lynx (hereafter satellite locations). Satellite transmitter collars were first used for lynx in April 2000. These satellite collars also contained a VHF transmitter which also allowed locating lynx from the air or ground. All locations were recorded in Universal Transverse Mercator (UTM) coordinates using the CONUS NAD27 datum.

Flights to obtain lynx aerial locations were typically conducted on a weekly basis throughout most summer and winter months and twice a week during the den search field season (May 15 – June 30), depending on weather and availability of planes and pilots. Flights were typically concentrated in the high elevation (> 2700 m) southwest quadrant of Colorado which encompasses the core lynx release and research area (Figure 1). Flights during the den seasons were conducted to obtain locations on all female lynx within the state wearing an active VHF transmitter. VHF transmitters were outfitted with sufficient batteries to last 60 months. The satellite transmitters were designed to provide locations on a weekly basis with sufficient batteries to last for 18 months.

Lynx may not be exhibiting typical behavior or habitat use within the first few months after their release in Colorado. Therefore, a subset of each of the aerial and satellite datasets was created that eliminated the first 180 days (approximately 6 months) of locations obtained for each lynx immediately after their initial release. As a result, the truncated aerial location dataset contained lynx locations from September 1999 through March 2007 while the truncated satellite location dataset began October 2000 and extended through March 2007.

Accuracy of both aerial and satellite locations varied with the environmental conditions at the time the location was obtained. Accuracy of aerial locations was influenced by weather with accuracy ranging from 50 - 500 meters. Satellite location accuracy was also influenced by atmospheric conditions and position of the satellites. Satellite location accuracy ranged from 150 meters -10 km.

Movement and Distribution.-- To document all known lynx locations maps were generated with all aerial and satellite locations displayed. Due to lynx movements outside of Colorado, particularly into the states of New Mexico, Utah and Wyoming we further evaluated lynx use throughout those three states, as well as the data would allow. All individual lynx located at least once in these 3 states (non-truncated datasets) were identified and tallied for each year. To document consistency and known use of these states after the initial effect of being reintroduced was minimized (i.e., 180 days post-release), each individual lynx located at least once in these states from the truncated datasets were identified and tallied.

Relative Use.-- To document relative use of areas by lynx, 90% kernel use-density surfaces were calculated for truncated satellite and aerial lynx locations using the ArcGIS Spatial Analyst Kernel Density Tool. Due to differences in data collection frequency and accuracy between datasets, the truncated satellite and truncated aerial data were analyzed separately for generating the lynx use-density surfaces.

These use-density surfaces fit a smoothly curved surface over each lynx location. The surface value was highest at the location of the point and diminished with increasing distance from the point. A fixed kernel was used with a smoothing parameter of 5 km, reaching 0 at the search radius distance from the point. Only a circular neighborhood was possible. The volume under the surface equaled the total value for the point. The use-density at each output GIS raster cell was calculated by adding the values of all the kernel surfaces from all the lynx point locations that overlaid each raster cell center. The kernel function was based on the quadratic kernel function described in Silverman (1986, p. 76, equation 4.5). The use-density surfaces were calculated at 100 m resolution. To enhance graphic displays of higher use-density areas, density values representing single locations were not displayed.

Home Range

Annual home ranges were calculated as a 95% utilization distribution using a kernel home-range estimator for each lynx we had at least 30 locations for within a year. A year was defined as March 15 – March 14 of the following year. Locations used in the analyses were collected from September 1999 – January 2006 and all locations obtained for an individual during the first six months after its release were eliminated from any home range analyses as it was assumed movements of lynx initially post-release may not be representative of normal habitat use. Locations were obtained either through aerial VHF surveys or locations or the midpoint (ArcView Movement Extension) of all high quality (accuracy rating of 0-1km) satellite locations obtained within a single 24-hour period. All locations used within a single home range analysis were taken a minimum of 24 hours apart.

Home range estimates were classified as being for a reproductive or non-reproductive animal. A reproductive female was defined as one that had kittens with her; a reproductive male was defined as a male whose movement patterns overlapped that of a reproductive female. If a litter was lost within the defined year a home range described for a reproductive animal were estimated using only locations obtained while the kittens were still with the female.

Survival

Multi-state mark-recapture models were used to estimate monthly mortality rates and described in detail in Devineau et al. 2008 (*in review*). This approach accommodated missing data and allowed exploration of factors possibly affecting lynx survival such as sex, time spent in pre-release captivity, movement patterns, and origin.

Mortality Factors

When a mortality signal (75 beats per minute [bpm] vs. 50 bpm for the Telonics™ VHF transmitters, 20 bpm vs. 40 bpm for the Sirtrack™ VHF transmitters, 0 activity for Sirtrack™ PTT) was heard during either satellite, aerial or ground surveys, the location (UTM coordinates) was recorded. Ground crews then located and retrieved the carcass as soon as possible. The immediate area was searched for evidence of other predators and the carcass photographed in place before removal. Additionally, the mortality site was described and habitat associations and exact location were recorded. Any scat found near the dead lynx that appeared to be from the lynx was collected.

All carcasses were transported to the Colorado State University Veterinary Teaching Hospital (CSUVTH) for a post mortem exam to 1) determine the cause of death and document with evidence, 2) collect samples for a variety of research projects, and 3) archive samples for future reference (research or forensic). The gross necropsy and histology were performed by, or under the lead and direct supervision of a board certified veterinary pathologist. At least one research personnel from the CDOW involved with the lynx program was also present. The protocol followed standard procedures used for thorough post-mortem examination and sample collection for histopathology and diagnostic testing (see Shenk 1999 for details). Some additional data/samples were routinely collected for research, forensics, and archiving. Other data/samples were collected based on the circumstances of the death (e.g., photographs, video, radiographs, bullet recovery, samples for toxicology or other diagnostic tests, etc.).

From 1999–2004 the CDOW retained all samples and carcass remains with the exception of tissues in formalin for histopathology, brain for rabies exam, feces for parasitology, external parasites for ID, and other diagnostic samples. Since 2005 carcasses are disposed of at the CSUVTH with the exception of the lower canine, fecal samples, stomach content samples and tissue or bone marrow samples to be delivered by CDOW to the Center for Disease control for plague testing. The lower canine, from all carcasses, is sent to Matson Labs (Missoula, Montana) for aging and the fecal and stomach content samples are evaluated for diet.

Reproduction

Females were monitored for proximity to males during each breeding season. We defined a possible mating pair as any male and female documented within at least 1 km of each other in breeding season through either flight data or snow-tracking data. Females were then monitored for site fidelity to a given area during each denning period of May and June. Each female that exhibited stationary movement patterns in May or June were closely monitored to locate possible dens. Dens were found when field crews walked in on females that exhibited virtually no movement for at least 10 days from both aerial and ground telemetry.

Kittens found at den sites were weighed, sexed and photographed. Each kitten was uniquely marked by inserting a sterile passive integrated transponder (PIT, Biomark, Inc., Boise, Idaho, USA) tag subcutaneously between the shoulder blades. Time spent at the den was minimized to ensure the least amount of disturbance to the female and the kittens. Weight, PIT-tag number, sex and any distinguishing characteristics of each kitten was also recorded. Beginning in 2005, blood and saliva samples were collected and archived for genetic identification.

During the den site visits, den site location was recorded as UTM coordinates. General vegetation characteristics, elevation, weather, field personnel, time at the den, and behavioral responses of the kittens and female were also recorded. Once the females moved the kittens from the natal den area, den sites were visited again and site-specific habitat data were collected (see Habitat Use section below).

Captures

Captures were attempted for either lynx that were in poor body condition or lynx that needed to have their radio-collars replaced due to failed or failing batteries or to radio-collar kittens born in Colorado once they reached at least 10-months of age when they were nearly adult size. Methods of recapture included 1) trapping using a Tomahawk™ live trap baited with a rabbit and visual and scent lures, 2) calling in and darting lynx using a Dan-Inject CO_2 rifle, 3) custom box-traps modified from those designed by other lynx researchers (Kolbe et al. 2003) and 4) hounds trained to pursue felids were also used to tree lynx and then the lynx was darted while treed. Lynx were immobilized either with Telazol (3 mg/kg; modified from Poole et al. 1993 as recommended by M. Wild, DVM) or medetomidine (0.09mg/kg) and ketamine (3 mg/kg; as recommended by L. Wolfe, DVM)) administered intramuscularly (IM) with either an extendible pole-syringe or a pressurized syringe-dart fired from a Dan-Inject air rifle.

Immobilized lynx were monitored continuously for decreased respiration or hypothermia. If a lynx exhibited decreased respiration 2mg/kg of Dopram was administered under the tongue; if respiration was severely decreased, the animal was ventilated with a resuscitation bag. If medetomidine/ketamine were the immobilization drugs, the antagonist Atipamezole hydrochloride (Antisedan) was administered. Hypothermic (body temperature < 95^{o} F) animals were warmed with hand warmers and blankets.

While immobilized, lynx were fitted with replacement Sirtrack™ VHF/satellite collar and blood and hair samples were collected. Once an animal was processed, recovery was expedited by injecting the equivalent amount of the antagonist Antisedan IM as the amount of medetomidine given, if medetomodine/ketemine was used for immobilization. Lynx were then monitored while confined in the box-trap until they were sufficiently recovered to move safely on their own. No antagonist is available for Telezol so lynx anesthetized with this drug were monitored until the animal recovered on its own in the box-trap and then released. If captured and in poor body condition, lynx were anesthetized with either Telezol (2 mg/kg) or medetomodine/ketemine and returned to the Frisco Creek Wildlife Rehabilitation Center for treatment.

HABITAT USE

Gross habitat use was documented by recording canopy vegetation at aerial locations. More refined descriptions of habitat use by reintroduced lynx were obtained through following lynx tracks in the snow (i.e., snow-tracking) and site-scale habitat data collection conducted at sites found through this method to be used by lynx. See Shenk (2006) for detailed methodologies.

DIET AND HUNTING BEHAVIOR

Winter diet of reintroduced lynx was estimated by documenting successful kills through snow-tracking. Prey species from failed and successful hunting attempts were identified by either tracks or remains. Scat analysis also provided information on foods consumed. Scat samples were collected wherever found and labeled with location and individual lynx identification. Only part of the scat was collected (approximately 75%); the remainder was left in place in the event that the scat was being used by the animal as a territory mark. Site-scale habitat data collected for successful and unsuccessful snowshoe hare kills were compared.

SNOWSHOE HARE ECOLOGY

To further our understanding of snowshoe hare ecology in Colorado, a study was conducted comparing snowshoe hare densities among mature stands of Engelmann spruce/subalpine fir, lodgepole pine (*Pinus contorta*) and Ponderosa pine (*Pinus ponderosa*). The highest hare densities were found in Engelmann spruce/subalpine fir stands and no hares found in Ponderosa pine stands (Zahratka and Shenk 2008). A second study was initiated in 2005 to evaluate the importance of young, regenerating lodgepole pine and mature Engelmann spruce / subalpine fir stands in Colorado by examining density and demography of snowshoe hares that reside in each (Ivan 2005).

Specifically, this study was designed to evaluate small and medium lodgepole pine stands and large spruce/fir stands where the classes “small”, “medium”, and “large” refer to the diameter at breast height (dbh) of overstory trees as defined in the United States Forest Service R2VEG Database (small = 2.54–12.69 cm dbh, medium = 12.70–22.85 cm, and large = 22.86–40.64 cm dbh; J. Varner, United States Forest Service, personal communication). The study design was also developed to identify which of the numerous hare density-estimation procedures available perform accurately and consistently using an innovative, telemetry augmentation approach as a baseline. In addition, movement patterns and seasonal use of deciduous cover types such as riparian willow were assessed. Finally, the study was designed to further expound on the relationship between density, demography, and stand-type by examining how snowshoe hare density and demographic rates vary with specific vegetation, physical, and landscape characteristics of a stand.

RESULTS

REINTRODUCTION

Effort

From 1999 through 2006, 218 wild-caught lynx were reintroduced into southwestern Colorado (Table 1). No lynx were released in 2007 or 2008. All lynx were released with either VHF or dual VHF/satellite radio collars so they could be monitored for movement, reproduction and survival. The CDOW does not plan to release any additional lynx in 2009.

Movement Patterns and Distribution

Numerous travel corridors were used repeatedly by more than one lynx. These travel corridors include the Cochetopa Hills area for northerly movements, the Rio Grande Reservoir-Silverton-Lizardhead Pass for movements to the west, and southerly movements down the east side of Wolf Creek Pass to the southeast through the Conejos River Valley. Lynx appear to remain faithful to an area during winter months, and exhibit more extensive movements away from these areas in the summer.

A total of 10,935 aerial and 26,082 satellite locations were obtained from the 218 reintroduced lynx, radio-collared Colorado kittens (*n* = 14) and unmarked lynx captured in Colorado (*n* = 2) as of August 27, 2008. The majority of these locations were in Colorado (Figure 2). Some reintroduced lynx dispersed outside of Colorado into Arizona, Idaho, Iowa, Kansas, Montana, Nebraska, Nevada, New Mexico, South Dakota, Utah and Wyoming (Figure 2). The majority of surviving lynx from the reintroduction effort currently continue to use high elevation (> 2900 m), forested terrain in an area bounded on the south by New Mexico north to Independence Pass, west as far as Taylor Mesa and east to Monarch Pass. Most movements away from the Core Release Area were to the north.

Relative Use

The lynx use-density surfaces resulting from the fixed kernel analyses provided relative probabilities of finding lynx in areas throughout their distribution. A single use-density surface was calculated separately for both the aerial (*n* = 8058) and satellite truncated datasets (*n* = 16240).

All 218 lynx released in Colorado, all radio-collared kittens and 2 captured unmarked adults were located at least once in Colorado. The majority of these lynx remained in Colorado. The use-density surfaces within Colorado were displayed separately for both the aerial (Figure 3) and satellite truncated datasets (Figure 4). Of the total locations available in the truncated datasets used to generate the use-density surfaces, 7953 of the aerial locations and 13,241 of the satellite locations were in Colorado. Aerial and satellite use-density surfaces indicated similar high use-density areas. Satellite locations indicated broader spatial use by lynx because satellite collars provided more locations than flights.

The use-density surface for lynx use in Colorado indicates two primary areas of use. The first is the Core Research Area (see Figure 1) and a secondary core centered in the Collegiate Peaks Wilderness (Figures 1, 3 and 4). High use is also documented for 1) the area east of Dillon, on both the north and south sides of I70 and 2) the area north of Hwy 50 centered around Gunnison and then north to Crested Butte. These last 2 high use areas are smaller in extent than the 2 core areas.

Relative use-density surfaces were also generated for New Mexico, Wyoming and Utah and presented in detail in Shenk (2007).

Home Range

Reproductive females had the smallest 90% utilization distribution annual home ranges ($\bar{x}$ = 75.2 km^2, SE = 15.9 km^2, *n* = 19), followed by attending males ($\bar{x}$ = 102.5 km^2, SE = 39.7 km^2, *n* = 4). Non-reproductive females had the largest annual home ranges ($\bar{x}$ = 703.9 km^2, SE = 29.8 km^2, *n* = 32) followed by non-reproductive males ($\bar{x}$ = 387.0 km^2, SE = 73.5 km^2, *n* = 6). Combining all non-reproductive animals yielded a mean annual home range of 653.8 km^2 (SE = 145.4 km^2, *n* = 38).

Survival

Detailed analyses of lynx mortality was completed and described in Devineau et al. 2008 (*in review*). Monthly mortality rate was lower inside the study area than outside, and slightly higher for male than for female lynx, although 95% confidence intervals for sexes overlapped. Mortality was higher immediately after release (first month = 0.0368 [SE = 0.0140] inside the study area, and 0.1012 [SE = 0.0359] outside the study area), and then decreased according to a quadratic trend over time.

As of August 27, 2008, CDOW was actively monitoring/tracking 45 of the 106 lynx still possibly alive (Table 2). There are 62 lynx that we have not heard signals on since at least August 27, 2007 and these animals are classified as 'missing' (Table 2). One of these missing lynx is a mortality of unknown identity, thus only 61 are truly missing. Possible reasons for not locating these missing lynx include 1) long distance dispersal, beyond the areas currently being searched, 2) radio failure, or 3) destruction of the radio (e.g., run over by car). CDOW continues to search for all missing lynx during both aerial and ground searches. Two of the missing lynx released in 2000 are thought to have slipped their collars.

Mortality Factors

Of the total 218 adult lynx released, we have 112 known mortalities as of August 27, 2008 (Table 2). Starvation was a significant cause of mortality in the first year of releases only. The primary known causes of death included 30.4% human-induced deaths which were confirmed or probably caused by collisions with vehicles or gunshot (Table 3). Malnutrition and disease/illness accounted for 18.8% of the deaths. An additional 36.6% of known mortalities were from unknown causes.

Mortalities occurred throughout the areas through which lynx moved, with 26.8% occurring outside of Colorado. The out of state mortalities included 14 in New Mexico, 4 in Wyoming, Utah and Nebraska, and 1 each in Arizona, Kansas, Iowa and Montana (Figure 2, Table 4).

Reproduction

Reproduction was first documented in 2003 when 6 dens and a total of 16 kittens were found in the lynx Core Release Area in southwestern Colorado. Reproduction was also documented in 2004, 2005 and 2006. No dens were found in 2007 or 2008 (Table 5).

Field crews weighed, photographed, PIT-tagged the kittens and checked body condition. Beginning in 2005, we also collected blood samples from the kittens for genetic work in an attempt to confirm paternity Kittens were processed as quickly as possible (11-32 minutes) to minimize the time the kittens were without their mother. While working with the kittens the females remained nearby, often making themselves visible to the field crews. The females generally continued a low growling vocalization the entire time personnel were at the den. In all cases, the female returned to the den site once field crews left the area. At all dens the females appeared in excellent condition, as did the kittens. The kittens weighed from 270-500 grams. Lynx kittens weigh approximately 200 grams at birth and do not open their eyes until they are 10-17 days old.

The percent of tracked females found with litters in 2006 was lower (0.095) than in the 3 previous years (0.413, SE = 0.032, Table 5). However, all demographic and habitat characteristics measured at the 4 dens that were found in 2006 were comparable to all other dens found. Mean number of kittens per litter from 2003-2006 was 2.78 (SE = 0.05) and sex ratio of females to males was equal ($\bar{x}$ = 1.14, SE = 0.14). More details of reproduction in 2003-06 were presented in Shenk (2007).

Den Sites.-- A total of 37 dens were found from 2003-2006. All of the dens except one have been scattered throughout the high elevation areas of Colorado, south of I-70. In 2004, 1 den was found in southeastern Wyoming, near the Colorado border. Dens were located on steep ($\bar{x}_{slope}$ = 30^o, SE=2^o), north-facing, high elevation ($\bar{x}$ = 3354 m, SE = 31 m) slopes. The dens were typically in Engelmann spruce/subalpine fir forests in areas of extensive downfall of coarse woody debris (Shenk 2006). All dens were located within the winter use areas used by the females. No dens were found in either 2007 or 2008 even though up to 34 adult females were monitored intensively during the denning period (Table 5).

Captures

Two adult lynx were captured in 2001 for collar replacement. One lynx was captured in a tomahawk live-trap, the other was treed by hounds and then anesthetized using a jab pole. Five adult lynx were captured in 2002; 3 were treed by hounds and 2 were captured in padded leghold traps. In 2004, 1 lynx was captured with a Belisle snare and 6 adult lynx were captured in box-traps. Trapping effort was substantially increased in winter and spring 2005 and 12 adult lynx were captured and re-collared. Eight reintroduced lynx were captured in winter and spring 2006. In 2007, 11 reintroduced adult lynx were captured and re-collared and an additional 10 in 2008. All lynx captured in Colorado from 2005-2008 were caught in box-traps.

In addition, as part of the collaring trapping effort, 14 Colorado-born kittens were captured and collared at approximately 10-months of age. Seven 2004-born kittens were collared in spring 2005, and 7, 2005-born kittens were collared in spring 2006. We were not successful at capturing and collaring any kittens born in 2006 in winter 2006-07. We did however, capture 2 adults (approximate age 2 years old) in winter 2006-07 that had no PIT-tags or radio collars. We assume these 2 lynx were from litters born in Colorado that were never found at dens (i.e., why there were no PIT-tags). All lynx captured for collaring or re-collaring were fitted with new Sirtrack ™ dual VHF/satellite collars and re-released at their capture locations.

Seven adult lynx were captured from March 1999-August 27, 2008 because they were in poor body condition (Table 6). Five of these lynx were successfully treated at the Frisco Creek Rehabilitation Center and re-released in the Core Release Area. One lynx, BC00F07, died from starvation and hypothermia within 1 day of capture at the rehabilitation center. Lynx QU04M07 died 3 days after capture at the rehabilitation center. Necropsy results documented starvation as the cause of death for this lynx that was precipitated by hydrocephalus and bronchopneumonia (unpublished data T. Spraker, CSUVTH).

Seven lynx were captured (either by CDOW personnel or conservation personnel in other states) because they were in atypical habitat outside the state of Colorado (Table 6). They were held at Frisco Creek Rehabilitation Center for a minimum of 3 weeks, fitted with new Sirtrack ™ dual VHF/satellite collars and re-released in the Core Release Area in Colorado. Five of these 7 lynx were still alive 6 months post-re-release but 3 had already dispersed out of Colorado and 1 stayed in Colorado through August 27, 2008. Two of these lynx died within 6 months of re-release: 1 died of starvation in Colorado and the other died of unknown causes in Nebraska. One lynx captured out of state and re-released currently remains in Colorado.

HABITAT USE

Landscape-scale daytime habitat use was documented from 9496 aerial locations of lynx collected from February 1999-June 30, 2007. Throughout the year Engelmann spruce - subalpine fir was the dominant cover used by lynx. A mix of Engelmann spruce, subalpine fir and aspen (*Populus tremuloides*) was the second most common cover type used throughout the year. Various riparian and riparian-mix areas were the third most common cover type where lynx were found during the daytime flights. Use of Engelmann spruce-subalpine fir forests and Engelmann spruce-subalpine fir-aspen forests was similar throughout the year. There was a trend in increased use of riparian areas beginning in July, peaking in November, and dropping off December through June.

Site-scale habitat data collected from snow-tracking efforts indicate Engelmann spruce and subalpine fir were also the most common forest stands used by lynx for all activities during winter in southwestern Colorado. Comparisons were made among sites used for long beds, dens, travel and where they made kills. Little difference in aspect, mean slope and mean elevation were detected for 3 of the 4 site types including long beds, travel and kills where lynx typically use gentler slopes ($\bar{x} = 15.7^{o}$) at an mean elevation of 3173 m, and varying aspects with a slight preference for north-facing slopes. See Shenk (2006) for more detailed analyses of habitat use.

DIET AND HUNTING BEHAVIOR

Winter diet of lynx was documented through detection of kills found through snow-tracking. Prey species from failed and successful hunting attempts were identified by either tracks or remains. Scat analysis also provided information on foods consumed. A total of 548 kills were located from February 1999-April 2008. We collected over 950 scat samples from February 1999-April 2008 that will be analyzed for content. In each winter, the most common prey item was snowshoe hare, followed by red squirrel (*Tamiusciurus hudsonicus*; Table 7). The percent of snowshoe hare kills found however, varied annually from a low of 55.56% in 1999 to a high of 90.77% in winter 2002-2003. An annual mean of 73.29% (SE = 4.67) snowshoe hare kills in the diet has been documented.

A comparison of percent overstory for successful and unsuccessful snowshoe hare chases indicated lynx were more successful at sites with slightly higher percent overstory, if the overstory species were Englemann spruce, subalpine fir or willow. Lynx were slightly less successful in areas of greater aspen overstory. This trend was repeated for percent understory at all 3 height categories except that higher aspen understory improved hunting success. Higher density of Engelmann spruce and subalpine fir increased hunting success while increased aspen density decreased hunting success.

SNOWSHOE HARE ECOLOGY

Two years of a 3-year study to evaluate snowshoe hare densities, demography and seasonal movement patterns among small and medium tree-sized lodgepole pine stands and mature spruce/fir stands have been completed and preliminary results presented (see Appendix I).

DISCUSSION

In an effort to establish a viable population of lynx in Colorado, CDOW initiated a reintroduction effort in 1997 with the first lynx released in winter 1999. From 1999 through spring 2007, 218 lynx were released in the Core Release Area.

Locations of each lynx were collected through aerial- or satellite-tracking to document movement patterns and to detect mortalities. Most lynx remain in the high elevation, forested areas in southwestern Colorado. The use-density surfaces for lynx use in Colorado indicate two primary areas of use. The first is the Core Research Area (see Figure 1) and a secondary core centered in the Collegiate Peaks Wilderness (Figures 1, 3, 4). High use is also documented for 1) the area east of Dillon, on both the north and south sides of I70 and 2) the area north of Hwy 50 centered around Gunnison and then north to Crested Butte. These last 2 high use areas are smaller in extent than the 2 core areas.

Dispersal movement patterns for lynx released in 2000 and subsequent years were similar to those of lynx released in 1999 (Shenk 2000). However, more animals released in 2000 and subsequent years remained within the Core Release Area than those released in 1999. This increased site fidelity may have been due to the presence of con-specifics in the area on release. Numerous travel corridors within Colorado have been used repeatedly by more than 1 lynx. These travel corridors include the Cochetopa Hills area for northerly movements, the Rio Grande Reservoir-Silverton-Lizardhead Pass for movements to the west, and southerly movements down the east side of Wolf Creek Pass to the southeast to the Conejos River Valley.

Lynx appear to remain faithful to an area during winter months, and exhibit more extensive movements away from these areas in the summer. Reproductive females had the smallest 90% utilization distribution home ranges ($\bar{x}$ = 75.2 km^2, SE = 15.9 km^2), followed by attending males ($\bar{x}$ = 102.5 km^2, SE = 39.7 km^2) and non-reproductive animals ($\bar{x}$ = 653.8 km^2, SE = 145.4 km^2). Most lynx currently being tracked are within the Core Release Area. During the summer months, lynx were documented to make extensive movements away from their winter use areas. Extensive summer movements away from areas used throughout the rest of the year have been documented in native lynx in Wyoming and Montana (Squires and Laurion 1999).

Current data collection methods used for the Colorado lynx reintroduction program were not specifically designed to address the reintroduced lynx movements or use of areas in other states. In particular, the core research and release area were in Colorado. Therefore, the number of aerial locations obtained would be far fewer in other states than in Colorado which would bias low the number of lynx and intensity of lynx use documented outside the state. In contrast, obtaining satellite locations is not biased by the location of the lynx. Satellite locations are, however, biased by the shorter time the satellite transmitters function, approximately 18 months versus 60 months for the VHF transmitters used to obtain the aerial locations. However, data collected to meet objectives of the lynx reintroduction program were used to provide information to help address the question of lynx use outside of Colorado. Due to the rarity of flights conducted outside Colorado, only use-density surfaces generated from satellite locations were used to document relative lynx use of areas in New Mexico, Utah and Wyoming.

New Mexico and Wyoming have been used continuously by lynx since the first year lynx were released in Colorado (1999) to the present. Lynx reintroduced in Colorado were first documented in Utah in 2000 and are still being documented there to date. In addition, all levels of lynx use-density documented throughout Colorado are also represented in New Mexico, Utah and Wyoming from none to the highest level of use (Shenk 2007). One den was found in Wyoming. Although no reproduction has been documented in New Mexico or Utah to date, documenting areas of the highest intensity of use and the continuous presence of lynx within these states for over six years does suggest the potential for year-round residency of lynx and reproduction in those states.

From 1999-August 2008, there were 112 mortalities of released adult lynx. Human-caused mortality factors are currently the highest causes of death with approximately 30.4% attributed to collisions with vehicles or gunshot. Starvation and disease/illness accounted for 18.8% of the deaths while 36.6% of the deaths were from unknown causes. Lynx mortalities were documented throughout all areas lynx used, including 30 (26.8%) occurring in other states (Figure 2, Table 3). Nearly half (14 of 30) of the out-of-state mortalities were documented in New Mexico. Monthly mortality rate was lower inside the study area than outside, and slightly higher for male than for female lynx, although 95% confidence intervals for sexes overlapped. Mortality was higher immediately after release (first month = 0.0368 [SE = 0.0140] inside the study area, and 0.1012 [SE = 0.0359] outside the study area), and then decreased according to a quadratic trend over time.

Reproduction is critical to achieving a self-sustaining viable population of lynx in Colorado. Reproduction was first documented from the 2003 reproduction season and again in 2004, 2005 and 2006. Lower reproduction occurred in 2006 (Table 5) but did include a Colorado-born female giving birth to 2 kittens, documenting the first recruitment of Colorado-born lynx into the Colorado breeding population. No reproduction was documented in 2007 or 2008. The cause of the decreased reproduction from 2006 - 08 is unknown. One possible explanation would be a decrease in prey abundance.

Additional reproduction is likely to have occurred in all years from females we were no longer tracking, and from Colorado-born lynx that have not been collared. The dens we find are more representative of the minimum number of litters and kittens in a reproduction season. To achieve a viable population of lynx, enough kittens need to be recruited into the population to offset the mortality that occurs in that year and hopefully even exceed the mortality rate to achieve an increasing population.

The use-density surfaces depict intensity of use by location. Why certain areas would be used more intensively than others should be explained by the quality of the habitat in those areas.

Characteristics of areas used by lynx, as documented through aerial locations and snow-tracking of lynx in the Colorado core research area, include mature Engelmann spruce-subalpine fir forest stands with 42-65% canopy cover and 15-20% conifer understory cover (Shenk 2006). Within these forest stand types, lynx appear to have a slight preference for north-facing, moderate slopes ($\bar{x}$ = 15.7°) at high elevations ($\bar{x}$ = 3173 m; Shenk 2006).

Snow-tracking of released lynx also provided information on hunting behavior and diet through documentation of kills, food caches, chases, and diet composition estimated through prey remains. The primary winter prey species (n = 548) were snowshoe hare (Table 7) with an annual $\bar{x}$ = 73.3% (SE = 4.7, n = 10) and red squirrel (annual $\bar{x}$ = 18.2%, SE = 4.2, n = 10). Thus, areas of good habitat must also support populations of snowshoe hare and red squirrel. In winter, lynx reintroduced to Colorado appear to be feeding on their preferred prey species, snowshoe hare and red squirrel in similar proportions as those reported for northern lynx during lows in the snowshoe hare cycle (Aubry et al. 1999). Environmental conditions in the springs and summers of 2003 and 2006 resulted in high cone crops during their following winters based on field observations, resulting in increased red squirrel abundance. This may partially explain the higher percent of red squirrel kills, and thus a lower percent of snowshoe hare kills, found in winters 2003-04 and 2006-07 (Table 7).

Caution must be used in interpreting the proportion of identified kills. Such a proportion ignores other food items that are consumed in their entirety and thus are biased towards larger prey and may not accurately represent the proportion of smaller prey items, such as microtines, in lynx winter diet. Through snow-tracking we have evidence that lynx are mousing and several of the fresh carcasses have yielded small mammals in the gut on necropsy. The summer diet of lynx has been documented to include less snowshoe hare and more alternative prey than in winter (Mowat et al., 1999). All evidence suggests reintroduced lynx are finding adequate food resources to survive.

Mowat et al. (1999) suggest lynx and snowshoe hare select similar habitats except that hares select more dense stands than lynx. Very dense understory limits hunting success of the lynx and provides refugia for hares. Given the high proportion of snowshoe hare in the lynx diet in Colorado, we might then assume the habitats used by reintroduced lynx also depict areas where snowshoes hare are abundant and available for capture by lynx in Colorado. From both aerial locations taken throughout the year and from the site-scale habitat data collected in winter, the most common areas used by lynx are in stands of Engelmann spruce and subalpine fir. This is in contrast to adjacent areas of Ponderosa pine, pinyon juniper, aspen and oakbrush. The lack of lodgepole pine in the areas used by the lynx may be more reflective of the limited amount of lodgepole pine in southwestern Colorado, the Core Release Area, rather than avoidance of this tree species.

Hodges (1999) summarized habitats used by snowshoe hare from 15 studies as areas of dense understory cover from shrubs, stands that are densely stocked, and stands at ages where branches have more lateral cover. Species composition and stand age appears to be less correlated with hare habitat use than is understory structure (Hodges 1999). The stands need to be old enough to provide dense cover and browse for the hares and cover for the lynx. In winter, the cover/browse needs to be tall enough to still provide browse and cover in average snow depths. Hares also use riparian areas and mature forests with understory. Site-scale habitat use documented for lynx in Colorado indicate lynx are most commonly using areas with Engelmann spruce understory present from the snow line to at least 1.5 m above the snow. The mean percent understory cover within the habitat plots is typically less than 15% regardless of understory species. However, if the understory species is willow, percent understory cover is typically double that, with mean number of shrubs per plot approximately 80, far greater than for any other understory species.

In winter, hares browse on small diameter woody stems (<0.25"), bark and needles. In summer, hares shift their diet to include forbs, grasses, and other succulents as well as continuing to browse on woody stems. This shift in diet may express itself in seasonal shifts in habitat use, using more or denser coniferous cover in winter than in summer. The increased use of riparian areas by lynx in Colorado from July to November may reflect a seasonal shift in hare habitat use in Colorado. Major (1989) suggested lynx hunted the edge of dense riparian willow stands. The use of these edge habitats may allow lynx to hunt hares that live in habitats normally too dense to hunt effectively. The use of riparian areas and riparian-Engelmann spruce-subalpine fir and riparian-aspen mixes documented in Colorado may stem from a similar hunting strategy. However, too little is known about habitat use by hares in Colorado to test this hypothesis at this time.

Lynx also require sufficient denning habitat. Denning habitat has been described by Koehler (1990) and Mowat et al. (1999) as areas having dense downed trees, roots, or dense live vegetation. We found this to be in true in Colorado as well (Shenk 2006). In addition, the dens used by reintroduced lynx were at high elevations and on steep north-facing slopes. All females that were documented with kittens denned in areas within their winter-use area.

SUMMARY

From results to date it can be concluded that CDOW developed release protocols that ensure high initial post-release survival of lynx, and on an individual level, lynx demonstrated they can survive long-term in areas of Colorado. We also documented that reintroduced lynx exhibited site fidelity, engaged in breeding behavior and produced kittens that were recruited into the Colorado breeding population. What is yet to be demonstrated is whether current conditions in Colorado can support the recruitment necessary to offset annual mortality in order to sustain the population. Monitoring of reintroduced lynx will continue in an effort to document such viability.

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Table 1. Number of wild-caught male (M) and female (F) Canada lynx (*Lynx canadensis*) from Alaska (AK) and Canada (BC = British Columbia, MB = Manitoba, QU = Quebec and YK = Yukon) released in southwestern Colorado per year from 1999–2006.

Year	%Released	Sex	State / Province of Origin					Total
			AK	BC	MB	QU	YK	
1999	19	F	13	5			4	22
		M	7	6			6	19
2000	25	F	6	9			20	35
		M	4	9			7	20
2003	15	F		10		7		17
		M		10	1	5		16
2004	17	F		7		10		17
		M		13		7		20
2005	17	F		4	3	8	3	18
		M		9		8	3	20
2006	6	F		4			3	7
		M		5			2	7
	Total		30	91	4	45	48	218

Table 2. Status of adult Canada lynx (*Lynx canadensis*) reintroduced to Colorado as of August 27, 2008.

Lynx	Females	Males	Unknown	TOTALS
Released	115	103		218
Known Dead	62	49	1	112
Possible Alive	53	54		106
Missing	27	35		61[a]
Monitoring/tracking	26	19		45

[a] 1 is unknown mortality

Table 3. Causes of death for all Canada lynx (*Lynx canadensis*) released into southwestern Colorado 1999-2006 as of August 27, 2008.

Cause of Death	Mortalities		
	Total (%)	In Colorado (%)	Outside Colorado (%)
Unknown	41 (36.6)	27 (32.91)	14 (46.7)
Gunshot	15 (13.4)	9 (11.0)	6 (20.0)
Hit by Vehicle	14 (12.5)	9 (11.0)	5 (16.7)
Starvation	11 (9.8)	10 (12.2)	1 (3.3)
Other Trauma	8 (7.1)	7 (8.5)	1 (3.3)
Plague	7 (6.3)	7 (8.5)	0 (0)
Probable Gunshot	5 (4.5)	4 (4.9)	1 (3.3)
Predation	5 (4.5)	5 (6.1)	0 (0)
Probable Predation	3 (2.7)	2 (2.4)	1 (3.3)
Illness	3 (2.7)	2 (2.4)	1 (3.3)
Total Mortalities	112	82 (73.2)	30 (26.8)

Table 4. Known lynx mortalities (*n* = 30) and causes of death documented by state outside of Colorado from February 1999 – August 27, 2008.

Lynx ID	State	Date Mortality Recorded	Cause of Death
AK99F8	New Mexico	7/30/1999	Starvation
Unknown	New Mexico	2000	Hit by Vehicle
AK99M11	New Mexico	1/27/2000	Unknown
YK99M06	New Mexico	6/19/2000	Probable Gunshot
AK99F13	New Mexico	6/22/2000	Unknown
YK00F04	New Mexico	4/20/2001	Gunshot
BC99M04	New Mexico	6/7/2002	Gunshot
QU05M01	New Mexico	8/22/2005	Unknown
QU04F05	New Mexico	8/26/2005	Hit by Vehicle
QU03F07	New Mexico	9/15/2005	Unknown
BC00M04	New Mexico	7/19/2006	Unknown
YK06F01	New Mexico	10/19/2006	Unknown
BC03M08	New Mexico	10/19/2006	Unknown
BC06F07	New Mexico	1/8/2007	Gunshot
AK99M06	Nebraska	11/16/1999	Gunshot
AK99M01	Nebraska	1/11/2005	Snared (Other Trauma)
QU05M08	Nebraska	10/1/2006	Unknown
MB05F02	Nebraska	2/13/2007	Gunshot
BC00F14	Wyoming	7/28/2004	Unknown
QU04F07	Wyoming	9/21/2004	Unknown
BC06M10	Wyoming	8/15/2006	Vehicle Collision
QU04F02	Wyoming	3/14/2007	Unknown
AK00M03	Utah	7/2/2001	Unknown
QU05M03	Utah	10/26/2005	Unknown
YK06M01	Utah	12/4/2006	Unknown
YK00F07	Utah	8/6/2007	Unknown
YK99F01	Arizona	9/15/2005	Gunshot
YK00M03	Kansas	9/30/2005	Vehicle Collision
YK05M03	Montana	11/8/2005	Unknown
YK05M02	Iowa	8/6/2007	Vehicle Collision

Table 5. Lynx reproduction summary statistics for 1999-2008. No reproduction was expected in 1999 because it was the first year of lynx releases and most animals were released after breeding season.

Year	Females Tracked	Dens Found in May/June	Percent Tracked Females with Kittens	Additional Litters Found in Winter	Mean Kittens/Litter (SE)	Total Kittens Found	Sex Ratio M/F (SE)
2000	9	0	0.0	0		0	
2001	25	0	0.0	0		0	
2002	21	0	0.0	0		0	
2003	17	6	0.353	0	2.67 (0.33)	16	1.0
2004	26	11	0.462	2	2.83 (0.24)	39	1.5
2005	40	17	0.425	1	2.88 (0.18)	50	0.8
2006	42	4	0.095	0	2.75 (0.47)	11	1.2
2007	34	0	0.0	0		0	
2008	28	0	0.0	0		0	
TOTAL						116	1.14 (0.14)

Table 6. Lynx captured because they were in poor body condition or were in atypical habitat and their fates 6 months post re-release and as of August 28, 2008.

Lynx ID	Date of Capture	State Where Captured	Reason For Capture	Date of Re-release	Status 6 Months Post Re-release	Current Status
BC99F6	3/25/1999	Colorado	Poor body condition	5/28/1999	Dead	Died 7/19/1999 in Colorado from vehicle collision
AK99M9	3/24/2000	Colorado	Poor body condition	5/3/2000	Missing	Last located 5/3/2000, collar failure
AK99F2	4/18/2000	Colorado	Poor body condition	5/22/2000	Alive in Colorado	Last located 7/30/2003 in Colorado
BC00F7	2/11/2001	Colorado	Poor body condition	N/A	Dead	Died at Rehab Center on 2/12/2001
BC00M13	3/21/2001	Wyoming	Poor body condition	4/24/2001	Alive in Colorado	Last located 10/26/2004 in Colorado
BC03M08	9/5/2003	Colorado	Poor body condition	1/1/2004	Alive in Colorado	Died in New Mexico of unknown causes 10/19/06
QU04M07	2/2/2006	Colorado	Poor body condition	N/A	Dead	Died at Rehab Center on 2/5/2006 from hydrocephalous and pneumonia
BC04M01	11/5/2004	Utah	Atypical habitat	12/5/2004	Alive in Colorado	In Colorado as of 8/27/2008
QU04F02	4/10/2005	Nebraska	Atypical habitat	5/7/2005	Alive in Wyoming	Died 3/14/2007 in Wyoming (good habitat) of unknown causes
QU05M08	11/25/2005	Wyoming	Atypical habitat	4/18/2006	Dead	Died of unknown causes in Nebraska 10/1/2006
QU04M04	12/5/2006	Utah	Atypical habitat	1/20/2007	Dead in Colorado	Died of starvation in Colorado, found 3/19/07
YK00F07	12/12/2006	Utah	Atypical habitat	1/20/2007	Alive in Utah	Died in Utah of unknown causes 8/6/2007
YK05M02	1/1/2007	Kansas	Atypical habitat	2/2/2007	Alive in Iowa	Died in Iowa from vehicle collision 8/6/2007
BC04M08	1/22/2007	Wyoming	Atypical habitat	2/15/2007	Alive in Colorado	Died in Colorado from gunshot 1/4/2008

Table 7. Number of kills found each winter field season through snow-tracking of lynx and percent composition of kills of the three primary prey species.

		Prey (%)			
Field Season	n	Snowshoe Hare	Red Squirrel	Cottontail	Other
1999	9	55.56	22.22	0	22.22
1999-2000	83	67.47	19.28	1.20	12.05
2000-2001	89	67.42	19.10	8.99	4.49
2001-2002	54	90.74	5.56	0	3.70
2002-2003	65	90.77	6.15	0	3.08
2003-2004	37	67.57	27.03	2.70	2.70
2004-2005	78	83.33	10.26	0	6.41
2005-2006	50	90.00	0.08	0	0.02
2006-2007	41	61.00	39.0	0	0
2007-2008	42	59.00	33.3	0	7.4
Total/Mean	548	73.29 (SE=4.7)	18.2 (SE=4.2)	1.29 (SE=0.95)	6.21 (SE=2.22)

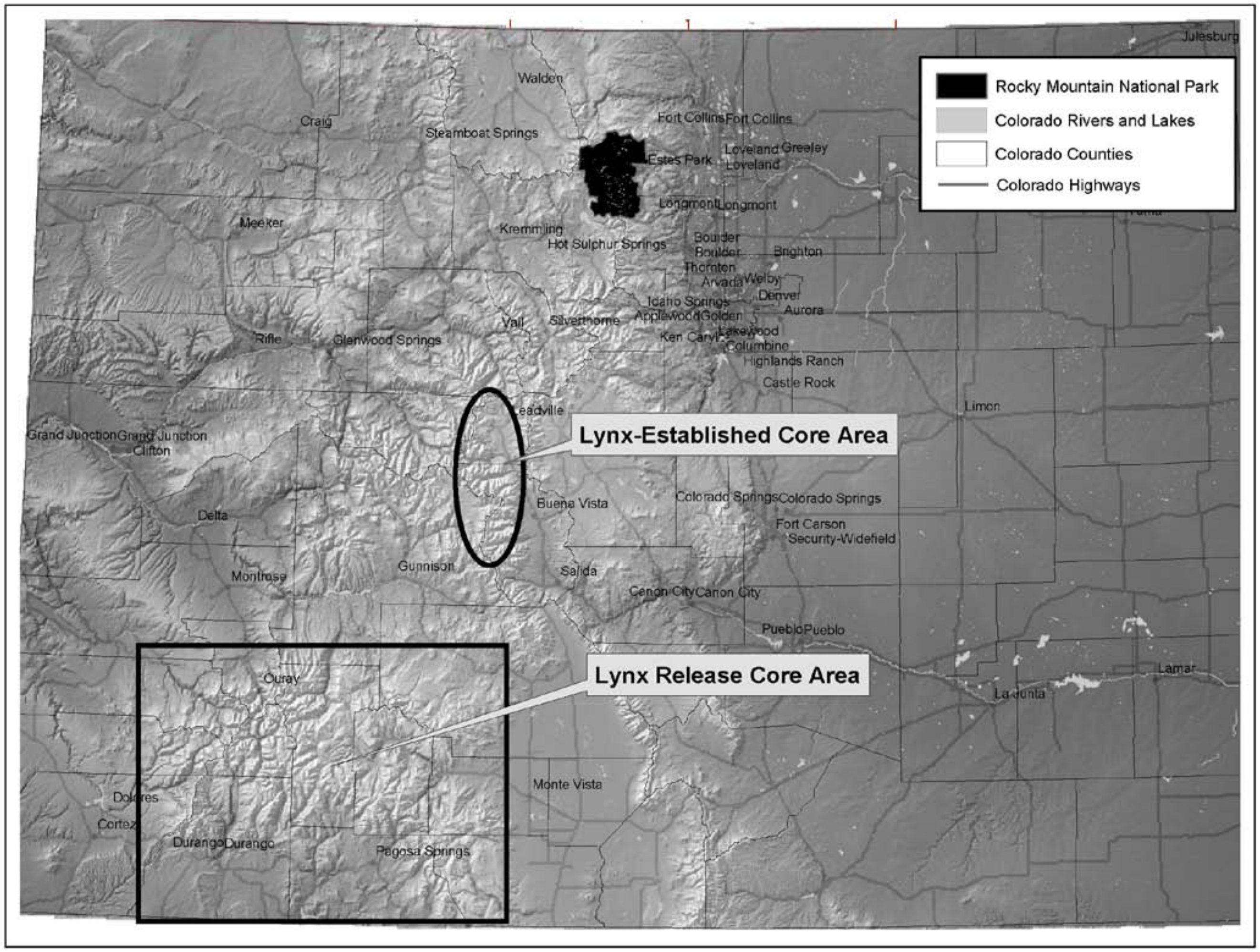

Figure 1. Lynx are monitored throughout Colorado and by satellite throughout the western United States. The lynx core release area, where all lynx were released, is located in southwestern Colorado. A lynx-established core use area has developed in the Taylor Park and Collegiate Peak area in central Colorado.

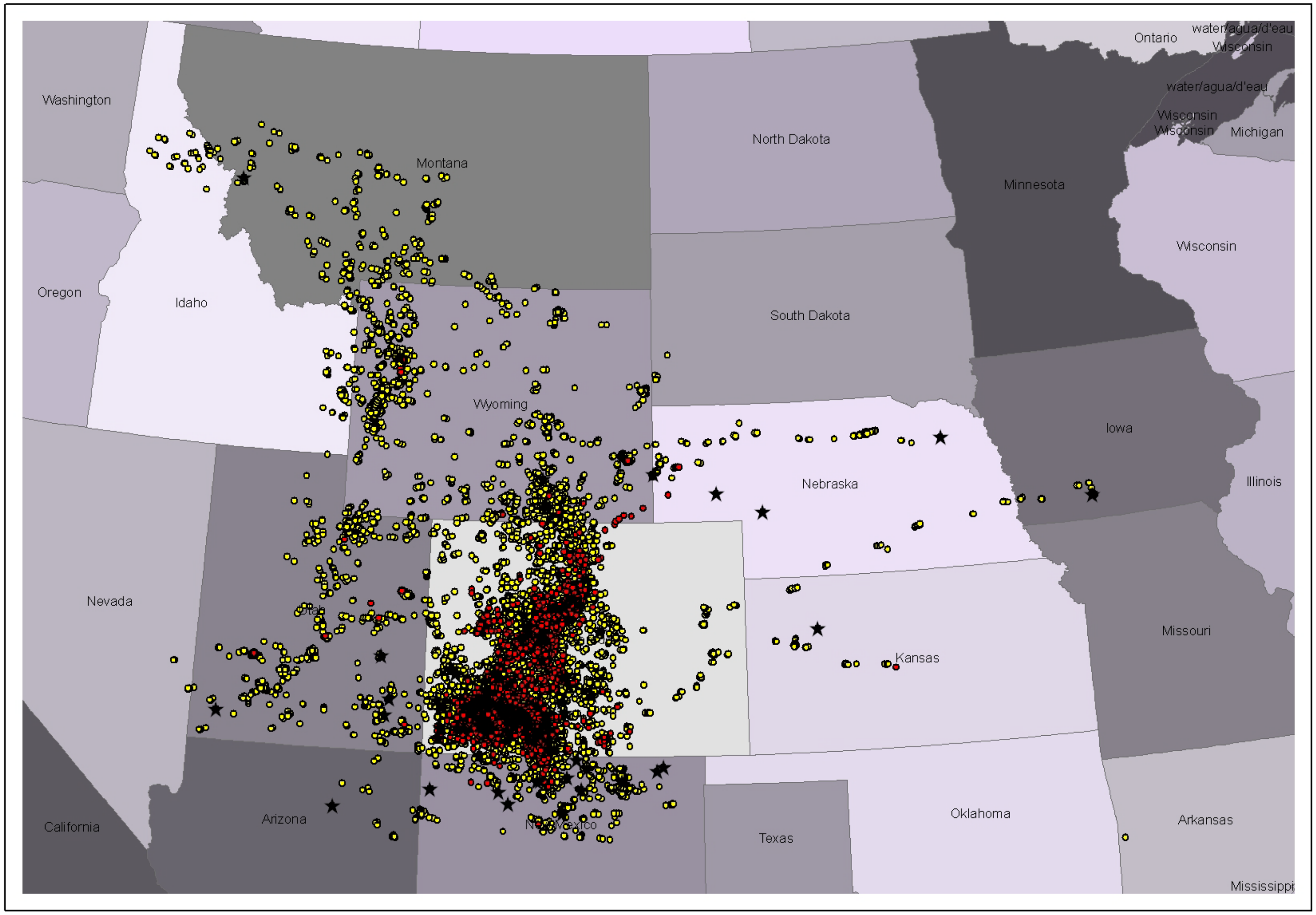

Figure 2. All documented lynx locations (non-truncated datasets) obtained from either aerial (red circles) or satellite (yellow circles) tracking from February 1999 through August 27, 2008. All known lynx mortality locations (n = 112) are displayed as black stars.

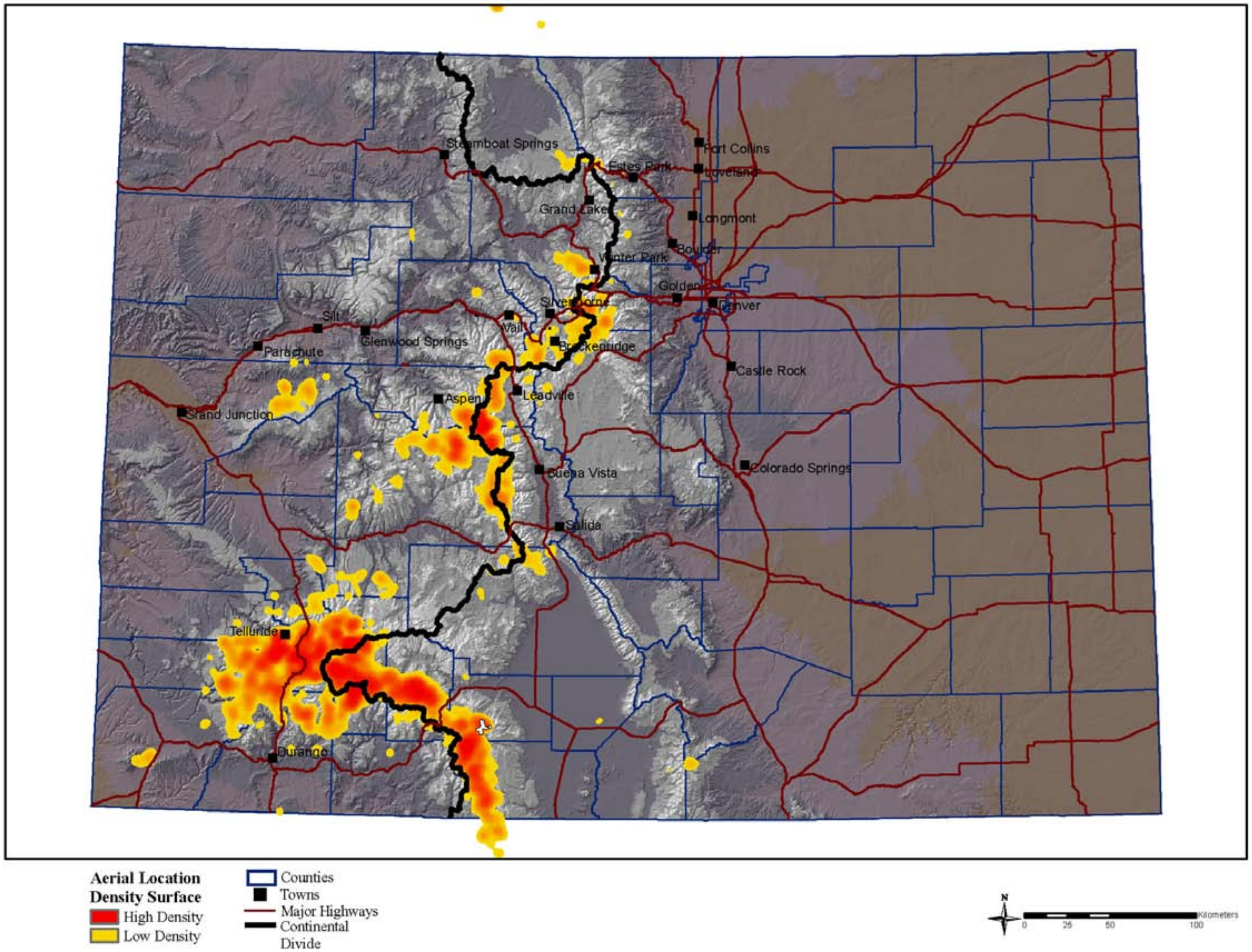

Figure 3. Use-density surface for lynx aerial locations (truncated dataset) in Colorado from September 1999-March 2007.

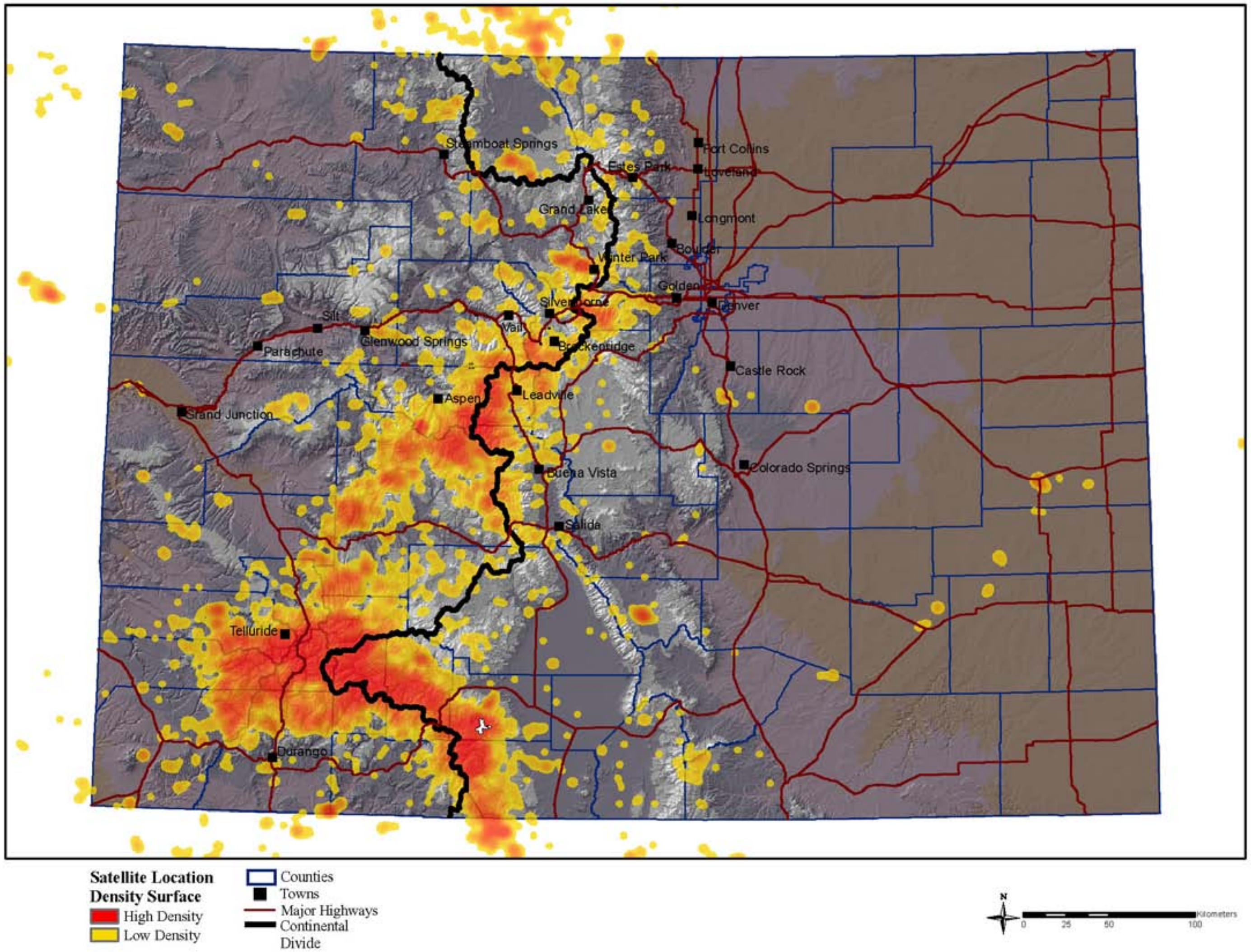

Figure 4. Use-density surface for lynx satellite locations (truncated dataset) in Colorado from September 1999-March 2007.

APPENDIX I

Colorado Division of Wildlife
July 2007 - June 2008

WILDLIFE RESEARCH REPORT

State of:	Colorado	:	Division of Wildlife
Cost Center:	3430	:	Mammals Research
Work Package:	0670	:	Lynx Conservation
Task No.:	2	:	Density, Demography, and Seasonal Movements
		:	Of Snowshoe Hare in Colorado
Federal Aid Project No.	N/A		

Period Covered: July 1, 2007- June 30, 2008

Author: J. S. Ivan, Ph.D. Candidate, Colorado State University

Personnel: Dr. T. Shenk of CDOW and Dr. G. C. White of Colorado State University.

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

A program to reintroduce the threatened Canada lynx (*Lynx canadensis*) into Colorado was initiated in 1997. Analysis of scat collected from winter snow tracking indicates that snowshoe hares (*Lepus americanus*) comprise 65–90% of the winter diet of reintroduced lynx. Thus, existence of lynx in Colorado and success of the reintroduction hinge at least partly on maintaining adequate and widespread hare populations. Beginning in July 2006, I initiated a study to assess the relative value of 3 stand types for providing hare habitat in Colorado. These types include mature, uneven-aged spruce/fir forests, sapling lodgepole pine forests ("small lodgepole"), and pole-sized lodgepole pine forests ("medium lodgepole"). Estimates and comparisons of survival, recruitment, finite population growth rate, and maximum (late summer) and minimum (late winter) snowshoe hare densities for each stand will provide the metrics for assessing these stands.

Thus far, snowshoe hare densities on the study area are low compared to densities reported elsewhere. Within the study area, hare densities during summer were highest in small lodgepole stands, followed by mature spruce/fir and medium lodgepole, respectively. This pattern was consistent through the first 2 summers of this project, although absolute hare densities declined considerably in summer 2007. Hare density in small and medium lodgepole stands equalized during both winters of the project. However, as with summer, overall density was much lower during the second winter compared to the first.

Hare survival from summer to winter has been relatively high. However the single winter to summer estimate I have to date is quite low. Extension of this time series will help determine whether low winter to summer survival is typical or somehow related to the decline in density.

WILDIFE RESEARCH REPORT

DENSITY, DEMOGRAPHY, AND SEASONAL MOVEMENTS OF SNOWSHOE HARES IN COLORADO

JACOB S. IVAN

P. N. OBJECTIVE

Assess the relative value of 3 stand types (mature spruce/fir, sapling lodgepole, pole-sized lodgepole) that purportedly provide high quality hare habitat by estimating survival, recruitment, finite population growth rate, and maximum (late summer) and minimum (late winter) snowshoe hare densities for each type.

SEGMENT OBJECTIVES

1. Complete mark-recapture work across all replicate stands during late summer (mid-July through mid-September) and winter (mid-January through March).
2. Obtain daily telemetry locations on radio-tagged hares for 10 days immediately after capture periods, as well as monthly between primary trapping sessions.
3. Locate, retrieve, and refurbish radio tags as mortalities occur.
4. Summarize initial sampling efforts and provide initial density estimates for Progress Reports for Colorado Division of Wildlife (CDOW).

INTRODUCTION

NEED

A program to reintroduce the threatened Canada lynx (*Lynx canadensis*) into Colorado was initiated in 1997. Since that time, 218 lynx have been released in the state, and an extensive effort to determine their movements, habitat use, reproductive success, and food habits has ensued (Shenk 2005, Shenk 2007). Analysis of scat collected from winter snow tracking indicates that snowshoe hares (*Lepus americanus*) comprise 65–90% of the winter diet of reintroduced lynx (T. Shenk, Colorado Division of Wildlife, unpublished data). Thus, as in the far north where the intimate relationship between lynx and snowshoe hares has captured the attention of ecologists for decades, it appears that the existence of lynx in Colorado and success of the reintroduction effort may hinge on maintaining adequate and widespread populations of hares.

Colorado represents the extreme southern range limit for both lynx and snowshoe hares (Hodges 2000). At this latitude, habitat for each species is less widespread and more fragmented compared to the continuous expanse of boreal forest at the heart of lynx and hare ranges. Neither exhibits dramatic cycles as occur farther north, and typical lynx (≤2–3 lynx/100km^2; Aubry et al. 2000) and hare (≤1–2 hares/ha; Hodges 2000) densities in the southern part of their range correspond to cyclic lows form northern populations (2-30 lynx/100 km^2, 1–16 hares/ha; Aubry et al. 2000, Hodges 2000, Hodges et al. 2001).

Whereas extensive research on lynx-hare ecology has occurred in the boreal forests of Canada, literature regarding the ecology of these species in the southern portion of their range is relatively sparse. This scientific uncertainty is acknowledged in the "Canada Lynx Conservation Assessment and Strategy," a formal agreement between federal agencies intended to provide a consistent approach to lynx conservation on public lands in the lower 48 states (Ruediger et al. 2000). In fact, one of the explicit guiding principles of this document is to "retain future options…until more conclusive information concerning lynx management is developed." Thus, management recommendations in this agreement are decidedly conservative, especially with respect to timber management, and are applied broadly to cover all habitats thought to be of possible value to lynx and hare. Accurate identification and detailed description of lynx-hare habitat in the southern Rocky Mountains would permit more informed and refined management recommendations.

A commonality throughout the snowshoe hare literature, regardless of geographic location, is that hares are associated with dense understory vegetation that provides both browse and protection from elements and predators (Wolfe et al. 1982, Litvaitis et al. 1985, Hodges 2000, Homyack et al. 2003, Miller 2005). In western mountains, this understory can be provided by relatively young conifer stands regenerating after stand-replacing fires or timber harvest (Sullivan and Sullivan 1988, Koehler 1990a, Koehler 1990b, Bull et al. 2005) as well as mature, uneven-aged stands (Beauvais 1997, Griffin 2004). Hares may also take advantage of seasonally abundant browse and cover provided by deciduous, open habitats (e.g., riparian willow [*Salix* spp.], aspen [*Populus tremuloides*]; Wolff 1980, Miller 2005). In drier portions of hare range, such as Colorado, regenerating stands can be relatively sparse, and hares may be more associated with mesic, late-seral forest and/or riparian areas than with young stands (Ruggiero et al. 2000).

Numerous investigators have sought to determine the relative importance of these distinctly different habitat types with regards to snowshoe hare ecology. Most previous evaluations were based on hare density or abundance (Bull et al. 2005), indices to hare density and abundance (Wolfe et al. 1982, Koehler 1990a, Beauvais 1997, Miller 2005), survival (Bull et al. 2005), and/or habitat use (Dolbeer and Clark 1975). Each of these approaches provides insight into hare ecology, but taken singly, none provide a complete picture and may even be misleading. For example, extensive use of a particular habitat type may not accurately reflect the fitness it imparts on individuals, and density can be high even in "sink" habitats (Van Horne 1983). A more informative approach would be to measure density, survival, and habitat use simultaneously in addition to recruitment and population growth rate through time. Griffin (2004) employed such an approach and found that summer hare densities were consistently highest in young, dense stands. However, he also noted that only dense mature stands held as many hares in winter as in summer. Furthermore hare survival seemed to be higher in dense mature stands, and only dense mature stands were predicted (by matrix projection) to impart a mean positive population growth rate on hares. Griffin's (2004) study occurred in the relatively moist forests of Montana, which share many similarities but also many notable differences with Colorado forests including levels of fragmentation, species composition, elevation, and annual precipitation.

Density estimation is a key component in assessing the value of a particular stand type and is the common currency by which hare populations are compared across time and space. However, it can be a difficult metric to estimate accurately. Abundance estimation based on capture-recapture methods is a well-developed field (Otis et al. 1978, White et al. 1982), but is often too costly and labor intensive to be implemented on scales necessary to effectively monitor density over a biologically meaningful area. Also, density can be difficult to assess from grid-trapping efforts because it is often unclear how much area was effectively sampled by the grid (Williams et al. 2002:314). Alternate approaches can produce density estimates that differ by an order of magnitude even when calculated from the same data (Zahratka 2004). Indices such as pellet plot counts and distance sampling of pellet groups can be used to estimate density, but each of these has limitations as well (Krebs et al. 1987, Eriksson 2006).

The study outlined below is designed principally to evaluate the importance of young, regenerating lodgepole pine (*Pinus contorta*) and mature Engelmann spruce (*Picea engelmannii*)/ subalpine fir (*Abies lasiocarpa*) stands in Colorado by examining density and demography of snowshoe hares that reside in each. Secondarily, I intend to quantify movement between these stands and other seasonally available types (e.g., willow). My hope is that information gathered from this research will be drawn upon as managers make routine decisions, leading to landscapes that include stands capable of supporting abundant populations of hares. I assume that if management agencies focus on providing habitat, hares will persist. I will use mark-recapture techniques as data from such an approach can provide information on both density and demography. In the future, I will address the "effective trapping area" issue using a new approach that augments mark-recapture data with telemetry locations of animals using the grid. However, for this report I used one of the more popular, traditional techniques. I determined that 2 classes of young, regenerating lodgepole stands could both provide adequate hare habitat. Thus, in addition to older spruce/fir forests, I am sampling "small" (2.54-12.69 cm dbh) and "medium" (12.70-22.85 cm dbh) stands regenerating from clearcutting that took place 20 and 40 years ago, respectively (Figure 1). Additionally, medium lodgepole stands were pre-commercially thinned 20 years ago; small lodgepole stands have not yet been thinned.

Hypotheses

1) In general, snowshoe hare density in Colorado will be relatively low (≤0.5 hares/ha) compared to densities reported in northern boreal forests, even immediately post-breeding when an influx of juveniles will bolster hare numbers.
2) Snowshoe hare density will be consistently highest in small lodgepole pine stands, followed by large spruce/fir and medium lodgepole pine, respectively.
3) Survival will generally be highest in mature (large) spruce/fir stands followed by small and medium lodgepole pine, respectively.
4) Finite population growth rate will be consistently at or above 1.0 in mature spruce/fir stands with survival contributing most significantly to the growth rate. Finite growth rates for the lodgepole pine stands will be more variable.
5) Snowshoe hares will significantly shift their home ranges to make use of abundant food and cover provided by riparian willow (and/or aspen) habitats in summer.
6) Snowshoe hare density, survival, and recruitment will be highly correlated with understory cover and stem density.

STUDY AREA

The study area stretches from Taylor Park to Pitkin in central Colorado (Figure 2). Elevation ranges from 2700 m to 4000 m. Sagebrush (*Artemisia spp.*) dominates broad, low-lying valleys. Most montane areas are covered by even-aged, large-diameter lodgepole pine forests with sparse understory. Moist, north-facing slopes and areas near tree line are dominated by large-diameter Engelmann spruce/subalpine fir. Interspersed along streams and rivers are corridors of willow. Patches of aspen occur sporadically on southern exposures. This area was chosen over other potential study areas in the state because 1) it contained numerous examples of the 3 stand types of interest (more southern regions lack naturally occurring stands of lodgepole pine), 2) it was not subject to confounding effects of large-scale mountain pine beetle outbreak as were more northern stands, and 3) an adequate number of radio frequencies were available to support a large study with hundreds of radio-tagged individuals.

Within the study area I selected sample stands based on the following: Potential replicate stands were required to be 1) close enough geographically to minimize differences due to climate, weather, and topography, but are far enough apart to be considered independent, 2) adjacent to one or more riparian willow corridors, 3) within 1 km of an access road for logistical purposes, 4) of suitable size and shape to admit a 16.5-ha trapping grid, and 5) consistent in their management history (i.e., replicate lodgepole pine stands were clear-cut and/or thinned within 1-2 years of each other).

I queried the U.S. Forest Service R2VEG GIS database using the criteria listed above to initially develop a suite of potential sample stands. I further narrowed this suite after obtaining updated stand-level information from local USFS personnel (Art Haines, Silviculturalist, USFS Gunnison Ranger

District, personal communication). Finally, I ground-truthed potential stands and qualitatively assessed their representativeness and similarity to other potential replicates. Given the numerous constraints imposed, very few stands met all criteria. Thus, I was unable to randomly select sample stands from a population of suitable stands. Rather, I subjectively chose the "best" stands from among the handful that met my criteria. Small lodgepole stands rarely occur on the landscape in patches large enough to fit a full trapping grid. To accommodate this, I sampled 6 replicate small lodgepole stands (rather than 3) using half-sized trapping grids.

METHODS

Experimental Design/Procedures

Variables.--The response variables of interest for this project include stand-specific snowshoe hare density (*D*), apparent survival (ϕ), recruitment (*f*), finite population growth rate (λ), and a metric of seasonal movement. Density is the number of hares per unit area and is estimated using a conventional techniques in this report. The stand-specific demographic parameters will be estimated primarily from capture-mark-recapture methods. As such, apparent survival is defined as the probability that a marked animal alive and in the population at time i survives and is in the population at time $i + 1$. Apparent survival encompasses losses due to both death and emigration. Estimates of recruitment, population growth, and seasonal movement are forthcoming and not provided in this report.

Potential explanatory variables for snowshoe hare density, demographics, and movement include general species composition and structural stage of each stand in which response variables are measured. Additionally, stem density, horizontal cover, and canopy cover (to a lesser extent) are highly correlated with snowshoe hare abundance and habitat use (Wolfe et al. 1982, Litvaitis et al. 1985, Hodges 2000, Zahratka 2004, Miller 2005). Thus, I further characterized vegetation in each stand by measuring stem density by size class (1-7 cm, 7.1-10 cm, and >10 cm), percent canopy cover, percent horizontal cover of understory and basal area. Basal area is an easily obtainable metric that may be correlated with the other variables and is recorded routinely during timber cruises, whereas the others are not. Thus, it might prove a useful link for biologists designing management strategies for snowshoe hare. Additionally, I recorded physical covariates such as ambient temperature, precipitation, and snow depth at each stand during sampling. These metrics were not included in the current preliminary analyses, but will be used as covariates in future models.

Sampling.--All trapping and handling procedures have been approved by the Colorado State University Animal Care and Use Committee and filed with the Colorado Division of Wildlife. Snowshoe hares breed synchronously and generally exhibit 2 birth pulses in Colorado (although in some years, some individuals may have 3 litters), with the first pulse terminating approximately June 5–20 and the second approximately July 15–25 (Dolbeer 1972). To obtain a maximum density estimate, I began data collection on the first suite of sites immediately following the second birth pulse in late July. Along with a crew of 5 technicians, I deployed one 7 × 12 trapping grid (50-m spacing between traps; grid covers 16.5 ha) in the large spruce/fir and medium lodgepole stands within the first suite, along with 2 6 × 7 grids in 2 small lodgepole stands. Grid set up and trap deployment followed Griffin (2004) and Zahratka (2004). Grid locations and orientation within each stand were chosen subjectively to accommodate logistical constraints and to ensure that hares using the grid had ample opportunity to use adjacent riparian willow zones. As traps were deployed, they were locked open and "pre-baited" with apple slices, hay cubes, and commercial rabbit chow. Traps were pre-baited in this manner for a total of 3 nights to maximize capture rates when trapping began. This minimized the number of trap-nights needed to capture the desired number of animals which in turn minimized trap-related injuries and minimized problems with predators keying into trap lines. During pilot work in winter 2005, I observed low but increasing capture rates (<0.20) during the first 3 nights of trapping, with higher, more stable capture probabilities after 3 days (approximately 0.35–0.45). Thus 3 days of pre-baiting seemed reasonable.

Traps were set on the afternoon of the 4^{th} day and checked early each morning and again in the evening on days 5–9. By checking traps in both morning and evening I prevented hares from being entrapped >13 hours, which should minimize capture stress. A crew of 2 people worked together on each grid to check traps and process captures as quickly as possible. All captured hares were coaxed out of the trap and into a dark handling bag by blowing quick shots of air on them from behind. Hares remained in the handling bag, physically restrained with their eyes covered, for the entire handling process. Each individual was aged, sexed, marked with a passive integrated transponder (PIT) tag and temporary ear mark (to track PIT tag retention), then released. Aging consisted of assigning each individual as either juvenile (<1 year old, <1000 g) or adult (≥1 year old, ≥1000 g) based on weight. This criterion is accurate through the end of September at which point juveniles are difficult to distinguish from adults (K. Hodges, University of British Columbia; P. Griffin, University of Montana, personal communication). After the first day of trapping, all captured hares were scanned for a PIT tag prior to any handling and those already marked were recorded and immediately released. Traps and bait were completely removed from the grid on day 10.

In addition to PIT tags and ear marks, I radio collared up to 10 hares captured on each grid with a 28-g mortality-sensing transmitter (BioTrack, LTD) to facilitate unbiased density estimation as well as assessment of seasonal movements. I expected heterogeneity in snowshoe hare movements and use of the grid area, with potential bias surfacing due to location at which a hare is captured (e.g., hares captured on the edge of a grid may use the grid area differently than those captured at the center), and differential behavioral responses to trapping (e.g., young individuals may have lower capture probabilities and thus may be more likely to be captured on later occasions). To guard against the first potential bias, I randomly selected a starting trap location each morning and ran the grid systematically from that point. Thus, the first several hares encountered (and collared) were as likely to be from the inner part of the grid as from the edge. To protect against the second potential source of bias, I refrained from deploying the final 3 collars until days 4 and 5 of the trapping session.

Immediately following the removal of traps, the field crew began work locating each radio-collared hare 1–2 times per day for 10 days. Most locations were obtained by triangulation from relatively close proximity, but some were obtained by “homing” on a signal (Samuel and Fuller 1996, Griffin 2004) taking care not to push hares while approaching them. Because hares are largely nocturnal (Keith 1964, Mech et al. 1966, Foresman and Pearson 1999), I made an effort to conduct telemetry work at various times of the night (safety and logistics permitting) and day to gather a representative sample of locations for each hare.

Crews gathered telemetry locations for radio-collared hares on the initial suite of sites for 10 days. Then the 10–day trapping procedure and 8 to 10–day telemetry work were repeated on the grids comprising suites 2 and 3(Figure 3). The entire process was repeated during the winter when densities should have been at a minimum. Thus, during the period covered by this report, sampling occurred from July 16 – September 14 and from January 20 – March 24, 2008. Sampling occurred across similar dates during FY06/07 and will continue during FY08/09. During the interim between intensive trapping and telemetry work, monthly telemetry checks were conducted from the air to track mortalities and facilitate retrieval of collars from dead hares. Telemetry work also occurred during “pre-baiting” days after the initial summer sampling session to determine which hares were still alive and immediately available to be sampled by the grid during the ensuing trapping period.

Vegetation sampling at each stand commenced in June 2008 and is nearly finished. I followed protocols established through previous snowshoe hare and lynx work in Colorado (Zahratka 2004, T.

Shenk, Colorado Division of Wildlife, personal communication). Specifically, on each of the 12 live-trapping grids, I laid out 5 × 5 grids (3-m spacing) of vegetation sampling points centered on 15 of the 84 trap locations (Figure 4; 9 points were sampled on each of the ½-sized small lodgepole stands). At each of the 25 vegetation sampling points, I recorded canopy cover (present or absent) using a densitometer. I quantified downed coarse wood along the center transect of the 25-point grid following Brown (1974). From the centerpoint (i.e., trap location) I measured 1) distance to the nearest woody stem 1.0–7.0 cm, 7.1−10.0 cm, and >10.0 cm in diameter at heights of 0.1 m and 1.0 m above the ground (to capture both summer and winter stem density; Barbour et al. 1999), 2) horizontal cover in 0.5-m increments above the ground up to 2 m (Nudds 1977), 3) basal area, and 4) slope.

Data Analysis

Density, Survival, and Population Growth.--I analyzed mark-recapture data in a robust design framework (Williams et al. 2002:523-554) treating summer and winter sampling occasions as primary periods, and the 5-day trapping sessions within each as secondary periods. As such, I assumed hare populations were demographically and geographically closed during the short 5-day mark-recapture sampling periods, but were open to immigration, emigration, births, and deaths between these occasions. I specified the Pradel Robust Design data type in Program MARK (White and Burnham 1999) and chose the Huggins closed capture model (Huggins 1989, 1991) to obtain abundance estimates for each grid from the secondary periods. I obtained estimates of apparent survival ($\hat{\phi}_i$) between each primary period. I employed a technique known as ½ Mean Maxmimum Distance Moved (MMDM; Wilson and Anderson 1985) to calculate the effective area trapped and obtain a density estimate for each grid from each secondary period. Future density analyses will employ a new estimator that employs telemetry data to correct for bias (Ivan 2005). I used Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 1998) to select appropriate models from alternatives that included all 8 closed capture models (Otis et al. 1978) in combination with models that allowed survival to be constant, vary with time, and/or vary with stand type.

RESULTS AND DISCUSSION

I captured 30 hares 73 times during July-September 2007. I captured 48 hares 71 times during January-March 2008. During summer, density estimates have thus far followed hypotheses 1) and 2) above (Figure 5). Specifically, hare densities were clearly highest in small lodgepole stands and quite low in medium lodgepole stands. Spruce/fir was intermediate in density. This pattern remained consistent between summer 2006 to summer 2007, although the absolute density of hares dropped considerably during summer 2007. Why this decline occurred is unclear, although disease outbreak, natural population cycles, and response to increased predation due to lynx reintroduction are possibilities. Note that even the highest densities recorded here correspond to low estimates observed in other parts of hare range (Hodges 2000).

Hare densities tend to equalize in lodgepole stands during winter (Figure 5). I submit that the interplay between food, cover, and snow depth provides a plausible explanation for this pattern. Medium lodgepole stands apparently provide very little forage/cover for hares during summer as the canopy in these stands is generally ≥1 meter off the ground. However, in winter, accumulated snow may make that canopy available again to hares. Conversely, small lodgepole stands provide abundant food and cover during summer, but accumulated snow during winter brings hares closer to the crowns of the young trees, which then provide less cover. Spruce/fir stands probably provide adequate access to both food and cover during both summer and winter due to their uneven-aged, multi-layered structure. Like the summer estimates, density during the second winter was much lower than during the first winter.

Hare survival from the first sampling season into the first winter was relatively high (Figure 6). However, survival from the first winter to the second summer declined drastically. Survival from the second summer to the second winter was again quite high. Whether this pattern is typical is unclear. Survival from winter to summer is commonly lower than from summer to winter. However, the low survival from the first winter to second summer is coincident with the dramatic decline in hare density observed on spruce/fir and small lodgepole grids. Thus, low survival for this period is possibly reflective of, or maybe even a driver for, the decline in density. Extension of the time series and a breakdown of survival by stand type should provide more evidence for one or the other of these explanations.

SUMMARY

- Snowshoe hare densities on my study sites appear to be relatively low compared to densities reported elsewhere. Densities during summer were highest in small lodgepole stands, followed by spruce/fir and medium lodgepole.
- During winter, densities equalize in lodgepole stands, possibly due to the interplay between snow depth and canopy height in small and medium lodgepole pine.
- Hare density declined considerably beginning in summer 2007.
- Summer to winter hare survival has been consistently high thus far in the study, but the lone winter to summer survival estimate is quite low. It is unclear whether winter to summer survival is typically this low or whether that estimate is related to coincident drop in density.

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Figure 1. Purported high quality snowshoe hare habitat in Colorado. From left to right: small lodgepole pine, medium lodgepole pine, and large Engelmann spruce/subalpine fir.

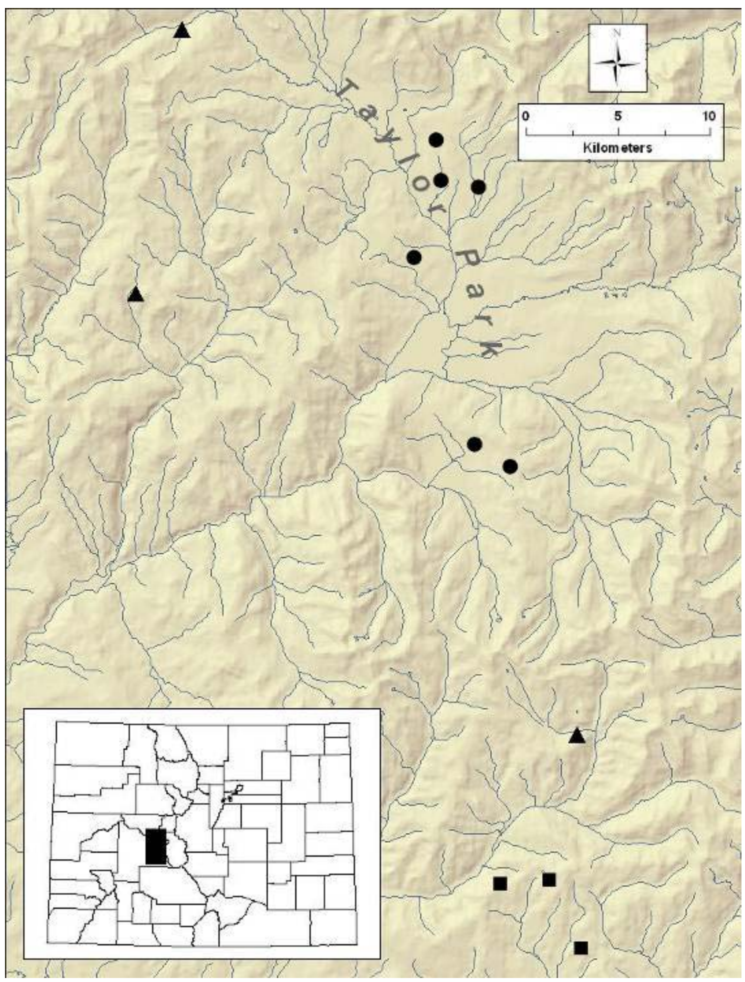

Figure 2. Study area near Taylor Park and Pitkin, Colorado including medium lodgepole (squares), small lodgepole (circles), and spruce/fir (triangles) stands selected for mark-recapture sampling.

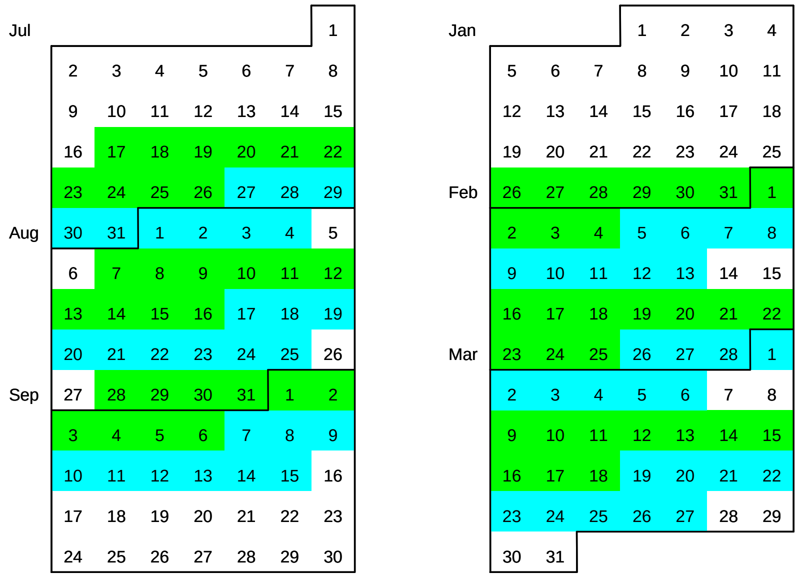

Figure 3. Approximate annual data collection schedule for trapping (■) and telemetry (■). Dates and weeks changed depending on calendar year and pay schedule. During telemetry work, the 6-person crew was divided into 2 teams, only one of which worked at any given time. Monthly locations on radio-collared hares were also collected in the interim between the intensive sampling periods indicated here.

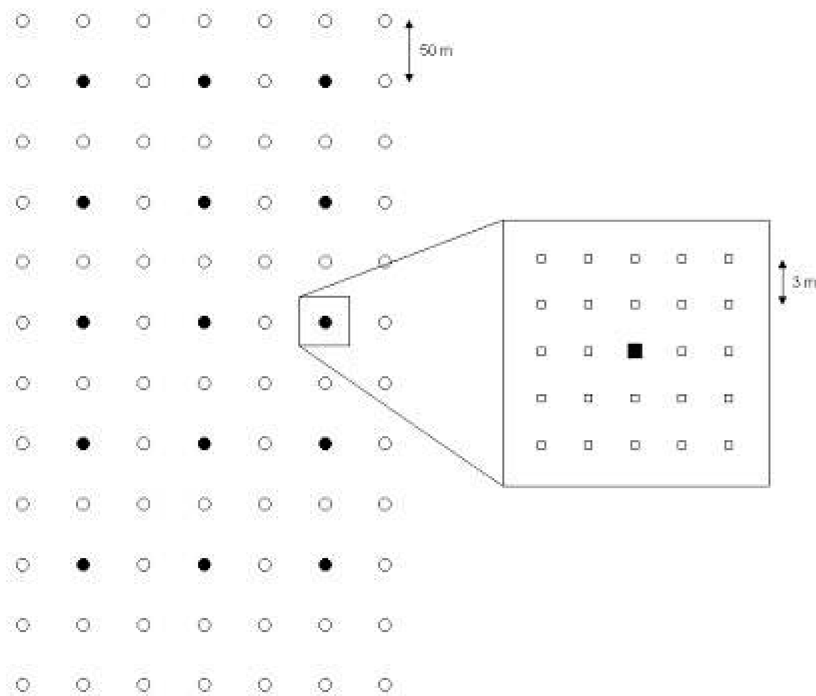

Figure 4. 15 trap locations (•) on 7 × 12 trapping grid where vegetation was sampled by measuring stem density, horizontal cover, downed woody material, and basal area. Additionally, the 25-point grid superimposed on each of the 15 trap locations (inset) was used to quantify canopy covert).

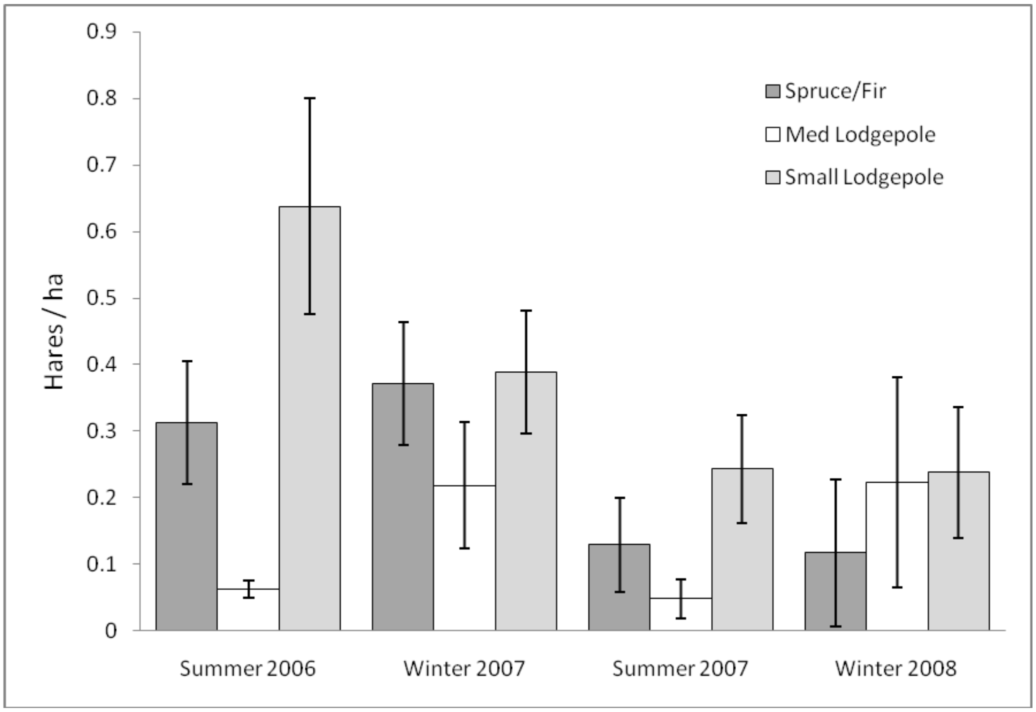

Figure 5. Snowshoe hare density and 95% confidence intervals in 3 types of stands in central Colorado as determined by ½ mean maximum distance moved, summer 2006 through winter 2008.

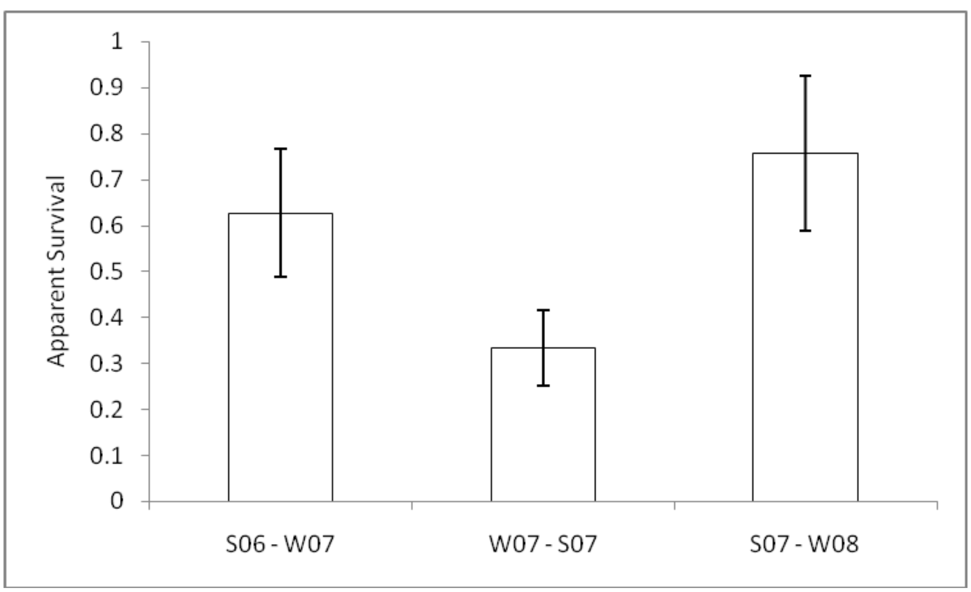

Figure 6. Snowshoe hare survival and 95% confidence intervals across summer (S) and winter (W) sampling seasons in central Colorado as determined by mark-recapture, 2006-2008.