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WILDLIFE RESEARCH REPORT

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ABSTRACT

In an effort to establish a viable population of 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 lynx were released in Colorado. We documented survival, movement patterns, reproduction, and landscape habitat-use through aerial (n = 9496) and satellite (n = 23,791) tracking. Most lynx remained near the core release area in southwestern Colorado. From 1999-June 2007, there were 98 mortalities of released adult lynx. Approximately 30.6% were human-induced which were attributed to collisions with vehicles or gunshot. Starvation and disease/illness accounted for 19.4% of the deaths while 35.7% of the deaths were from unknown causes. 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. From snow-tracking, the primary winter prey species (n = 506 kills) were snowshoe hare (*Lepus americanus*, annual $\bar{x}$ = 74.9%, SE = 4.6, n = 9) and red squirrel (*Tamiasciurus hudsonicus*, annual $\bar{x}$ = 16.5%, SE = 4.1, n = 9); 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 and areas of use in New Mexico, Utah and Wyoming. 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. The first year 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 was completed in 2006-2007 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 2006-07 field data collection on lynx habitat use at the landscape scale, hunting behavior, diet, mortalities, and movement patterns.
2. Complete winter 2006-07 lynx trapping field season to collar Colorado born lynx and re-collar adult lynx.
3. Complete spring 2007 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 first 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

Southwestern Colorado is characterized by wide plateaus, river valleys, and rugged mountains that reach elevations over 4200 m. Engelmann spruce-subalpine fir is the most widely distributed coniferous forest type at elevations most typically used by lynx. The Core Release Area is defined as areas bounded by the New Mexico state line to the south, Taylor Mesa to the west and Monarch Pass on the north and east and > 2900 m in elevation (Figure 1). 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

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). Specific release sites were those used in earlier years of the project and were selected based on land ownership and accessibility during times of release (Byrne 1998). Lynx were transported from the Frisco Creek Wildlife Rehabilitation Center, where they were held from their time of arrival in Colorado, to their release site in individual cages. Release site location was 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

Survival was estimated as ragged telemetry data using the nest survival models in Program MARK (White and Burnham 1999).

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

A study designed 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.

Specifically, the 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 density-estimation procedures available perform accurately and consistently using an innovative, telemetry augmentation approach as a baseline. 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 lynx were reintroduced into southwestern Colorado (Table 1). No lynx were released in 2007. 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 2008.

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 9496 aerial and 23791 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 June 30, 2007. 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).

Relative Use in Colorado.-- 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 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 in New Mexico.-- Combining the non-truncated aerial (n = 81) and satellite lynx location (n = 928) datasets, lynx used New Mexico consistently and with an increasing number of individuals from 1999 through 2006 (Table 2). Data for 2007 represents only a partial year and thus trend in numbers of individuals using New Mexico for 2007 cannot be made, however continued use of New Mexico into 2007 was documented Sixty lynx (37 females: 23 males) were found within New Mexico from February 1999 through March 2007 (Table 2). Excluding all aerial and satellite lynx locations collected in the first 180 days after release (truncated datasets; n = 61 aerial locations, n = 569 satellite locations), a total of 35 individual lynx (22 females: 13 males) were found within New Mexico from September 1999 through March 2007 (Table 3).

The decrease in number of lynx frequenting New Mexico in 2001 through 2003 (Tables 2 and 3) was more likely due to fewer satellite collars functioning in those years rather than indicating less use of the area by lynx. The satellite transmitters placed on lynx in 2000 were failing and no new lynx were released or re-collared in 2001 and 2002. This decrease in satellite locations is present throughout the lynx distribution and is also reflected in the numbers presented below for Utah and Wyoming

The use-density surface for lynx use in New Mexico indicates the primary area of use being located either immediately south of the Colorado border and south of the Conejos River Valley (an area of high use in Colorado) or east of Taos (Figure 5). The use-density surfaces throughout both Colorado and New Mexico are displayed so that lynx use within New Mexico can be directly compared to lynx use throughout Colorado (Figure 6).

Relative Use in Utah.-- Combining the non-truncated aerial (n = 10) and satellite lynx location (n = 574) datasets, lynx used the analysis area consistently and with an increasing number of individuals from 1999 through 2006 (Table 4). Data for 2007 represents only a partial year and thus trend in numbers of individuals using the state for 2007 cannot be made, however continued use of Utah into 2007 was documented. Twenty-two lynx (7 females: 15 males) were found within Utah from February 1999 through March 2007 (Table 4). Excluding all aerial and satellite lynx locations collected in the first 180 days after release (truncated datasets; n = 7 aerial locations, n = 399 satellite locations), 17 individual lynx (6 females: 11 males) were found within Utah from September 1999 through March 2007 (Table 5).

The use-density surface for lynx use in Utah indicates the primary area of use being located in the Uinta Mountains (Figure 7). The use-density surfaces throughout both Colorado and Utah are displayed so that lynx use within Utah can be directly compared to lynx use throughout Colorado (Figure 8).

Relative Use in Wyoming.-- Combining the non-truncated aerial (n = 34) and satellite lynx location (n = 1780) datasets, lynx used the analysis area consistently and with an increasing number of individuals from 1999 through 2006 (Table 6). Data for 2007 represents only a partial year and thus trend in numbers of individuals using the state for 2007 cannot be made, however continued use of the Wyoming into 2007 was documented. Thirty-three lynx (14 females: 19 males) were found within

Wyoming from February 1999 through March 2007 (Table 6). Excluding all aerial and satellite lynx locations collected in the first 180 days after release (truncated datasets; n = 28 aerial locations, n = 1533 satellite locations), 27 individual lynx (13 females: 14 males) were found within Wyoming from September 1999 through March 2007 (Table 7).

The use-density surface for lynx use in Wyoming indicates the primary area of use being located either immediately north of the Colorado border in the Medicine Bow National Forest or in the northwest quadrant of the state including areas in Yellowstone and Teton National Parks and the Laramie Range (Figure 9). The use-density surfaces throughout both Colorado and Wyoming are displayed so that lynx use within Wyoming can be directly compared to lynx use throughout Colorado (Figure 10).

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

Initial survival rate estimates for reintroduced lynx were completed, however, further analyses need to be conducted before estimates will be presented. As of June 30, 2007, CDOW was actively monitoring/tracking 71 of the 120 lynx still possibly alive (Table 8). There are 50 lynx that we have not heard signals on since at least June 30, 2006 and these animals are classified as 'missing' (Table 8). One of these missing lynx is a mortality of unknown identity, thus only 49 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 98 known mortalities as of June 30, 2007 (Table 9). The primary known causes of death included 30.6% human-induced deaths which were confirmed or probably caused by collisions with vehicles or gunshot. Starvation and disease/illness accounted for 19.4% of the deaths; starvation was a significant cause of mortality in the first year of releases only. An additional 35.7% of known mortalities were from unknown causes.

Mortalities occurred throughout the areas where lynx moved, including 13 in New Mexico, 4 in Wyoming and Nebraska, 3 in Utah and 1 each in Arizona, Kansas and Montana (Figure 2, Table 10).

Reproduction

Field crews weighed, photographed, PIT-tagged the kittens and took hair, blood and saliva samples from the kittens for genetic work in an attempt to confirm paternity. Lynx kittens weigh approximately 200 grams at birth and do not open their eyes until they are 10-17 days old. 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.

2003.-- Nine pairs of lynx were documented during the 2003 breeding season (March and April) from the 17 females we were monitoring. In May and June, 6 dens and a total of 16 kittens were found in the lynx Core Release Area in southwestern Colorado (Table 11, Figure 1). The kittens weighed from 270-500 grams. The dens were scattered throughout the Core Release Area, with no dens found outside the core area. All the dens were in Engelmann spruce/subalpine fir forests in areas of extensive downfall. Elevations ranged from 3240-3557 m.

Four of the 6 females that we know had kittens in summer 2003 were still with kittens at the end of April 2004. Two of those females still had 2 kittens with them at that time. Visual observations in February 2004 of one female with 2 kittens indicated all 3 were in good body condition. The mortality of female YK00F16 and her 1 kitten in October 2003 from plague was not due to poor habitat or prey conditions, and thus we might assume she would have raised the 1 kitten to this stage as well. Three probable kitten deaths from female YK00F19 were from 1 litter that most likely failed very early. Through snow-tracking in winter 2003-04 an unknown female (no radio frequency heard in the area of the tracks) we also documented 1-2 additional kittens born spring 2003 and still alive in winter 2004.

Of the 16 kittens we found in summer 2003, we documented the following by April 2004: 6 confirmed alive, 7 confirmed dead, and 3 some evidence dead. Although we tried, we were not able to capture any of the 6 surviving kittens to fit them with radio-collars for subsequent monitoring.

2004.-- In Spring 2004, 26 females from the releases in 1999, 2000 and 2003 had active radio-collars. Of these, we documented 18 possible mating pairs of lynx during breeding season. All 4 of the females that had kittens with them through winter 2003-04 bred again spring 2004; 2 with the same male they successfully bred with spring 2003. During May-June 2004 we found 11 dens and a total of 30 kittens (Table 11). The kittens weighed from 250-770 grams. Three of the 11 females with kittens were from the 2003 releases. Three additional litters were documented after denning season through either observation of a female lynx with kittens or snow-tracking females with kittens that were not one of the 11 females found on dens. From the size of the kittens they would have been born during the normal denning season in May or June. Nine additional kittens were observed from these litters for a total of 39 known kittens born in 2004. Two of these additional litters were documented from direct follow-ups to sighting made by the public and reported to CDOW.

Two females that had kittens in 2003 and reared at least part of their litters through March 2004, bred and had kittens again in 2004. Two of the litters documented by direct observation or snow-tracking are from females whose collars were no longer functioning. Seven kittens born in 2004 were captured at approximately 10-months of age and fitted with dual satellite/VHF collars. Six of the 7 were still alive and being monitored as of June 30, 2006. The cut collar of one kitten CO04M15 was left at the Silverton Post Office on October 25, 2005. We assume this lynx is dead.

2005.-- In spring 2005 we had 40 females from the releases in 1999, 2000, 2003 and 2004 that had active radio-collars. We documented 23 possible mating pairs of lynx during breeding season. During May-June 2005 we visited 16 dens and found a total of 46 kittens (Table 11). An additional female (BC03F10) had a den we were not able to get to during May or June due to high water during spring run-off. Female BC03F03 was hit and killed on I-70 on 5/19/2005. She had 2 fetuses in her uterus, so would have contributed to reproduction this year had she lived.

All of the 2005 dens were scattered throughout the high elevation areas of Colorado, south of I-70. Most of the dens were in Engelmann spruce/subalpine fir forests in areas of extensive downfall. Elevations ranged from 3117-3586 m. Four of the females would not leave the den until we reached out to pick up a kitten.

One female, YK00F10 has had litters 3 years in a row. In 2003 she had 4 kittens and raised 2 through the winter. In 2004 she had 2 kittens and raised both through the winter, in 2005 she had 4 kittens again. She has had all 3 litters in the same general area and has had the same mate for 3 years. Eight additional females had their second litter in Colorado in 2005. Three females from the 2004 releases had litters in 2005. Year 2005 was the second consecutive year that we had females released the prior spring find a territory and a mate within a year and produced live young. In reproduction season 2004 we had 3 females released in spring 2003 that also produced live young the next year. Of those 3, 2 successfully raised at least part of their litters through winter 2005.

Seven kittens born in 2005 were captured at approximately 10-months of age and fitted with dual satellite/VHF collars. One of the 7 was still alive and being monitored as of June 30, 2007.

2006.-- In spring 2006, 42 females were being monitored. We found 4 dens in May and June 2006 with 11 kittens total (Table 11). Lynx CO04F07, a female lynx born in Colorado in 2004, was the mother of one of these litters which documented the first recruitment of Colorado-born lynx into the Colorado breeding population. There were at least 2 surviving kittens as of spring 2007. We were unsuccessful in capturing these kittens for collar placement.

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 11). However, all demographic and habitat characteristics measured at the 4 dens that were found in 2006 were comparable to all other dens found (Table 11). 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).

2007.-- During May and June 2007 we monitored 34 females for reproduction (Table 11). No dens were found.

Den Sites.-- A total of 37 dens have been 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.

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. All lynx captured in Colorado from 2005-2007 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-June 30, 2007 because they were in poor body condition (Table 12). Five of these lynx were successfully treated at the Frisco Creek Rehabilitation Center and re-released in the Core Release Area. One lynx, BC00F7, 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 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 12). 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 2 stayed in Colorado through June 30, 2007. Two lynx died within 6 months of re-release: 1 died of starvation in Colorado and the other died of unknown causes in Nebraska. Two lynx captured out of state and re-released currently remain 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°) 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 506 kills were located from February 1999-April 2007. We collected over 900 scat samples from February 1999-April 2007 that will be analyzed for content. In each winter, the most common prey item was snowshoe hare, followed by red squirrel (*Tamiusciurus hudsonicus*; Table 13). 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.

SNOWSHOE HARE ECOLOGY

The first year 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 was completed and preliminary results presented (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 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 (Tables 2, 6). Lynx reintroduced in Colorado were first documented in Utah in 2000 (Table 4) 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 (Figures 5, 7, 9). 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.

The use-density surface for lynx use in New Mexico indicates the primary areas of use being located immediately south of the Colorado border and south of the Conejos River Valley (an area of high use in Colorado) or east of Taos (Figure 5). In Utah, the primary area of use is located in the Uinta Mountains (Figure 7). Lynx use in Wyoming is focused in 2 primary areas, the Medicine Bow National Forest in south-central Wyoming and in the northwest quadrant of the state including areas in Yellowstone and Teton National Parks and the Laramie Range (Figure 9).

From 1999-June 2007, there were 98 mortalities of released adult lynx. Human-caused mortality factors are currently the highest causes of death with approximately 30.6% attributed to collisions with vehicles or gunshot. Starvation and disease/illness accounted for 19.4% of the deaths while 35.7% of the deaths were from unknown causes. Lynx mortalities were documented throughout all areas lynx used, including 28 (28.6%) occurring in other states (Figure 2, Table10). Half of the out-of-state mortalities were documented in New Mexico.

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 11) 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. The cause of the decreased reproduction in 2006 and 2007 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 = 506) were snowshoe hare (Table 12) with an annual $\bar{x}$ = 74.9% (SE = 4.6, n = 9) and red squirrel (annual $\bar{x}$ = 16.5%, SE = 4.1, n = 9). 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 12).

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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Tanya M. Shenk, Wildlife Researcher

Table 1. Lynx released in Colorado from February 1999 through June 30, 2007. No lynx were released in 2001, 2002 or 2007.

Year	Females	Males	TOTAL
1999	22	19	41
2000	35	20	55
2003	17	16	33
2004	17	20	37
2005	18	20	38
2006	6	8	14
TOTAL	115	103	218

Table 2. All individual lynx (*n* = 60) documented through either aerial or satellite locations (non-truncated datasets) by year in New Mexico from February 1999 – March 2007.

Lynx ID	Year								
	1999	2000	2001	2002	2003	2004	2005	2006	2007
AK99F10	X								
AK99F13		X							
AK99F17	X								
AK99F3		X							
AK99F5					X		X		
AK99F8	X								
AK99M11		X							
AK99M26	X								
AK99M9		X							
BC99M4	X			X					
YK99F3		X							
YK99M3	X								
YK99M6	X	X							
YK99M7	X								
AK00F2								X	X
AK00F5							X		
BC00F10		X							
BC00F14				X					
BC00F6		X							
BC00F8		X	X			X	X		
BC00M04								X	
BC00M11		X						X	
BC00M4		X						X	
YK00F11							X		
YK00F2				X	X				
YK00F4			X						
YK00F7								X	
BC03F03					X	X			
BC03F04					X				
BC03F06						X			
BC03F08					X				
BC03M02					X	X			
BC03M05					X				
BC03M08						X	X	X	
QU03F01					X				
QU03F04						X	X		
QU03F07					X	X	X		
BC04F02						X	X		
BC04F03						X			
BC04F05						X			
BC04M02						X			
BC04M13						X	X		
QU04F05						X	X		
QU04F08						X			
QU04F09						X			
QU04M02						X			
QU04M04						X			
BC05F04							X		
BC05M02							X		
QU05F03							X		
QU05M01							X		
QU05M05							X	X	
YK05F01							X		
YK05M01							X	X	
BC06F05								X	
BC06F07								X	X
BC06F09								X	
BC06M12								X	
YK06F01								X	
YK06M01								X	
Total Lynx	8	11	2	3	9	17	17	14	2

Table 3. All individual lynx (*n* = 35) documented at least 180 days after their initial release (truncated datasets) through either aerial or satellite locations, by year in New Mexico from September 1999 – March 2007.

Lynx ID	Year							
	2000	2001	2002	2003	2004	2005	2006	2007
AK99F13	X							
AK99F3	X							
AK99F5				X		X		
AK99M11	X							
AK99M9	X							
BC99M4			X					
YK99F3	X							
YK99M6	X							
AK00F2							X	X
AK00F5						X		
BC00F14			X					
BC00F8		X			X	X		
BC00M04							X	
BC00M11							X	
BC00M4							X	
YK00F11						X		
YK00F2			X	X				
YK00F4		X						
YK00F7							X	
BC03F03					X			
BC03F06					X			
BC03M02					X			
BC03M08					X	X	X	
QU03F04					X	X		
QU03F07					X	X		
BC04F02					X	X		
BC04M13					X	X		
QU04F05					X	X		
QU04F08					X			
QU04F09					X			
QU05M05							X	
YK05M01							X	
BC06F07							X	X
BC06M12							X	
YK06F01							X	
Total Lynx	6	2	3	2	12	10	11	2

Table 4. All individual lynx (n = 22) documented through either aerial or satellite locations (non-truncated datasets) by year in Utah from February 1999 – March 2007.

Lynx ID	Year							
	2000	2001	2002	2003	2004	2005	2006	2007
AK99F5						X		
AK00F5								X
AK00M3		X						
BC00M09					X			
BC00M13	X							
YK00F7							X	X
BC03F03				X				
BC03M06								X
BC03M08				X				
BC03M10								X
QU03F03					X	X		
BC04M01					X	X		
QU04M04							X	
QU04M05					X			
BC05M01								X
BC05M03						X	X	
CO05F20							X	
QU05F05						X	X	
QU05M03						X		
QU05M08						X		
YK05M01							X	
YK06M01							X	
Total Lynx	1	1	0	2	4	7	7	5

Table 5. All individual lynx (n = 17) documented at least 180 days after their initial release (truncated datasets) through either aerial or satellite locations, by year in Utah from September 1999 – March 2007.

Lynx ID	Year							
	2000	2001	2002	2003	2004	2005	2006	2007
AK99F5						X		
AK00F5								X
AK00M3		X						
BC00M09					X			
YK00F7							X	X
BC03M06								X
BC03M10								X
QU03F03					X	X		
BC04M01					X	X		
QU04M04							X	
BC05M01								X
BC05M03						X	X	
CO05F20							X	
QU05F05						X	X	
QU05M03						X		
YK05M01							X	
YK06M01							X	
Total Lynx	0	1	0	0	3	6	7	5

Table 6. All individual lynx (n = 33) documented through either aerial or satellite locations (non-truncated datasets) by year in Wyoming from February 1999 – March 2007.

Lynx ID	Year						
	1999	2001	2003	2004	2005	2006	2007
AK99M6	X						
BC00F14			X	X			
BC00M13		X		X			
YK00F11						X	
BC03F03				X			
BC03M02				X			
BC03M06				X			
BC03M09			X	X			
QU03M01				X			
BC04F02					X		
BC04M01				X			
BC04M08				X	X	X	
BC04M13					X		
CO04F10				X			
CO04M05				X			
CO04M06				X			
QU04F01				X	X	X	
QU04F02				X	X	X	X
QU04F07				X			
QU04M04					X	X	
QU04M05				X	X	X	
BC05M03					X	X	
BC05M08					X		
MB05F01						X	
MB05F02						X	X
MB05F03						X	
QU05F04					X	X	X
QU05F05					X	X	
QU05F08					X	X	X
QU05M08					X	X	
YK05M03					X		
BC06M10						X	
BC06M13						X	X
Total Lynx	1	1	2	16	14	16	5

Table 7. All individual lynx (n = 27) documented at least 180 days after their initial release (truncated datasets) through aerial or satellite locations, by year in Wyoming from September 1999 – March 2007.

	Year					
Lynx ID	2001	2003	2004	2005	2006	2007
BC00F14		X	X			
BC00M13	X		X			
YK00F11					X	
BC03F03			X			
BC03M02			X			
BC03M06			X			
BC03M09		X	X			
QU03M01			X			
BC04F02				X		
BC04M08			X	X	X	
BC04M13				X		
CO04F10			X			
CO04M05			X			
CO04M06			X			
QU04F01			X	X	X	
QU04F02			X	X	X	X
QU04M04				X	X	
QU04M05			X	X	X	
BC05M03					X	
MB05F01					X	
MB05F02					X	X
MB05F03					X	
QU05F04				X	X	X
QU05F05				X	X	
QU05F08				X	X	X
QU05M08				X	X	
BC06M13					X	X
Total Lynx	1	2	14	11	15	5

Table 8. Status of adult lynx reintroduced to Colorado as of June 30, 2007.

Lynx	Females	Males	Unknown	TOTALS
Released	115	103		218
Known Dead	54	43	1	98
Possible Alive	61	60		120
Missing	23	27		49[a]
Monitoring/tracking	38	33		71

[a] 1 is unknown mortality

Table 9. Causes of death for all lynx released into southwestern Colorado 1999-2006 as of June30, 2007.

Cause of Death	Mortalities		
	Total (%)	In Colorado (%)	Outside Colorado (%)
Unknown	35 (35.7)	20 (57.1)	15 (42.9)
Gunshot	13 (13.3)	7 (53.8)	6 (46.2)
Hit by Vehicle	12 (12.2)	8 (66.7)	4 (33.3)
Starvation	10 (10.2)	9 (90.0)	1 (10.0)
Other Trauma	8 (8.1)	7 (87.5)	1 (12.5)
Plague	7 (7.1)	7 (100)	0 (0)
Probable Gunshot	5 (5.1)	4 (80)	1 (20)
Predation	3 (3.1)	3 (100)	0 (0)
Probable Predation	3 (3.1)	3 (100)	0 (0)
Illness	2 (2.0)	2 (100)	0 (0)
Total Mortalities	98	70 (71.4)	28 (28.6)

Table 10. Known lynx mortalities (n = 28) and causes of death documented by state outside of Colorado from February 1999 – June 30, 2007.

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
YK99F01	Arizona	9/15/2005	Gunshot
YK00M03	Kansas	9/30/2005	Vehicle Collision
YK05M03	Montana	11/8/2005	Unknown

Table 11. Lynx reproduction summary statistics for 2003-2007. No reproduction was documented from 1999-2002 or in 2007.

Year	Females Tracked	Dens Found in May/June	Percent Tracked Females with Kittens	Additional Litters Found in Winter	Mean Kittens Per Litter (SE)	Total Kittens Found	Sex Ratio M/F (SE)
2003	17	6	0.353		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		2.75 (0.47)	11	1.2
2007	34	0	0.0			0	
Total						116	1.14 (0.14)

Table 12. 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 June 30, 2007.

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 6/30/2007
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
YK00F7	12/12/2006	Utah	Atypical habitat	1/20/2007	Alive in Utah	In Utah as of 6/30/2007
YK05M02	1/1/2007	Kansas	Atypical habitat	2/2/2007	Alive in Iowa	In Iowa as of 6/30/2007
BC04M08	1/22/2007	Wyoming	Atypical habitat	2/15/2007	Alive in Colorado	In Colorado as of 6/30/2007

Table 13. 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

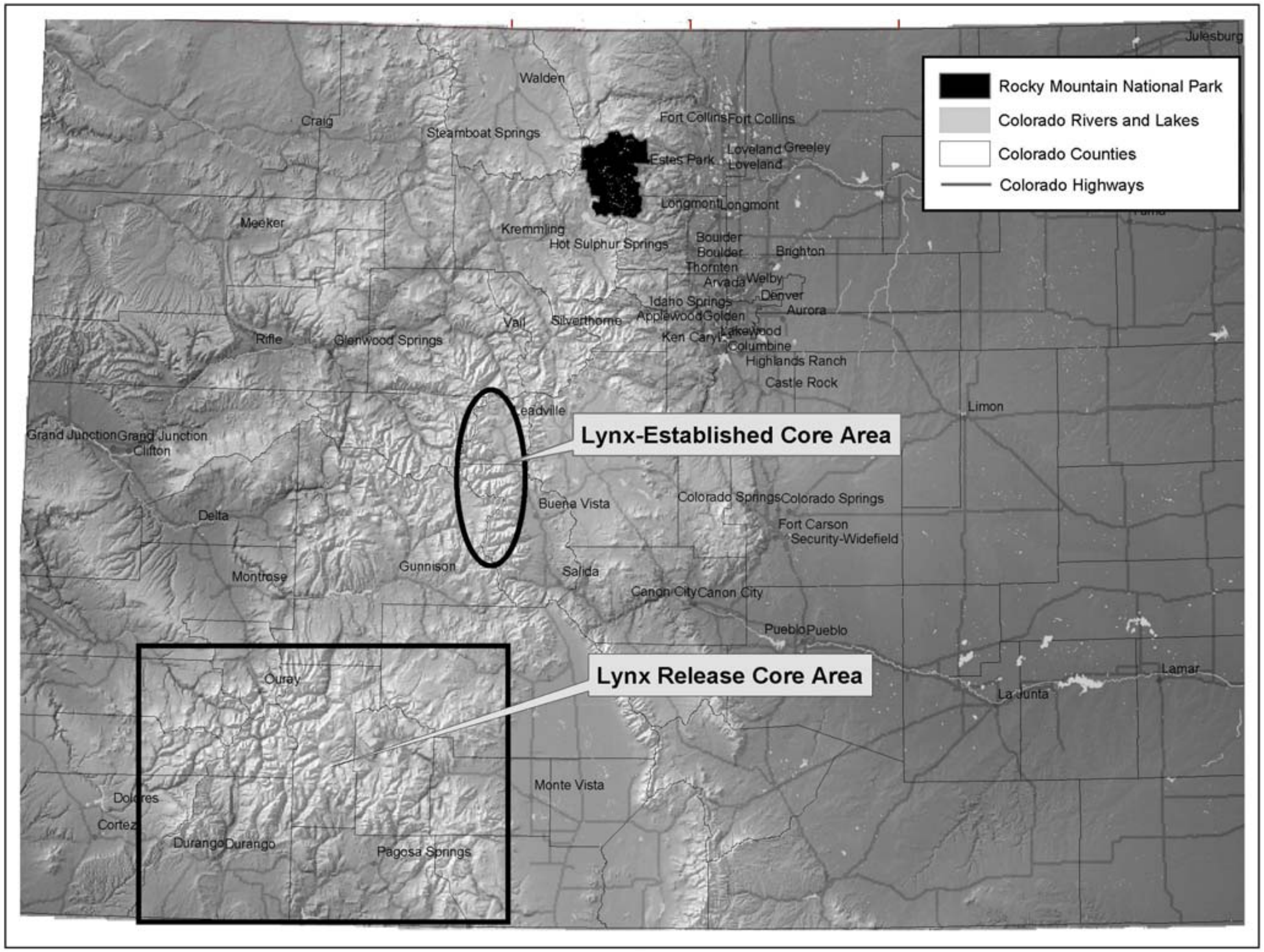

Figure 1. Lynx are monitored throughout Colorado and by satellite throughout the western United States. The lynx core release area, where all lynx were released, is located in southwestern Colorado. A lynx-established core use area has developed in the Taylor Park and Collegiate Peak area in central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

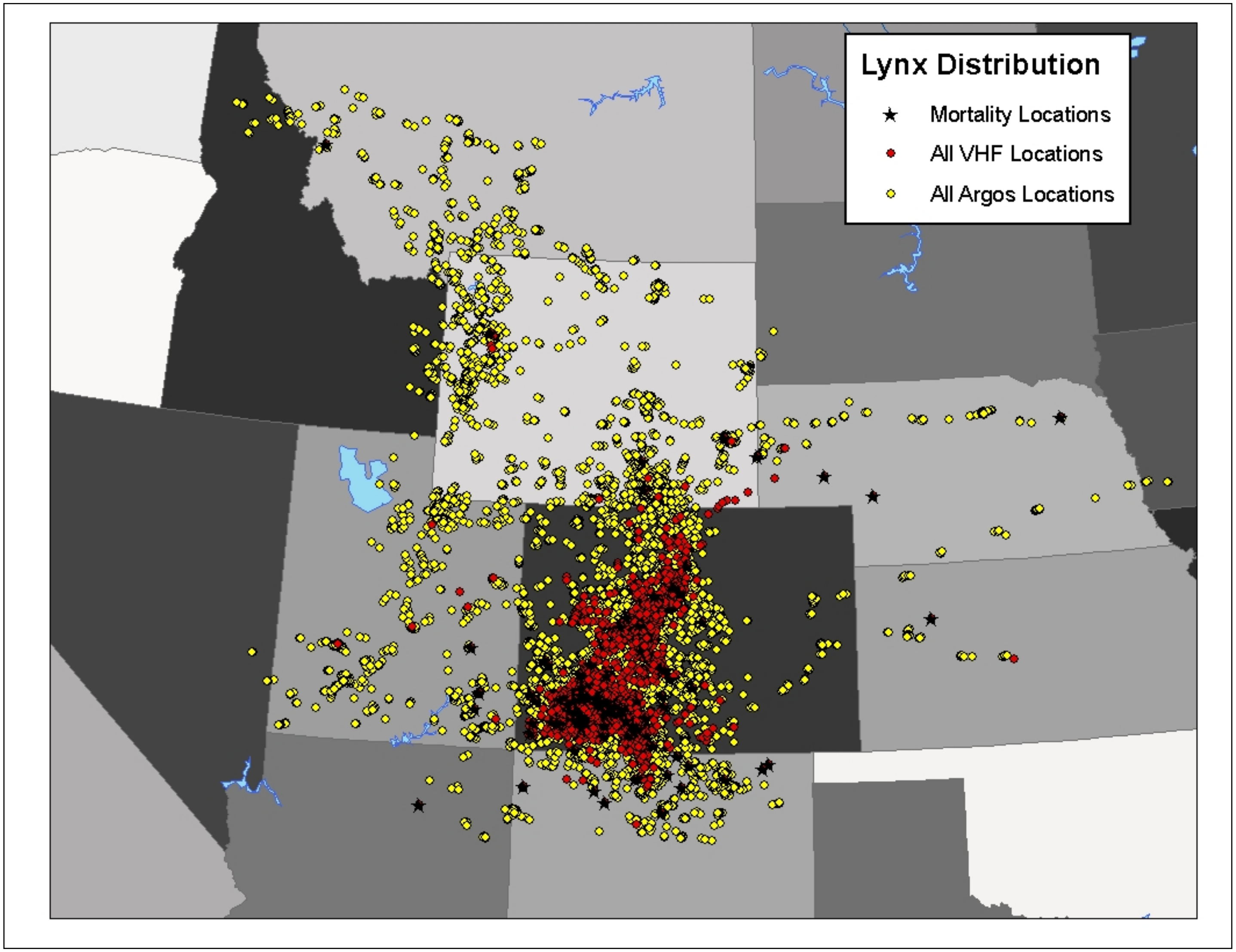

Figure 2. All documented lynx locations (non-truncated datasets) obtained from either aerial (yellow circles) or satellite (red circles) tracking from February 1999 through June 30, 2007. All known lynx mortality locations (n = 97) are displayed as stars.

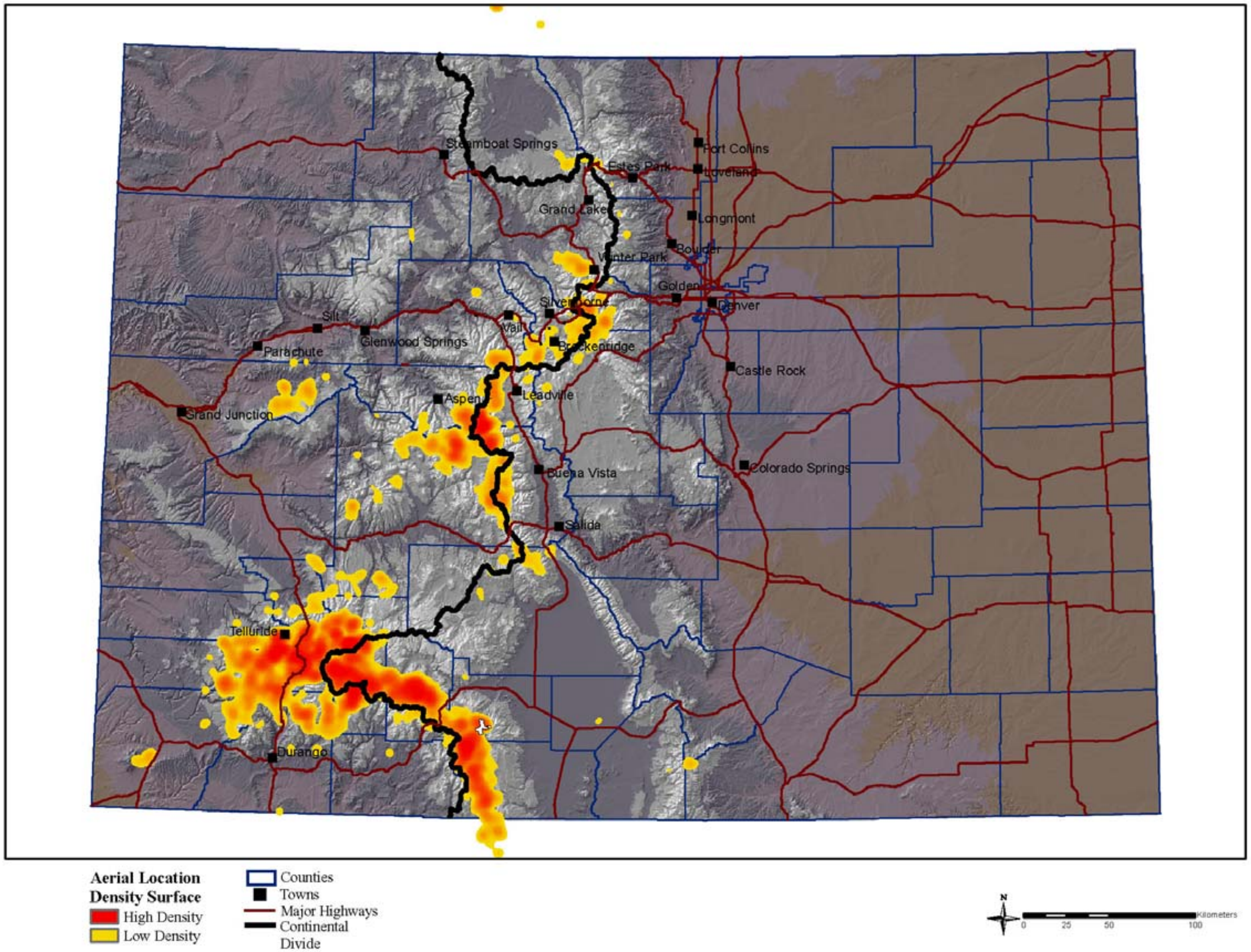

Figure 3. Use-density surface for lynx aerial locations (truncated dataset) in Colorado from September 1999-March 2007

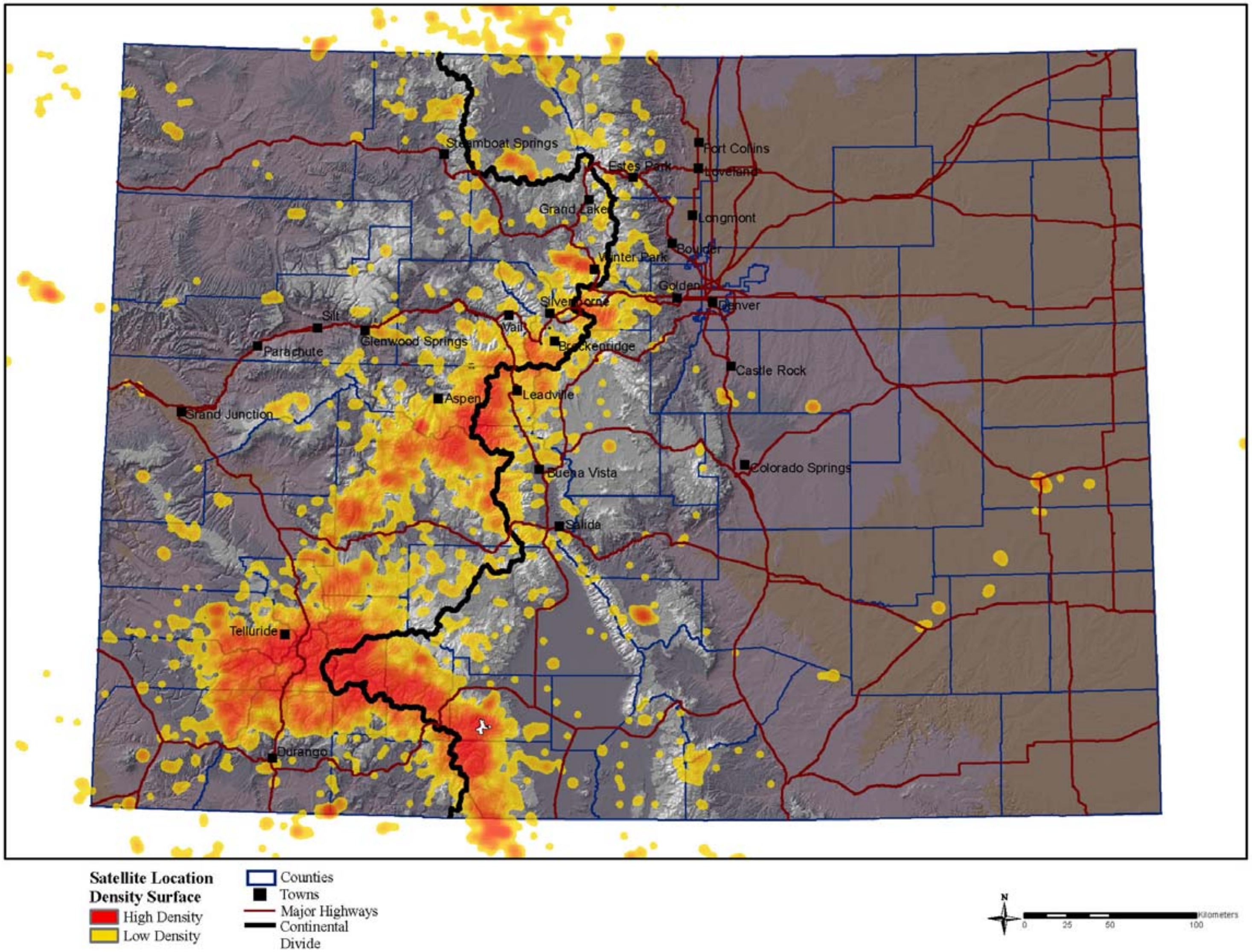

Figure 4. Use-density surface for lynx satellite locations (truncated dataset) in Colorado from September 1999-March 2007.

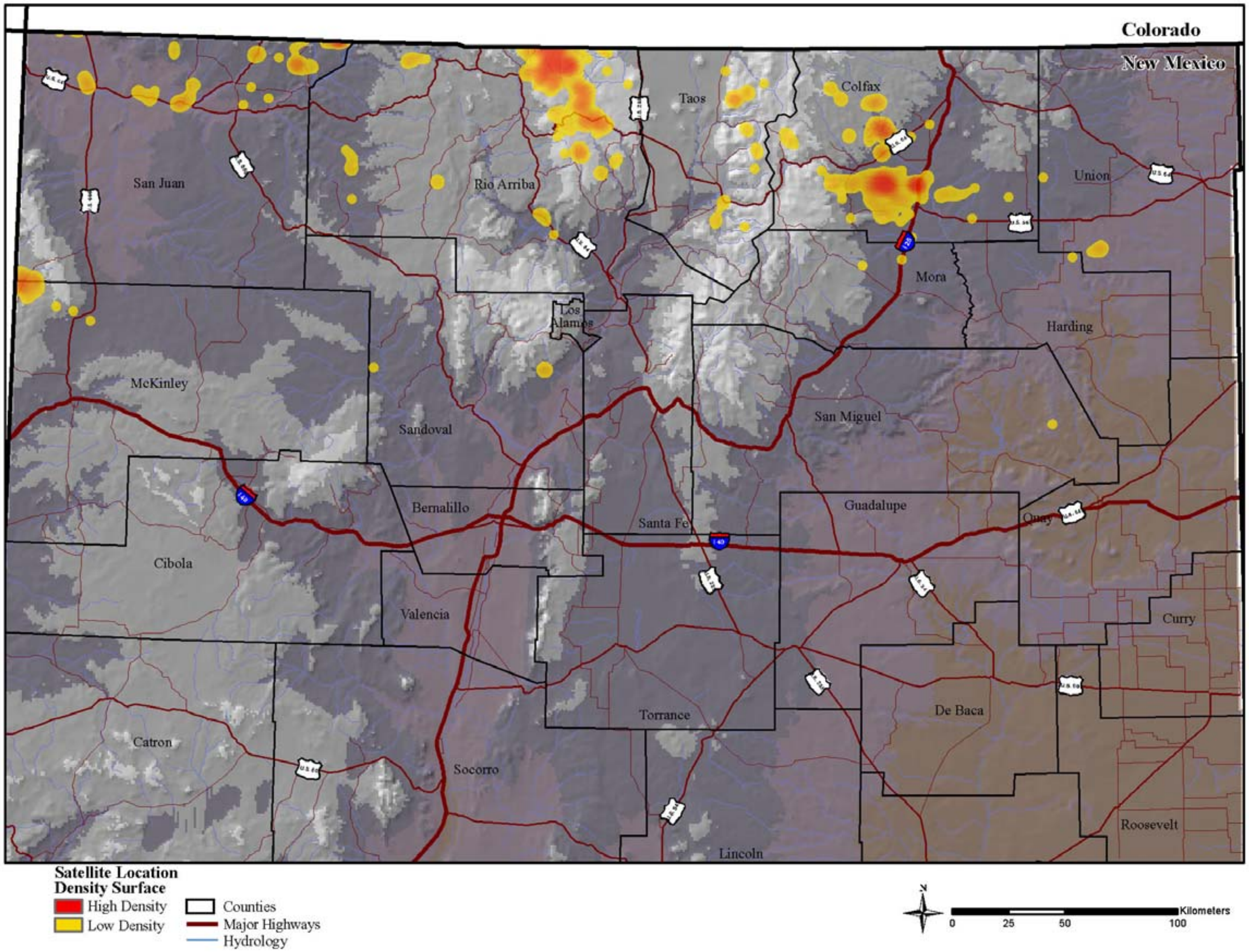

Figure 5. Use-density surface for lynx satellite locations (truncated dataset) in New Mexico from September 1999-March 2007

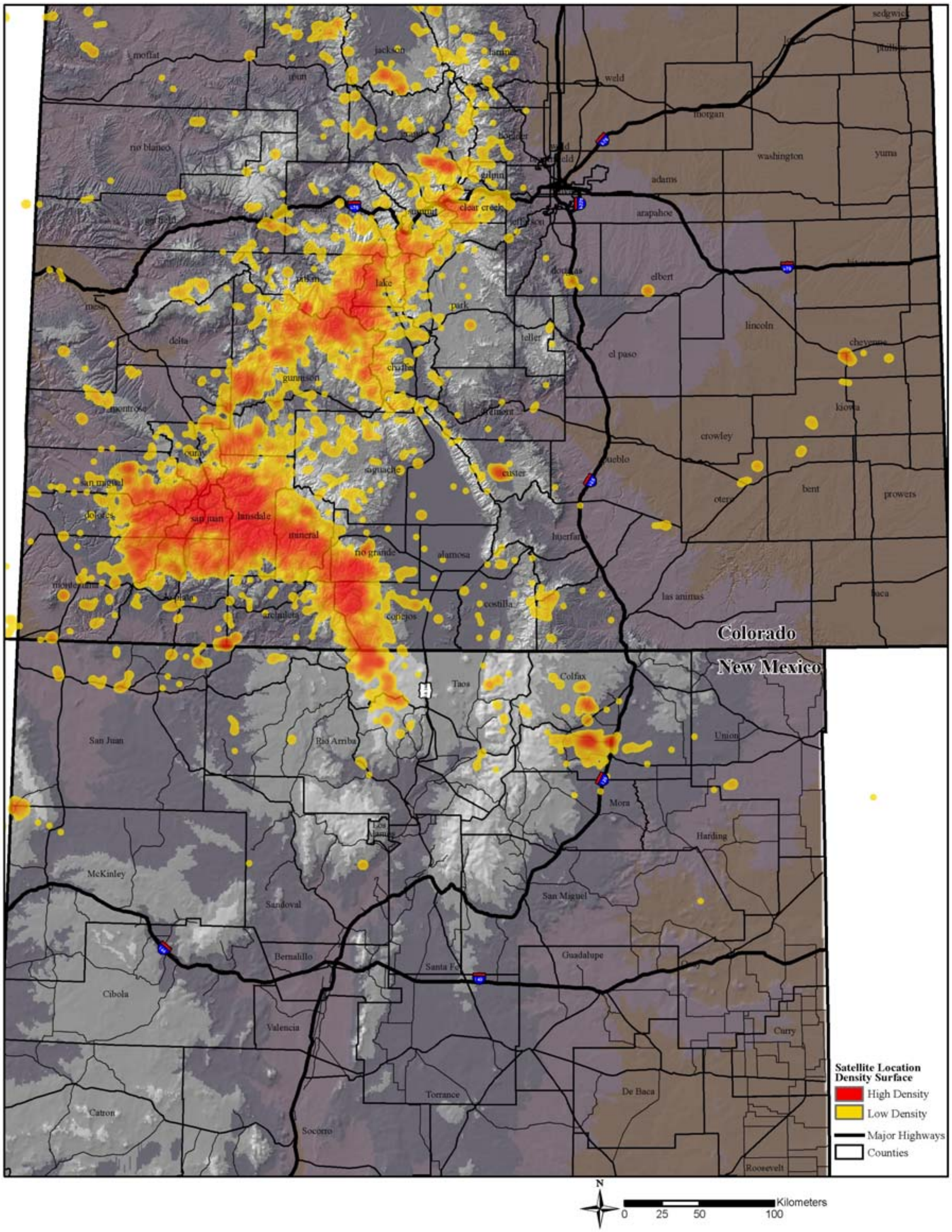

Figure 6. Use-density surface for lynx satellite locations (truncated dataset) in Colorado and New Mexico from September 1999-March 2007.

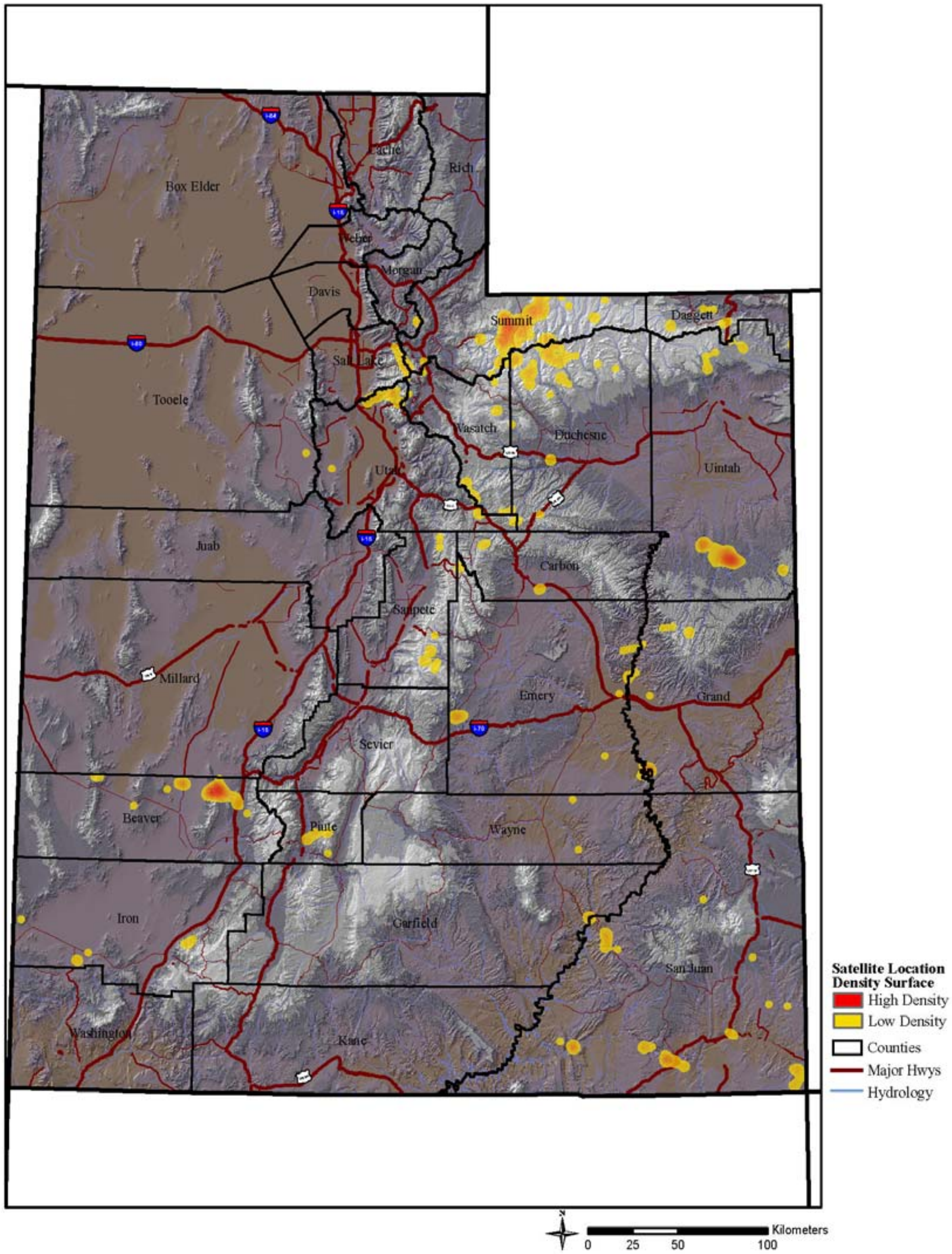

Figure 7. Use-density surface for lynx satellite locations (truncated dataset) for Utah from September 1999-March 2007.

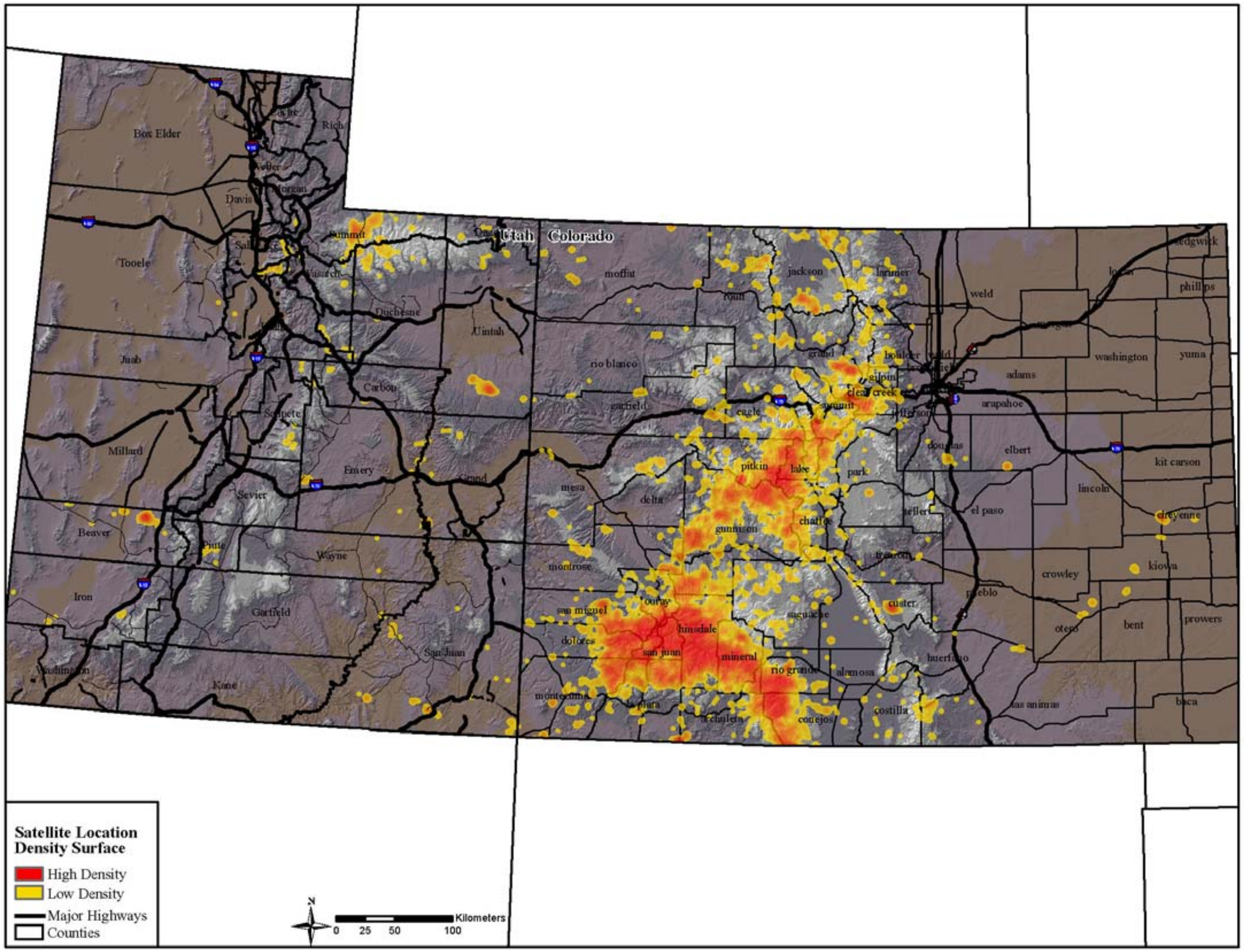

Figure 8. Use-density surface for lynx satellite locations (truncated dataset) in Colorado and Utah from September 1999-March 2007.

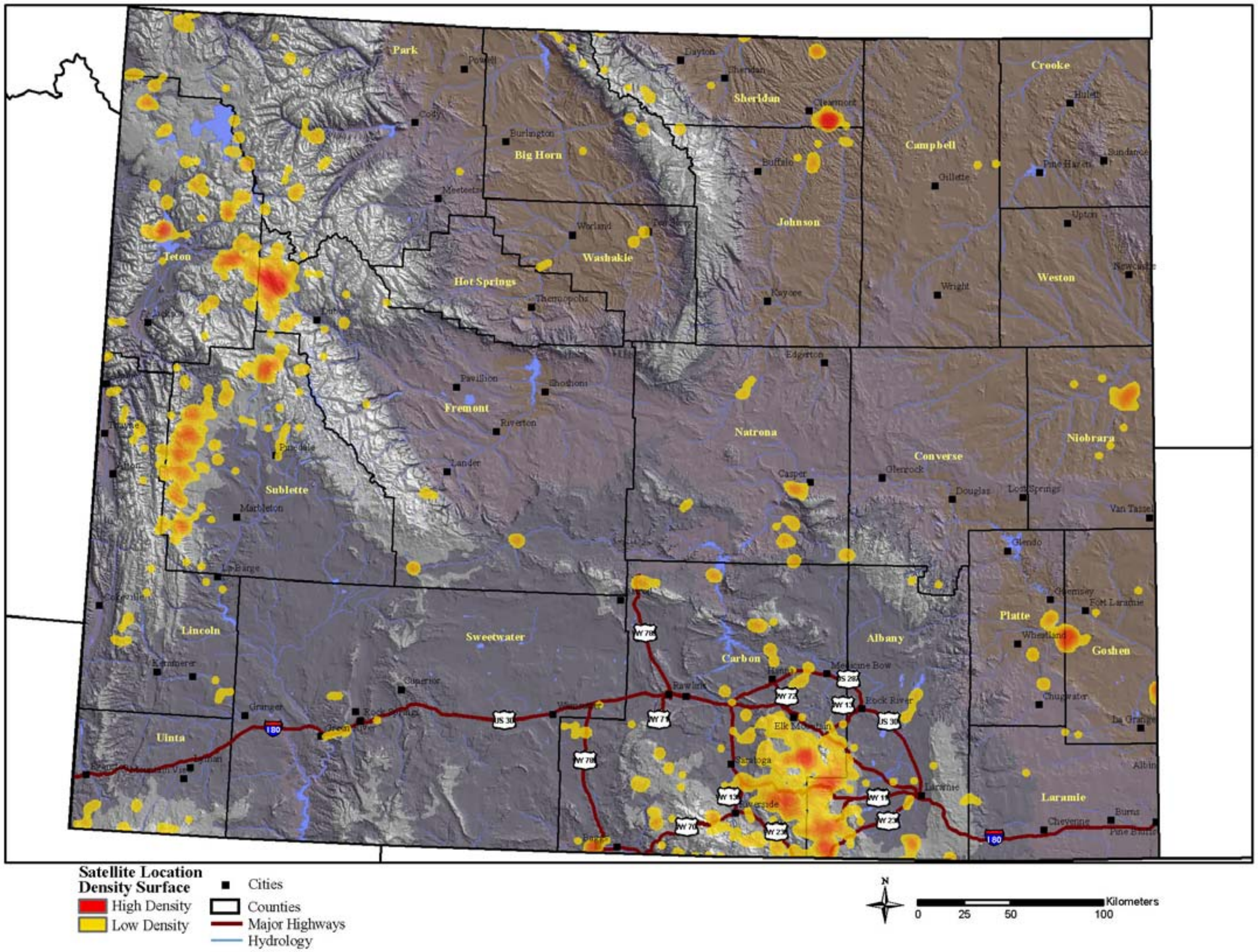

Figure 9. Use-density surface for lynx satellite locations (truncated dataset) in Wyoming from September 1999-March 2007.

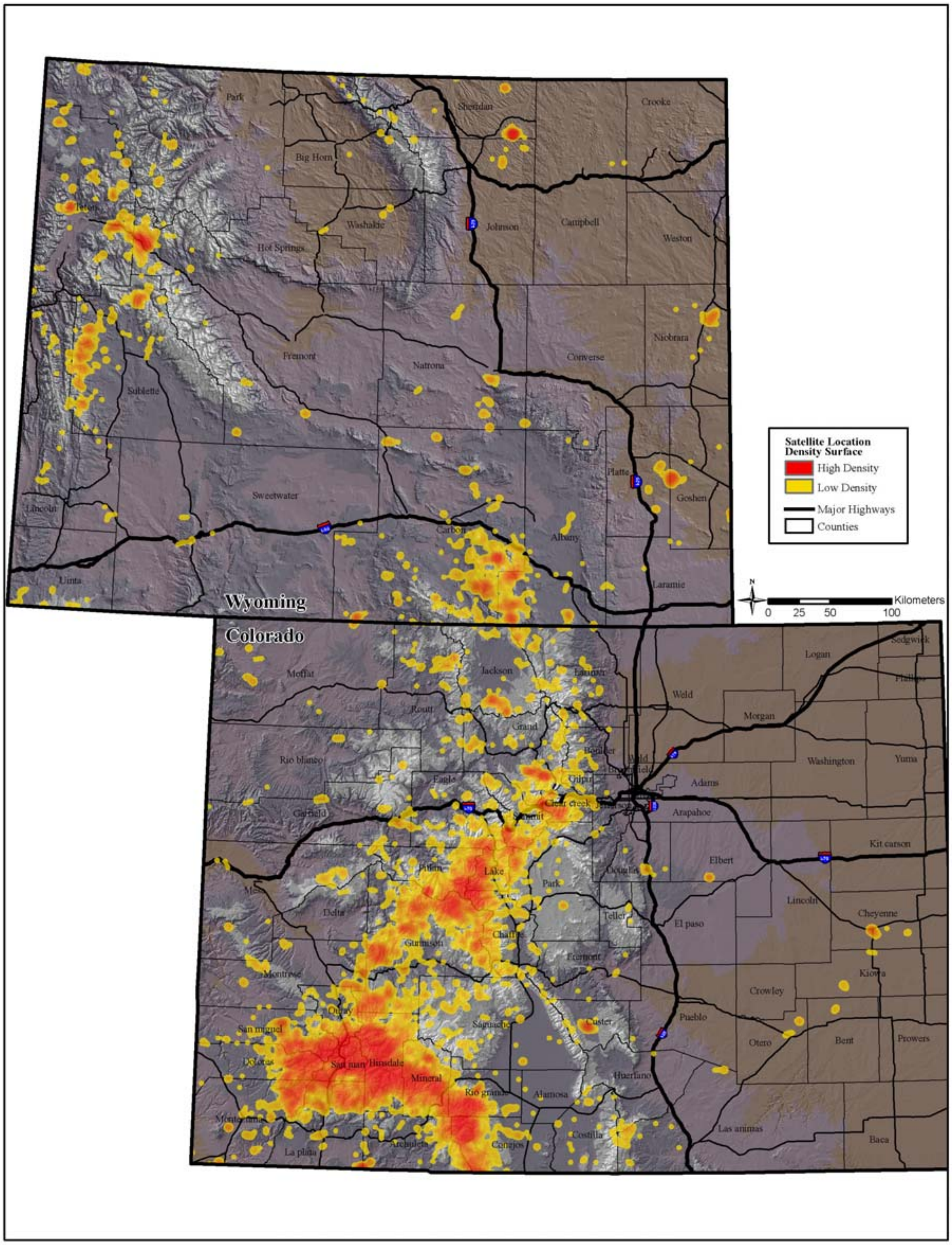

Figure 10. Use-density surface for lynx satellite locations (truncated dataset) in Colorado and Wyoming from September 1999-March 2007.

APPENDIX I

Colorado Division of Wildlife
July 2006 - June 2007

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:	N/A	:

Period Covered: July 1, 2006- June 30, 2007

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

Personnel: T. M. Shenk, CDOW and 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 with the first lynx release in 1999. Analysis of scat collected from winter snow tracking indicated that snowshoe hares (*Lepus americanus*) comprised 65–90% of the winter diet of reintroduced lynx. Thus, existence of lynx in Colorado and success of the reintroduction effort hinge at least in part on maintaining adequate and widespread populations of hares. Beginning in July 2006, I initiated a study to assess the relative value of 3 forest stand types (mature ["large"] spruce/fir, sapling ["small"] lodgepole pine, pole-sized ["medium"] lodgepole pine) that purportedly provide high quality hare habitat in Colorado. 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 value. Number of individuals captured, number of captures, and number of locations obtained per hare during the first year of the project appear adequate for attaining the objectives of this study. Some hare deaths due to capture myopathy (most likely cause) occurred during initial trapping periods in both the summer and winter sampling seasons. However, changes to the trapping protocol, trapping schedule, and bait provided seem to have alleviated the problem. Densities during summer were highest in small lodgepole stands (0.47 hares/ha, 95% CI: 0.41-0.54), followed by large spruce/fir (0.18 hares/ha, 95% CI: 0.12-0.25) and medium lodgepole (0.02 hares/ha, 95% CI: 0.01-0.03). During winter, densities in small lodgepole stands dropped and became more variable across replicates (0.18 hares/ha, 95% CI: 0.01-0.35). Medium lodgepole stands gained hares (0.07 hares/ha, 95% CI: 0.05-0.10). Spruce/fir stands remained at the same density as during summer (0.17 hares/ha, 95% CI: 0.11-0.23).

WILDIFE RESEARCH REPORT

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

JACOB S. IVAN

P. N. OBJECTIVE

Assess the relative value of 3 forest stand types (old spruce/fir, sapling lodgepole, pole-sized lodgepole) that purportedly provide high quality snowshoe hare (*Lepus americanus*) 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 Wildlife Research Reports for Colorado Division of Wildlife (CDOW).

INTRODUCTION

A program to reintroduce the threatened Canada lynx (*Lynx canadensis*) into Colorado was initiated in 1997 with the first lynx released in 1999. Since that time, 204 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 2006). 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, the existence of lynx in Colorado and success of the reintroduction effort may also 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 species exhibits dramatic cycles as occur farther north, and typical lynx ($\leq$2–3 lynx/100km^2; Aubry et al. 2000) and hare ($\leq$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. This has caused controversy where recommendations conflict with competing resource management goals. 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 1990, Koehler 1990, 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 1990, 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, density can be a difficult metric to estimate accurately. Density 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). Different 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).

Pellet plot counts are typically conducted by laying out numerous rectangular or circular plots along transect lines randomly placed within a study site. All pellets occurring within the plot are counted and removed on an annual basis. The mean number of pellets per plot is then inserted into a regression equation that gives an estimate of hare density (Krebs et al. 1987). Estimates from this technique correlate well with density estimates derived from simultaneous mark-recapture studies occurring in the same area (Krebs et al. 2001, Murray et al. 2002, Mills et al. 2005, Homyack et al. 2006). However, because fecal deposition rates can vary by season and diet, and because pellet decomposition rates can vary with altitude, climate, aspect, precipitation, and cover type, region-specific, stand-specific, and/or season-specific equations should be developed before this technique is employed for a given area and season (Krebs et al. 2001, Prugh and Krebs 2004, Murray et al. 2005). Density estimates vary with plot size and shape, requiring equations specific to these geometric considerations as well (McKelvey et al. 2002). Pellet counts tend to yield more precise and unbiased density estimates when plots are visited and cleared more than once per year (e.g., plots cleared in the fall and then counted in the spring to estimate winter density) because variability in deposition and decomposition rates is reduced (Homyack et al. 2006). However, this requires considerably more work and expense than an annual survey. Some studies have conducted pellet plot counts without first clearing plots (e.g., Bartmann and Byrne 2001). This saves time and money, but requires the ability to discern fresh (this year) pellets from old pellets, which can be difficult and is generally not a recommended approach (Prugh and Krebs 2004, Murray et al. 2005).

Distance sampling is a well-developed method for estimating the density of objects in a given area (Buckland et al. 2001). In general, observers walk a pre-defined sampling transect and record each object of interest along with the perpendicular distance of that object from the transect line. This information is then used to develop a detection function which is in turn used to estimate density (Buckland et al. 2001). The method assumes all objects on the line are seen with certainty, objects are not double-counted, distance measures are accurate, and transect lines are located randomly within a study area (Buckland et al. 2001). Recently, distance sampling has been used to indirectly estimate hare density by first estimating the pellet group density of hares, then using fecal deposition and decomposition rates as a link back to hare density (Eriksson 2006). In general, distance sampling is more efficient than pellet plot counts as it does not require the tedious layout of hundreds of plots or counting individual pellets. This advantage is most recognizable in situations where pellet groups occur at low densities. Conversely, at extremely high densities, it may become difficult to distinguish pellet groups, and plots may be preferable (Marques et al. 2001). Regardless, distance sampling of pellet groups to estimate animal density also requires habitat and season specific decomposition and defecation rates, which can be difficult to obtain (Marques et al. 2001).

For this project, I have chosen to provide land managers with information relating demographic rates, as well as density, to forest stand characteristics. Thus, I will use mark-recapture techniques as data from such an approach can provide information on both density and demography. 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.

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 (Figure 1). 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.

Specifically, I will 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). I also intend to identify which of the numerous density-estimation procedures available perform accurately and consistently using an innovative, telemetry augmentation approach as a baseline. I will assess movement patterns and seasonal use of deciduous cover types such as riparian willow. Finally, I will 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.

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

7 x 12 trapping grid. To accommodate this, I sampled 6 replicate small lodgepole stands (rather than 3) using 6 x 7 trapping grids (1/2 size).

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 will be estimated using a variety of conventional techniques as well as a rigorous method that incorporates radio telemetry. 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. Recruitment is the number of new animals in the population at time *i* + 1 per animal in the population at time *i*. New recruits can arise from on-site reproduction as well as immigration. The finite population growth rate is the number of animals in a given age class at time *i* + 1 divided by the number present at time *i*. Shifts in home range will be assessed by comparing the seasonal proportion of telemetry locations in deciduous habitats using multi-response permutation procedures (MRPP; Zimmerman et al. 1985, White and Garrott 1990).

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 will further characterize 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 will record physical covariates such as ambient temperature, precipitation, and snow depth at each stand during sampling periods as well as precipitation 1-3 years prior to sampling. Finally, I will calculate potentially important landscape metrics such as patch size and level of fragmentation.

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. Traps were deployed in all 4 stands in a single day. As traps are deployed, they were locked open and “pre-baited” with apple slices and commercial rabbit chow. During winter, hay cubes were added to traps as well (see Discussion). On days 2-4, the crew continued pre-baiting, replacing apples and rabbit chow as necessary. The purpose of this extended pre-baiting was 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 trapping-related stress as well as the likelihood that

American marten (*Martes americana*) keyed into trap lines and preyed on entrapped hares, as has occurred in previous studies (J. Zahratka, personal communication). 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 seems reasonable.

Traps were set on the afternoon of the 4th day and checked early each morning and again in the evening on days 5–9. By checking traps in both morning and evening I prevent 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.

The crew gathered telemetry locations for radio-collared hares on the initial sites for 8 to 10 days. Then the 10–day trapping procedure and 8 to 10–day telemetry work were repeated on the 3 grids comprising suite 2 (Figure 3). The cycle was repeated once more for grids in suite 3 (Figure 3). The entire process was repeated during the winter when densities should have been at a minimum.

In summary, for any given 9-week sampling period, I collected data from 12 total grids, 1 spruce/fir, 1 medium lodgepole, and 2 small lodgepole across 3 replicates. Sampling will occur during 2 such 9-week periods each year – once in late summer and once in late winter – and will continue for 3 years. 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 was also occur 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 will follow 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 will lay out 5 × 5 grids (3-m spacing) of vegetation sampling points centered on 15 of the 84 trap locations (Figure 4; 9 points will be sampled on each of the ½-sized small lodgepole stands). At each of the 25 vegetation sampling points, I will record: 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 [0.1 m] and winter [1.0 m] stem density; Barbour et al. 1999), 2) horizontal cover in 0.5-m increments above the ground up to 2 m (Nudds 1977), and 3) canopy cover [present or absent] using a densitometer. Additionally, at the center of all 15 vegetation sampling grid points (i.e., at the trap location), I will measure basal area using an angle gauge. These measurements will be gathered once at the start of the project, unless conditions change due to disturbance such as fire. Temperature will be monitored hourly at each grid during the 6-week intensive sampling periods using data loggers. During winter sampling periods, snow depth measurements will be recorded daily at the same 15 trap locations used to quantify the vegetative attributes of that stand.

Data Analysis

Density.--I assumed that hare populations were demographically and geographically closed during the short 5-day mark-recapture sampling periods. To obtain a density estimate for each grid, I used the Huggins closed capture model (Huggins 1989, 1991) in Program MARK (White and Burnham 1999) with some modifications. The basic Huggins estimator (no individual covariates) is based on the fact that if p_j is the probability that a hare in the population is captured (and marked) for the first time on trapping occasion *j*, then $p^* = 1-(1-p_1)...(1-p_5)$ is the probability that an individual is captured at least once during a 5-day trapping period (i.e., *j* = 1,…,5). Accordingly, the basic Huggins estimator for population size, $\hat{N}$, is $\hat{N} = M_{t+1}/p^*$ where M_{t+1} is the total number of hares captured. The estimator can be re-written to allow each of the M_{t+1} individuals captured to have their own p^*. In that case, $\hat{N} = \sum_{i=1}^{M_{t+1}} 1/p_i^*$. Presumably hares that reside near the edge of a grid encounter fewer traps and are less likely to be captured than hares residing near the center of a grid. To account for this, I took advantage of the Huggins model with individual covariates to model p^* by using the logit link function of program MARK to model p_i^* as a function of d_i, where d_i is distance from the edge of the grid for hare *i* based on mean capture coordinates. A naïve density estimate for each grid would then be $\hat{D} = \hat{N}/A$ where *A* is the area of the grid. However, this gives full credit to all hares, even those whose home range only partially overlaps the grid, which results in a density estimate that is biased high. To correct for this bias, I determined the proportion, $(\tilde{p}_k)$, of telemetry locations for each of the *k* = 1,…,10 radio-collared hares that fell within the "naïve grid area." By incorporating data from multiple grids, a logistic regression model was developed to estimate $\tilde{p}_i$ for all M_{t+1} animals captured on a grid based on distance from the edge of the grid for hare *i* (d_i). Replacing the numerator (i.e., 1) in the Huggins estimator with $(\tilde{p}_i)$, gives a density estimate, $\hat{D} = \left(\sum_{i=1}^{M_{t+1}} \tilde{p}_i / p_i^* \right) \Big/ A$.

The above-stated approach assumes that radio-collared hares neither gravitate toward nor avoid the former grid area after the 5 days of trapping, 10–20 locations per hare is enough to provide a reasonable representation of the proportion of time they spend on the grid, and their use of the grid area is representative of other hares that were captured but not collared (i.e., that the logistic regression model of $\tilde{p}_i$ is a useful model). I contend that this type of estimate from grid-based trapping can be construed as a relatively unbiased estimate of density. Using these point estimates and their associated confidence intervals, I compared hare density among seasons and stand types. I will also compare these "true" density estimates to those that would have been obtained using other available methods such as ½ mean maximum distance moved (Wilson and Anderson 1985, Williams et al. 2002:314-315), full mean maximum distance moved (Parmenter et al. 2003), ½ trap interval (Parmenter et al. 2003), "nested grids" (White et al. 1982:120-131), and Program DENSITY (Efford et al. 2004).

Demography.--I will analyze mark-recapture data using Pradel temporal symmetry models (Pradel 1996, Nichols and Hines 2002) in a robust design framework (Williams et al. 2002:523-554), which will be available in Program MARK by summer 2006. Thus, I will treat summer and winter sampling occasions as primary periods, and the 5-day trapping sessions within each as secondary periods. The Pradel temporal symmetry models employ both forward and reverse-time evaluation of capture histories to provide estimates of apparent survival ($\hat{\phi}$) and seniority ($\hat{\gamma}$). Apparent survival, ϕ_i, is the probability that a marked animal alive and in the population at time *i* survives and is in the population at time *i* + 1. The seniority parameter, γ_i, is the reverse-time analogue of survival. Reading backward through a capture history, it is the probability that a marked animal alive and in the population at time *i* was alive and in the sampled population at time *i* − 1. If *N* is the number of animals present in the population, $N_i\phi_i \approx N_{i+1}\gamma_{i+1}$ and $N_{i+1}/N_i = \phi_i/\gamma_{i+1} = \lambda_i$. Also, if f_i is recruitment rate, or the number of recruits at time *i* + 1 per animal present at time *i*, then $N_{i+1} = N_i\phi_i + N_i f_i$. Rearranging and substituting into the previous equation gives $f_i = \phi_i\left(1/\gamma_i - 1\right)$. Thus, using Pradel models, one can estimate recruitment and finite population growth rate in addition to survival (Pradel 1996, Nichols and Hines 2002).

I will use Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 1998) to determine whether models with time-dependent parameters or constant parameters are best supported by the data. I will derive estimates of the above-mentioned parameters from the best model or from model averaging. I anticipate pooling capture data across sites to obtain $\hat{\phi}_i$, $\hat{\lambda}_i$, and $\hat{f}_i$ for each stand type for each interval between primary sampling periods (5 estimates of each). I also anticipate simply estimating these parameters for "generic hares", treating both juveniles and adults as a single group or age class. Given that juveniles are morphometrically indistinguishable from adults by their first fall of life (K. Hodges, University of British Columbia; P. Griffin, University of Montana, personal communication), adult and juvenile survival rates are similar (Griffin 2004), and there is little evidence for age-specific differences in pregnancy rates or litter size (Dolbeer 1972), this approach seems justified. However, if I happen to capture sufficient numbers of juveniles and adults, the design I have laid out here allows for treating the age classes separately. This, in turn, may permit me to decompose the contribution that f_i makes to λ_i into the portion of that contribution due to on-site reproduction and that due to immigration (Nichols et al. 2000). Similarly, it may also be possible using my telemetry data to decompose apparent survival, ϕ_i, into emigration and mortality. Such fortuitous situations would facilitate the identification of source and sink habitats if they exist.

Seasonal Movements.--I will assess whether snowshoe hares seasonally shift their home ranges using the multi-response permutation procedure (MRPP; Zimmerman et al. 1985, White and Garrott 1990:134-135). Under this approach, telemetry locations are grouped by season (summer and winter), and an MRPP statistic is calculated as the weighted average of the distance between all possible pairs of locations within groups compared to the average distance between all possible pairs ignoring groups. The null hypothesis is that the distribution of locations is the same for both groups (seasons). Sufficiently small values of the test statistic suggest that within group distances are smaller than distances measured ignoring groups, which is evidence against the null in favor of a group (seasonal) effect. P-values are obtained by calculating the percentile of the observed test statistic relative to all possible test statistics that could be computed by re-arranging the data into all possible groups of 2. The MRPP procedure is sensitive and can detect even small changes in use of an area (White and Garrott 1990:136). I propose a priori that changes in proportional use of deciduous habitats <0.10 in magnitude are unlikely to be biologically significant.

Vegetation.--I will calculate mean stem density, horizontal cover, canopy cover, and basal area for each season–stand type as well as temperature, precipitation, snow depth information, and landscape metrics. These will be entered into the MARK design matrix as covariates to population size (~density) and survival in a random effects analysis. As such, I will be able to quantify the amount of variation in population size or survival that is due to differences in vegetation, landscape, or weather relative to the amount left to other causes.

Sample size.--I conducted power analyses to determine the probability of discerning meaningful differences in density and survival for hares occupying different stand types. For density, I postulated that foraging lynx likely do not discriminate among stands that differ by only a few hares. However, it seems probable that if hare density in one stand is twice that of another, a lynx would choose the former given the opportunity. Thus, I conducted power calculations to determine the probability of distinguishing differences in densities between 2 stand types in which one had twice the density of hares as the second. Specifically, using the Huggins closed capture model (Huggins 1989, Huggins 1991) in Program MARK, I specified the number of hares (*N*) present in each of 2 groups (i.e., 2 stand types), allowed capture (*p*) and recapture (*c*) probabilities to vary with time but constrained them to be equal and the same for each group, then simulated this scenario 1000 times for a range of realistic capture probabilities. For each simulation I calculated a 95% confidence interval for the mean difference in $\hat{N}$ between the 2 groups and determined the proportion of all simulations in which this confidence interval did not include zero. This proportion is the power, or probability of discerning a difference between the 2 groups when one actually exists. I compared 2-fold differences in density at the low (5 vs. 10 hares/grid) and high (15 vs. 30 hares/grid) end of the range of hare numbers and I expect to observe (Zahratka 2004). I also simulated the power to detect differences between 17 and 39 hares/grid, corresponding to recently published cut-points for low and high hare densities in the context of lynx conservation (Mills et al. 2005). Given capture/recapture probabilities I observed during winter 2005 (approximately 0.35–0.45), I expect to have reasonable power to detect 2-fold differences in density even if I encounter relatively few hares per grid (Figure 5).

I conducted power analyses for survival in a similar manner using the Huggins estimator (Huggins 1989, Huggins 1991) in a robust design framework (Williams et al. 2002:524-556). For this analysis, I specified 3 primary periods (e.g., 3 years) with 5 secondary occasions for each. I established either 30 or 45 hares in each of 2 groups (i.e., pooled an expected 10-15 hares/grid across the 3 grids in a given habitat type), specified a different survival rate for each, and allowed *p* and *c* to vary with time but constrained them to be equal and the same for each group as before. I then specified a general model that assumed survival rates varied among groups and a second, reduced model that assumed survival rates were the same for each group. After 1000 simulations under a given scenario of hare numbers, capture probabilities, and survival rates, I conducted a likelihood ratio test between each pair of general and reduced models. As before, I used the proportion of significant tests as an estimate of power to detect differences in survival.

I compared survival rates of 0.4 vs. 0.5, 0.3 vs. 0.5, and 0.2 vs. 0.5. These rates span the range of annual hare survival rates reported in the literature (Dolbeer 1972, Dolbeer and Clark 1975, Griffin 2004). Also, because each comparison is anchored at 0.5, these calculations provide a conservative estimate of power due to the nature of binomial probabilities. That is, I would be more likely to distinguish the difference between 0.1 and 0.2 than between 0.4 and 0.5 even though the difference in both cases is 0.1 because the sampling variance of the estimate for the same sample size is maximal at 0.5 and declines to 0 for survival rates of 0 or 1. Results indicate that I have ≥80% chance of discerning real differences in survival of ≥0.3 (Figure 6), but only 40-65% chance (depending on number of hares captured) of detecting a difference of 0.2, and very little chance of detecting differences smaller than 0.2. However, I plan to combine my telemetry data with my trapping data in the MARK Robust design model using separate groups for each data type. This should enhance my precision and power, thus making the prospect of detecting differences as small as 0.2 a possibility.

To complete a power analysis for $\hat{\lambda}$ requires running simulations of Pradel models in a robust design framework. This capability is not yet available in Program MARK, so such an analysis has not been completed. Sampling 15 vegetation plots per trapping grid provided reasonably precise characterizations of similar stands in similar locations during a previous study (Zahratka 2004). I trust this level of sampling will be adequate for the present study as well. If not, more plots can be established at a later date given that vegetative characteristics are unlikely to change appreciably over a few years.

RESULTS AND DISCUSSION

Much of the analysis presented above is not possible or meaningful without several seasons of data, especially the survival, recruitment, and growth rate models. Below, I present a basic summary, relevant observations, and initial density estimates from the inaugural year of this project.

I captured 75 hares 166 times during July-September 2006. I captured 99 hares 243 times during January-March 2007 (Table 1). Fourteen of these individuals were captured during both the summer and winter sampling sessions. During summer, I captured over twice as many individuals in small lodgepole stands as in spruce/fir. I captured only a few individuals in medium lodgepole stands. During winter, captures were more evenly distributed among the stands (Table 1).

During the initial trapping session of the summer trapping period, 6 hares were captured, handled, and released (seemingly without harm) but were found dead in traps 1-3 days later. I collected the carcasses and submitted them for necropsy. Cause of death was attributed to capture myopathy, which is relatively common in lagomorphs (Laurie Baeten DVM, and Lisa Wolfe DVM, Colorado Division of Wildlife, personal communication). I subsequently altered my trapping protocol to further minimize both the amount of time a hare could be entrapped as well as the handling time at each capture. No trap deaths occurred during the remainder of the sampling season aside from 4 hares that succumbed to predation while inside traps.

During the initial 2 trapping sessions of the winter trapping period, 6 more hares were captured, handled, and released multiple times, again with seemingly little adverse reaction, only to be found dead on a subsequent trapping occasion. Several more hares died during the 10-day telemetry session immediately following trapping. These "telemetry deaths" could have been due to natural causes, effects of capture, or a combination of both. Again, carcasses were submitted for necropsy, and again capture myopathy was cited as a potential cause of death. Further examination of the data indicated that hares trapped ≥3 days in a row were much more likely to die in a trap or during telemetry than other hares. Thus, I further modified the trapping protocol by locking traps open on day 3 of the 5-day trapping period so that hares could not be trapped more than 2 days in a row. Additionally, I began providing hay cubes in the traps as roughage to complement the high quality alfalfa pellets and apples. After implementing these changes, I did not observe any further trap-deaths or telemetry-deaths for the rest of the season.

I averaged 9.9 and 6.3 locations per radio-tagged hare during the summer and winter sampling sessions, respectively (Table 2). Thus, "proportion of time on grid," which is critical to my density estimation procedure, was based on relatively few points per individual for the first 2 sampling periods, and I was unable to attain my goal of 10-20 locations per individual. Following the winter field season, I conducted a series of simulations to examine the effects of sample size on precision of density estimates. I found that 1) the variability between hares ("proportion on grid" ranges from 0.00-1.00) overwhelms the variability within hares (i.e., the binomial variance for proportion of time on grid for any single individual, which decreases as number of locations increases), and 2) given a fixed effort, the variance of the density estimate is minimized by increasing the number of individuals collared as opposed to increasing the number of locations per individual. Thus, it is better to radio-tag more hares and get fewer locations than to tag fewer hares and get more locations. I will continue to deploy as many collars as possible, and will strive for 10-20 locations per individual, but the level of sampling achieved during the first 2 field seasons appears sufficient to detect the large differences in density that occur on the landscape.

During summer, density estimates followed hypotheses 1) and 2) above. Specifically, hare density in small lodgepole stands was twice that observed in spruce/fir, which was more than twice that observed in medium lodgepole stands (Figure 7). However, even the relatively high density found in the small lodgepole stands was relatively low compared to densities that have been reported in other parts of hare range (Griffin 2004, Hodges 2000). However, different methods for computing density make this type of comparison difficult.

During winter, hare densities remained the same in spruce/fir stands. Hare density in medium lodgpole stands more than doubled, although still remained relatively low compared to other stand types. Density in the small lodgepole stands dropped significantly compared to summer levels and was more variable among replicates. Hare density is likely driven by availability of food and cover. I submit that the interplay between food, cover, and snow depth provides a plausible explanation for the density patterns observed during the first year of this study. Spruce/fir stands probably provide adequate access to both necessities during both summer and winter due to their uneven-aged, multi-layered structure. Medium lodgepole stands, on the other hand, 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 bring that canopy back into reach for hares. Conversely, small lodgepole stands provided 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.

SUMMARY

- The number of snowshoe hares captured, the number of captures, and the number of locations obtained per hare during the first year appeared adequate for attaining the objectives of this study.
- Some deaths due to capture myopathy (most likely cause) occurred during initial trapping periods in each sampling season. Changes to the trapping protocol, trapping schedule, and bait provided seem to have alleviated the problem.
- Snowshoe hare densities during summer were highest in small lodgepole stands, followed by large spruce/fir and medium lodgepole. During winter, densities in small lodgepole stands dropped and became more variable across replicates. Medium lodgepole stands gained hares. Spruce/fir stands remained at the same density as during summer.

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Table 1. Number of snowshoe hares (*Lepus americanus*) captured during 5-day trapping sessions conducted during July-September 2006 and January-March 2007 on 3 medium lodgepole, 3 spruce/fir, and 6 small lodgepole stands on the Gunnison National Forest, Taylor Park and Pitkin, Colorado.

	Number of Hares Captured (Total Captures)		
	Summer 2006	Winter 2007	Both Summer and Winter
Medium Lodgepole	3	24	2
Small Lodgepole	50	40	10
Spruce/Fir	22	35	2

Table 2. Number of snowshoe hares (*Lepus americanus*) radio-collared and tracked during 10-day sessions immediately following 5-day trapping periods July-September 2006 and January-March 2007 on the Gunnison National Forest, Taylor Park and Pitkin, Colorado.

	Summer 2006	Winter 2007
Number of Hares Collared	41	79
Number of Locations	407	510
Number of Locations/Hare	9.9	6.5

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.

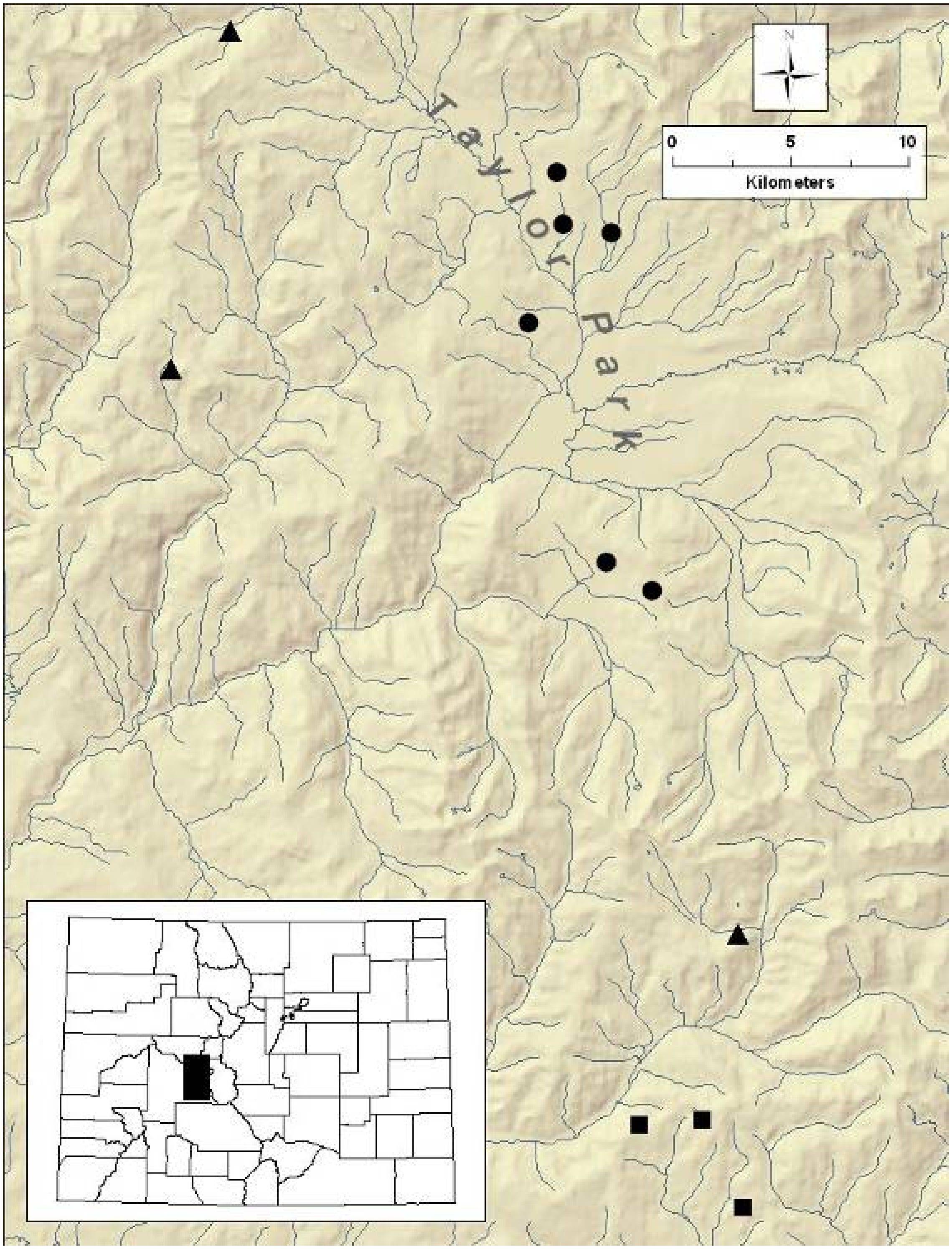


Figure 2. Study area near Taylor Park and Pitkin, Colorado including medium lodgepole (squares), small lodgepole (circles), and spruce/fir (triangles) stands selected for mark-recapture sampling.

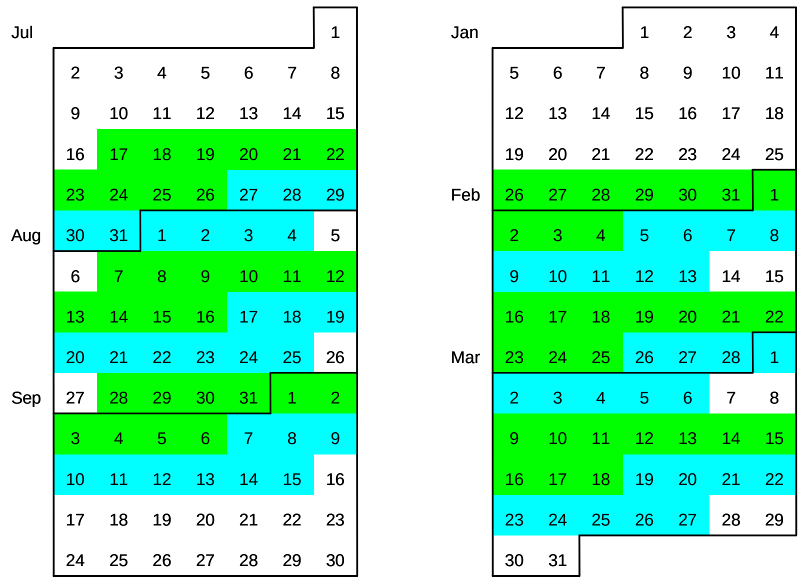


Figure 3. Approximate annual data collection schedule for trapping (■) and telemetry (■). Dates and weeks will change depending on calendar year and pay schedule. During telemetry work, the 6-person crew will be divided into 2 teams, only one of which will be working at any given time. Monthly locations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

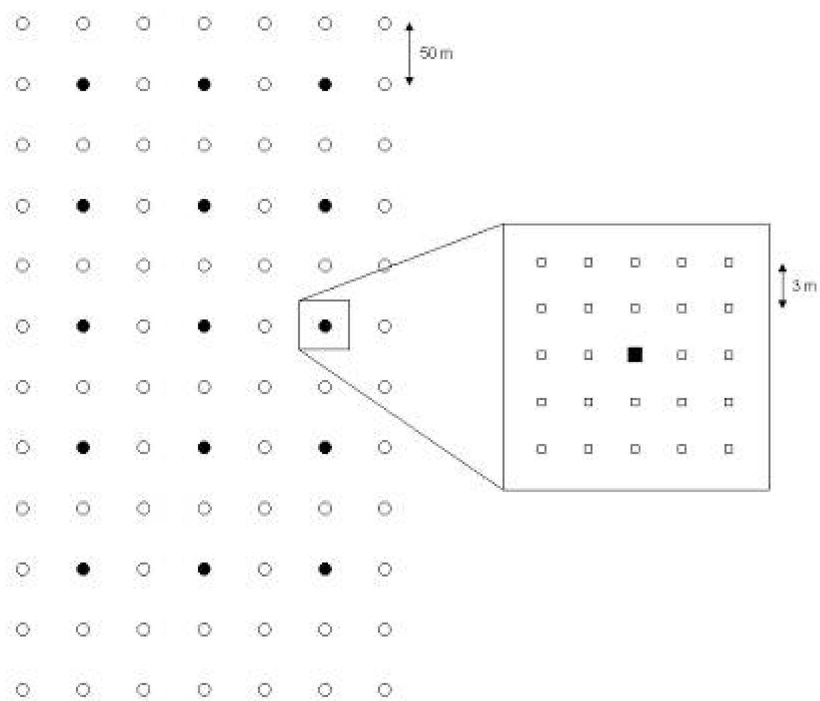


Figure 4. 15 trap locations (•) on 7 × 12 trapping grid where vegetation will be sampled by measuring stem density horizontal cover, and canopy cover at the 25 points on each 5 × 5 subgrid (inset). In addition, basal area will be measured at the trap location (■) on which each of the 15 subgrids are centered.

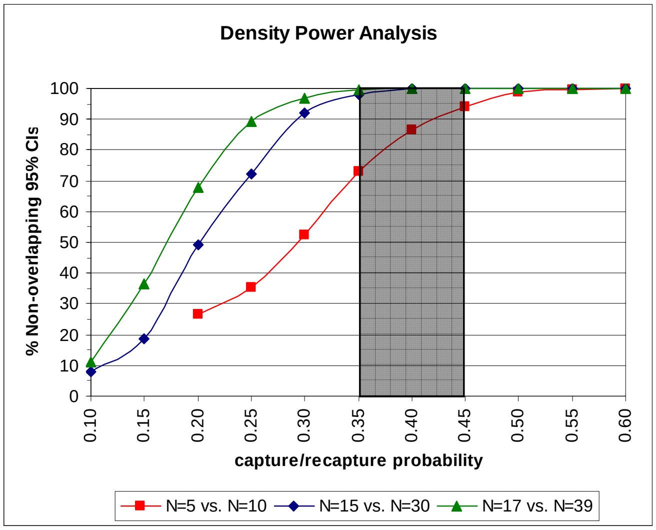
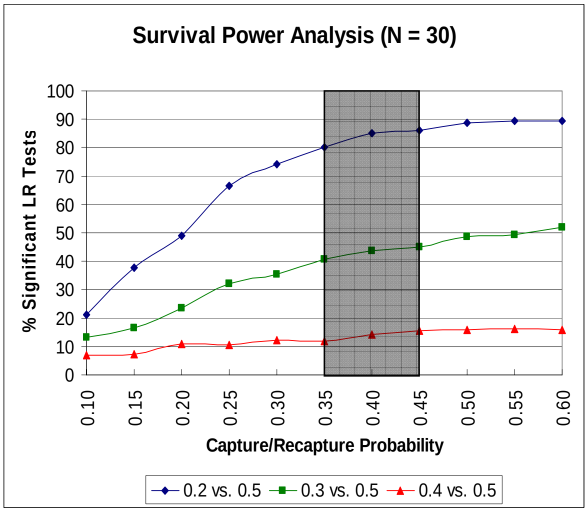


Figure 5. Power for distinguishing differences in snowshoe hare density between 2 habitat types when a difference actually exists. Gray area indicates the capture probability realized by the 3rd day of trapping during a pilot study in winter 2005. *N* indicates number of hares per grid, a range of roughly 0.1 (*N* = 5) to 0.7 hares/ha (*N* = 39).



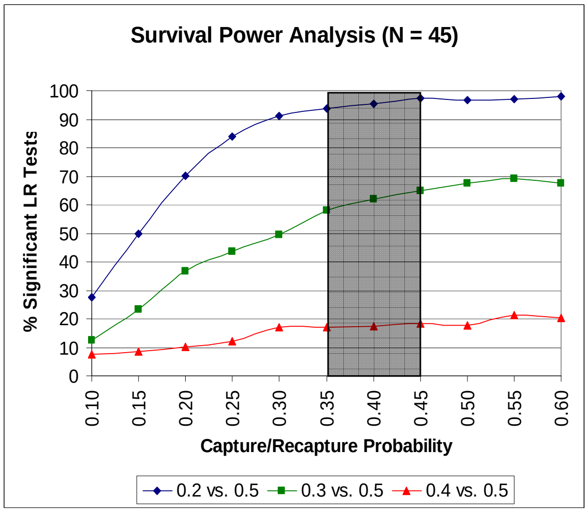


Figure 6. Power, or probability of distinguishing differences in snowshoe hare survival between 2 habitat types when differences actually exist. *N* = 30 (left) and *N* = 45 (right) correspond to reasonable estimates of the number of hares I expect to capture in each habitat type. Gray area indicates the capture probability realized by the 3rd day of trapping during a pilot study in winter 2005.

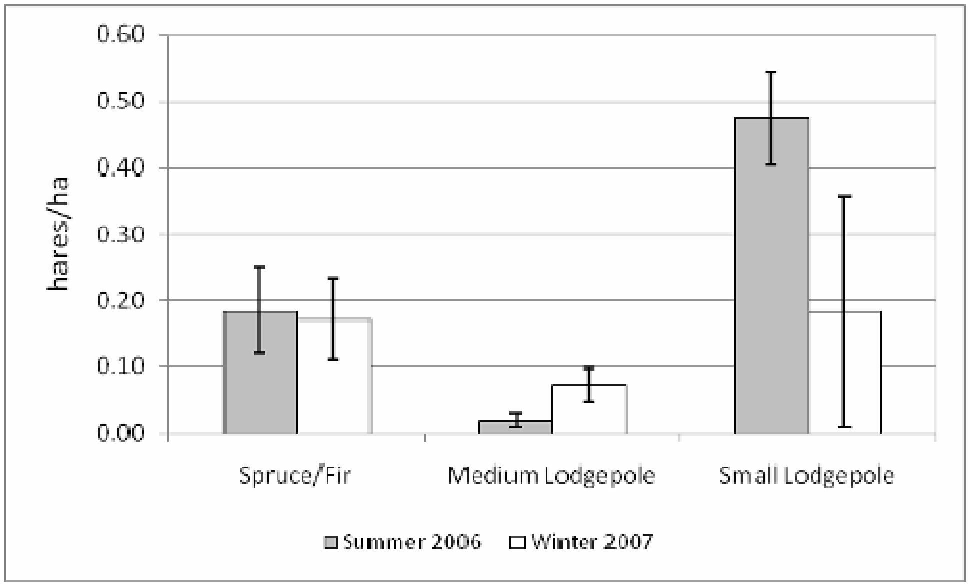


Figure 7. Snowshoe hare density and 95% confidence intervals in 3 types of stands in central Colorado as determined by mark-recapture with telemetry augmentation, July-September 2006 and January-March 2007.