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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 1999-2005, 204 lynx were released in Colorado. Fourteen additional animals (8 males: 6 females) were released in spring 2006 resulting in a total of 218 lynx reintroduced to southwestern Colorado. We documented survival, movement patterns, reproduction, and habitat-use through aerial (n = 8680) and satellite (n = 18, 963) tracking. Most lynx remained near the core release area in southwestern Colorado. From 1999-2006, there were 80 mortalities of released adult lynx. Approximately 31.3% were human-induced which were attributed to collisions with vehicles or gunshot. Malnutrition and disease/illness accounted for 21.3% of the deaths while 32.5% 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 and 2005. Four dens with 11 kittens were found in 2006. 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. From snow-tracking, the primary winter prey species (n = 426) were snowshoe hare (*Lepus americanus*, annual $\bar{x}$ = 75.1%, SE = 5.17) and red squirrel (*Tamiasciurus hudsonicus*, annual $\bar{x}$ = 15.3%, SE = 3.09); other mammals and birds formed a minor part of the winter diet. Mature Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest stands with 42-65% canopy cover and 15-20% conifer understory cover were 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. 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 initiated in 2005 and will continue through 2009. Results to date have demonstrated that CDOW has developed 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 lynx 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. Release additional adult lynx captured in Canada in southwestern Colorado during spring 2006.
2. Complete winter 2005-06 field data collection on lynx habitat use, hunting behavior, diet, mortalities, and movement patterns.
3. Complete winter 2005-06 lynx trapping field season to collar Colorado born lynx and re-collar adult lynx.
4. Complete spring 2006 field data on lynx reproduction.
5. Summarize and analyze data and publish information as Progress Reports, peer-reviewed manuscripts for appropriate scientific journals, or CDOW technical publications.
6. Complete a study plan to evaluate snowshoe hare densities, demography and seasonal movement patterns among small and medium tree-sized lodgepole pine stands and mature spruce/fir stands.

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.

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 2006 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.

Distribution and Movement Patterns

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.

To determine general movement patterns of reintroduced lynx, regular locations of released lynx were collected through a combination of aerial, satellite and ground radio-tracking. Locations were recorded in UTM coordinates and general habitat descriptions for each ground and aerial location were recorded.

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.

Snow-tracking

Locations from aerial- and satellite-tracking were used to help ground-trackers locate lynx tracks in snow. Snowmobiles, where permitted, were used to gain the closest possible access to the lynx tracks without disturbing the animal. From that point, the tracking team used snowshoes to access tracks. Once tracks were found, the ground crew back- or forward-tracked the animal if it was far enough away not to be disturbed. Back-tracking generally avoided the possibility of disturbing the lynx by moving away from the animal rather than towards the animal. However, monitoring of the lynx through radio-telemetry was used to assure that the ground crew was staying a sufficient distance away from the lynx in the event the lynx might double back on its tracks. Radio-telemetry was also used in forward-tracking to make sure the team did not disturb the animal. If it appeared the lynx began to move in response to the observers, the observers stopped following the tracks. If the lynx began to move and the movement did not appear to be a response to the observers, the ground crew continued following the track.

An attempt was made in Season 1 (February-May 1999) and Season 2 (December 1999-April 2000) to snow-track each lynx. In Season 3 (December 2000-April 2001), we attempted to snow-track all lynx within the Core Release Area. In tracking Season 4 (December 2001-April 2002), Season 5 (December 2002-April 2003), Season 6 (December 2003-April 2004), Season 7 (December 2004-April 2005) and Season 8 (December 2005-March 2006) we attempted to track all accessible lynx in the Core Release Area and some lynx north of the Core Release Area. Ground crews were instructed to track lynx only where it was safe to travel. Restrictions to safe travel included avalanche danger and extremely rugged terrain. Ground crews worked in pairs and were fully equipped for winter back-country survival.

Data Collection

For each day of tracking the date, lynx being tracked, slope, aspect, UTM coordinates, elevation, general habitat description, and summary of the days tracking were recorded. Aspect was defined as the direction of 'downhill' or 'fall line' on a slope. This is the direction along the ground in a dihedral angle between the horizontal and the plane of the ground surface. Units were compass degrees. Slope was defined as the dihedral angle between the horizontal and the plane of the ground surface (e.g., 45°).

Once a track was located there were 2 types of 'sites' that were encountered. Site I areas needed documentation but either did not reflect areas lynx selected for specific habitat features, or were sites that occurred too frequently to measure each in detail. These sites included the start and end of the track being followed, the location of scat, and short-duration beds defined as being small in size (approximating an area a lynx would crouch), and with little ice formed in the bed indicating little time spent there. Site II areas included areas that might reflect specific habitat features lynx selected for and included locations where the following were found: kills, start of chases, territory marks (e.g., spray sites, buried scat, scat placed on prominent locations), long-duration beds (encompasses an area where a lynx would have lain for an extended period, iced bottom), and road crossing (both sides of road). In addition, habitat plots were conducted along lynx travel routes if no other sites were sampled in the last hour.

At each of the 2 types of sites the date, lynx tracked, slope, aspect, forest structure class, UTM coordinates, and elevation were recorded. Forest structure classes included grass/forb, shrub/seedling, sapling/pole, mature, and old growth as defined in Table 1. For Site I areas, the only additional data that was collected was identification of what the site was used for (e.g., short-duration bed), and a brief description of the site. Habitat plots (see below) were conducted at Site II areas.

Description of the Habitat Plot

The habitat plot consisted of a 12 m x 12 m square defined by a series of 25 points placed in 5 rows of 5 with the center point being on the object that defined the site (e.g., a kill)(Figure 2). Each point was 3 m apart. The 12 m x 12 m sampling square exceeded the minimum requirement of 0.01 ha. recommended by Curtis (1959) for sampling trees.

Measurements taken at each of the 25 points included:

1. Snow depth - measured vertically by an avalanche probe marked in cm.
2. Understory - measured from top of snow to 150 cm above snow in a column of 3-cm radius around the avalanche probe. Because understory measurements were influenced by vegetation outside the perimeter of the 25 sampling points (12 m x 12 m) the area used for estimating undersory cover was 15 m by 15 m. At each point, crews recorded all shrubs, trees and coarse woody debris (CWD) that fell within this column and was visible above the snow. Crews also recorded number of branches of each species that fell within the column at 3 different height categories (0-0.5 m, 0.51-1.0 m, 1.01-1.5 m).

3. Overstory: measured at 150 cm above snow with a sighting tube. The tube was made of PVC pipe, with a curved viewing end and a crosshair made of wire on the opposite end. The sighting tube was attached to the avalanche probe used to measure snow depth. Species that hit the crosshair were recorded at each of the 25 points in the vegetation plot. Ganey and Block (1994) found this method of measuring canopy cover (with 20 sample points per plot; Laymon 1988) provided greater precision among observers.
4. Species composition: all the different species of tree or shrub that hit the crosshair of the sighting tube at each of the 25 points were recorded.
5. Tree composition of the vegetation plot was recorded by species and diameter at breast height (DBH). Snow depth was used in conjunction with this recorded DBH to estimate true DBH. Within the 12 m x 12 m square all conifers and deciduous trees were recorded by DBH size class (A = 0-6 in, B = 6.1-12 in, C = 12.1 -18 in, D = 18.1-24 in, E = > 24 in). Area for the tree composition analysis was 12 m x 12 m.

Understory was estimated as: 1) percent occurrence within the vegetation plot (number of points with understory/total number of points surveyed) and 2) mean percent occurrence and variance by species and height category over the total points sampled within the vegetation plot. Overstory was estimated as percent occurrence over the vegetation plot (number of points with overstory/total number of points surveyed).

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 plan was designed to evaluate the importance of young, regenerating lodgepole pine (*Pinus contorta*) and mature Engelmann spruce / subalpine fir stands in Colorado by examining density and demography of snowshoe hares that reside in each.

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 will be 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 2005 204 lynx were reintroduced into southwestern Colorado. An additional 14 lynx were released in April 2006 (6 females: 8 males), bringing the total number of lynx released in Colorado to 218 (Table 2). Lynx released in 2006 were captured in British Columbia and Yukon. These 14 lynx were released in the Core Release Area of southwestern Colorado at or near previously used release sites in southwestern Colorado. Lynx were released with 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 2007.

Distribution and Movement Patterns

A total of 8680 aerial VHF locations for all 218 reintroduced lynx have been collected to date (June 30, 2006). An additional 18,963 satellite locations have been collected. Most lynx released in 2006 remained in southwestern Colorado. The majority of surviving lynx from the entire reintroduction effort continue to use high elevation (> 2900 m), forested areas from New Mexico north to Gunnison, west as far as Taylor Mesa and east to Monarch Pass. Most movements away from the Core Release Area were to the north.

Numerous travel corridors have been 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. Such movement patterns have also been documented by native lynx in Wyoming and Montana (Squires and Laurion 1999).

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, 2006, CDOW was actively tracking 95 of the 138 lynx still possibly alive. There are 43 lynx that we have not heard signals on since at least June 30, 2005 and these animals are classified as 'missing' (Table 3). One of these missing lynx is a mortality of unknown identity, thus only 42 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 from 1999-2006 there are 80 known mortalities as of June 30, 2006. Causes of death are listed in Table 4. Starvation was a significant cause of mortality in the first year of releases only. Mortalities occurred throughout the areas through which lynx moved. Approximately 31.3% were human-induced which were attributed to collisions with vehicles or gunshot. Malnutrition and disease/illness accounted for 21.3% of the deaths while 32.5% of the deaths were from unknown causes (Table 4).

Reproduction

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 5, Figure 1). At all dens the females appeared in excellent condition, as did the kittens. The kittens weighed from 270-500 grams. Lynx kittens weigh approximately 200 grams at birth and do not open their eyes until they are 10-17 days old.

The 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. Field crews weighed, photographed, PIT-tagged the kittens and took hair samples from the kittens for genetic work in an attempt to confirm paternity. Kittens were processed as quickly as possible (11-32 minutes) to minimize the time the kittens were without their mother. While working with the kittens the females remained nearby, often making themselves visible to the field crews. The females generally continued a low growling vocalization the entire time personnel were at the den. In all cases, the female returned to the den site once field crews left the area.

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 6). At all dens the females appeared in excellent condition, as did the kittens. The kittens weighed from 250-770 grams. Three of the 11 females with kittens were from the 2003 releases (Table 6). 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 7). At all dens the females appeared in excellent condition, as did the kittens. 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.

We weighed, photographed, PIT-tagged the kittens and recorded sex. We also took blood samples from the kittens for genetic work in an attempt to confirm paternity. While we were working with the kittens the females remained nearby, often remaining visible to us. The females generally continued a low growling vocalization the entire time we were at the den. In all cases, the female returned to the den site once we left the area.

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. We weighed, photographed, and PIT-tagged the kittens, recorded sex and took hair samples from the kittens for genetic work in an attempt to confirm paternity. Four of the females would not leave the den until we reached out to pick up a kitten. While we were working with the kittens the females remained nearby, often remaining visible to us. The females generally continued a low growling vocalization the entire time we were at the den. In all cases, the female returned to the den site once we left the area.

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, 2006.

2006.--In spring 2006, 42 females were being monitored. We found 4 dens in May and June 2006 with 11 kittens total (Table 8). 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.

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 9). However, all demographic and habitat characteristics measured at the 4 dens that were found in 2006 were comparable to all other dens found (Table 9). 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).

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 (Figure 3). The dens were typically in Engelmann spruce/subalpine fir forests in areas of extensive downfall of coarse woody debris (Figures 4, 5, 6). 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 other 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. All lynx captured in 2005 and 2006 were caught in box-traps. All captured lynx were fitted with new Sirtrack ™ dual VHF/satellite collars.

Seven adult lynx were captured from March 1999-June 30, 2006 because they were in poor body condition. 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. Lynx QU04M07 died on February 5, 2006 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). Two lynx were captured because they were in atypical habitat outside the state of Colorado. They were held at Frisco Creek Rehabilitation Center for a minimum of 3 weeks and re-released in the Core Release Area in Colorado. Prior to release these lynx were fitted with new Sirtrack ™ dual VHF/satellite collars.

In addition, 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 collared in spring 2006.

HABITAT USE

Landscape-scale daytime habitat use was documented from 7421 aerial locations of lynx collected from February 1999-June 30, 2005. Throughout the year Engelmann spruce / subalpine fir was the dominant cover used by lynx. A mix of Engelmann spruce, subalpine fir and aspen (*Populus tremuloides*) was the second most common cover type used throughout the year. Various riparian and riparian-mix areas were the third most common cover type where lynx were found during the daytime flights. Use of Engelmann spruce-subalpine fir forests and Engelmann spruce-subalpine fir-aspen forests was similar throughout the year. There was a trend in increased use of riparian areas beginning in July, peaking in November, and dropping off December through June.

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

Mean percent total overstory was higher for long bed and kill sites than travel or den sites (Figure 4). Engelmann spruce provided a mean of 35.87% overstory for kills and long beds, with travel sites averaging 28% and den sites having the lowest mean percent overstory of 23% (Figure 4). Mean percent subalpine fir or aspen overstory did not vary across use sites (Figure 4). Willow overstory was highly variable and no dens were located in willow overstory.

A total of 1841 site-scale habitat plots were completed in winter from December 2002 through April 2005. The most common understory species at all 3 height categories above the snow (low = 0-0.5m, medium = 0.51 - 1.0 m, high = 1.1 - 1.5 m) was Engelmann spruce, subalpine fir, willow (*Salix* spp.) and aspen (Figure 5). Various other species such as Ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), cottonwood (*Populus sargentii*), birch (*Betula* spp.) and others were also found in less than 5% of the habitat plots. If present, willow provided the greatest percent cover within a plot followed by Engelmann spruce, subalpine fir, aspen and coarse woody debris for long beds, kills and travel sites. Areas documented in willow used by lynx are typically on the edge of willow thickets as tracks are quickly lost within the thicket. Den sites had significantly higher percent understory cover for all three height categories. Understory at den sites was primarily made up of coarse woody debris (Figure 5).

The most common tree species documented in the site-scale habitat plots was Engelmann spruce Figure 6). Subalpine fir and aspen were also present in >35% of the plots. Most habitat plots were vegetated with trees of DBH < 6" (Figure 6). As DBH increased, percent occurrence decreased within the plot. Although decreasing in abundance as size increased, most lynx use sites had trees in each of the DBH categories, indicating mature forest stands except for dens. Den sites had a broad spectrum of Engelmann spruce tree sizes, including > 18" but no large subalpine fir or aspen trees. While Engelmann spruce and subalpine fir occurred in similar densities for kills, long beds and travel sites, den sites had twice the density of subalpine firs found at all other sites (Figure 6).

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 400 kills were located from February 1999-April 2005. We collected 671 scat samples from February 1999-April 2004 that will be analyzed for content. In each winter, the most common prey item was snowshoe hare, followed by red squirrel (Table 10).

A comparison of percent overstory for successful and unsuccessful snowshoe hare chases indicated lynx were more successful at sites with slightly higher percent overstory, if the overstory species were Englemann spruce, subalpine fir or willow. Lynx were slightly less successful in areas of greater aspen overstory (Figure 7). This trend was repeated for percent understory at all 3 height categories (Figure 8) except that higher aspen understory improved hunting success. Higher density of Engelmann spruce and subalpine fir increased hunting success while increased aspen density decreased hunting success (Figure 9).

SNOWSHOE HARE ECOLOGY

A study plan was completed to evaluate snowshoe hare densities, demography and seasonal movement patterns among small and medium tree-sized lodgepole pine stands and mature spruce/fir stands (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 2005, 204 lynx were released in the Core Release Area. The reintroduction effort was augmented with the release of 14 additional animals in April 2006, bringing the total to 218 lynx reintroduced to southwestern Colorado.

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. Dispersal movement patterns for lynx released in 2000 and subsequent years were similar to those of lynx released in 1999. 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 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. 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). Human-caused mortality factors such as gunshot and vehicle collision are currently the highest causes of death.

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. Reproduction in 2006 included a Colorado-born female giving birth to 2 kittens, documenting the first recruitment of Colorado-born lynx into the Colorado breeding population. Additional reproduction is likely to have occurred in all years from females we are 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 for an increasing population.

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. 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.

Snow-tracking of released lynx provided information on hunting behavior and diet through documentation of kills, food caches, chases, and diet composition estimated through prey remains. Snow-tracking results indicate the primary winter prey species are snowshoe hare and red squirrel, with other mammals and birds forming a minor part of the winter diet. 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). 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.

SUMMARY

From results to date it can be concluded that CDOW has developed release protocols that ensure high initial post-release survival, and on an individual level lynx have demonstrated they can survive long-term in areas of Colorado. It has also been documented that reintroduced lynx could exhibit site fidelity, engage in breeding behavior and produce kittens that are 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 for a population to sustain itself. Monitoring of reintroduced lynx will continue in an effort to document such viability.

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Table 1. Definitions of forest structure classes used to describe habitat sites (Thomas 1979).

Forest Structure	Class Definition
Grass/forb	The grass/forb stage is created naturally by a catastrophic event, such as wildfire, and is typified by the near complete absence of snags, litter or down material in the aspen and ponderosa pine types, or vice versa in the lodgepole or subalpine forest types.
Shrub/seedling	The shrub/seedling stage occurs when tree seedlings or shrubs grow up to 2.5 cm at diameter breast height (DBH), either naturally or artificially through planting.
Sapling/pole	The sapling/pole stage is a young stage where tree DBH's range from 2.5-17.5 cm with tree heights ranging 1.8-13.5 m. These trees are 5-100 years of age, depending on species and site condition.
Mature	The mature stage occurs when tree diameters reach a relatively large size (25-50 cm) and the trees are usually 90 or more years old. Forest stands begin to experience accelerated mortality from disease and insects.
Old-growth	The old-growth stage occurs when a mature stand is at advanced age (100 years for aspen or 200 years for spruce), is very slow growing, and has advanced degrees of disease, insects, snags, and down, dead material. An exception to this occurs in ponderosa pine and aspen types where these old-growth stands typically experience low densities of down dead material or snags.

Table 2. Lynx released in Colorado from February 1999 through June 30, 2006.

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 3. Status of adult lynx reintroduced to Colorado as of June 30, 2006.

	Females	Males	Unknown	TOTALS
Released	115	103		218
Known Dead	46	33	1	80
Possible Alive	69	70		138
Missing	20	24		43[a]
Tracking	49	46		95

[a] 1 is unknown mortality

Table 4. Causes of death for lynx released into southwestern Colorado from 1999-2006 as of June30, 2006.

Cause of Death	Number of Mortalities
Unknown	26
Hit by Vehicle	11
Starvation	10
Shot	9
Other Trauma	7
Probable Shot	5
Plague	5
Predation	3
Probable Predation	2
Illness	2
Total Mortalities	80

Table 5. Lynx reproduction documented in 2003.

Female	Release Year	Date Den Found	Number of Kittens		
			Females	Males	Total
BC00F8	2000	5/21/03	?	?	2
BC00F19	2000	5/26/03	1	1	2
YK00F16	2000	6/19/03	1	1	2
YK99F1	1999	6/10/03	2	1	3
YK00F19	2000	6/11/03	1	2	3
YK00F10	2000	5/31/03	2	2	4
		TOTAL	7	7	16

Table 6. Lynx reproduction documented in 2004.

Female ID	Release Year	Previous Litters	Date Den Found	Date Kittens Found	Number of Kittens		
					Females	Males	Total
YK00F2	2000		5/28/2004		3	1	4
AK00F2	2000		5/31/2004		2	1	3
YK00F1	2000		6/1/2004		3		3
YK00F15	2000		6/4/2004		1	2	3
BC00F14	2000		6/7/2004		1	2	3
BC00F18	2000		6/10/2004		4		4
YK00F10	2000		6/17/2004		1	1	2
BC03F02	2003		6/25/2004			2	2
BC03F10	2003		6/26/2004		2		2
BC03F09	2003		6/29/2004		1	1	2
YK00F7	2000		6/30/2004		1	1	2
YK99F1	1999		6/2004	Dec 2004			2
Unknown				Sept 2004			4
Unknown				Feb 2005			3
TOTAL					19	11	39

Table 7. Lynx reproduction documented in 2005.

Female ID	Release Year	Previous Litters	Date Den Found	Date Kittens Found	Number of Kittens Males	Females	Total
AK00F02	2000	2004	5/21/2005		2	1	3
YK00F15	2000	2004	5/28/2005		1	1	2
YK00F10	2000	2003, 2004	6/1/2005		2	2	4
YK00F11	2000		6/9/2005			2	2
YK00F01	2000	2004	6/10/2005		2	1	3
YK00F07	2000	2004	6/14/2005		1	2	3
BC00F18	2000	2004	6/24/2005		1	1	2
BC03F02	2003	2004	5/25/2005		1	1	2
BC03F01	2003		5/27/2005		2	2	4
QU03F06	2003		6/5/2005		3		3
QU03F04	2003		6/14/2005		1	2	3
QU03F07	2003		6/16/2005		3	1	4
BC03F09	2003	2004	6/27/2005		1	1	2
BC03F10	2003	2004	6/2005	12/20/2005			2
BC04F01	2004		6/11/2005		2	1	3
BC04F03	2004		6/19/2005		1	3	4
BC04F05	2004		6/23/2005		3		3
BC04F04	2004			12/10/2005		1	1
TOTAL					26	22	50

Table 8. Lynx reproduction in 2006.

Female ID	Release Year	Year Born in Colorado	Previous Litters	Date Den Found	Number of Kittens Males	Females	Total
AK00F15	2000		2004, 2005	5/21/2006	1	3	4
AK00F05	2000		2004	6/7/2006	1	2	3
BC03F10	2003		2004, 2005	6/9/2006	1	1	2
CO04F07		2004		6/17/2006	2		2
TOTAL					5	6	11

Table 9. Lynx reproduction summary statistics for 2003-2006.

Year	# Females Tracked	# Dens Found in May/June	% Tracked Females with Kittens	Additional Litters Found in Winter	Mean # Kittens/Litter	Total Kittens Found	Sex Ratio M/F
2003	17	6	0.353		2.67 (SE = 0.33	16	1.0
2004	26	11	0.462	2	2.83 (SE = 0.24)	39	1.5
2005	40	17	0.425	1	2.88 (SE = 0.18)	50	0.8
Mean 2003-05			0.413 (SE =0.032)				
2006	42	4	0.095		2.75 (SE = 0.47)	11	1.2
Mean 2003-06			0.334 (SE = 0.083)		2.78 (SE = 0.05)	TOTAL 116	1.14 (SE = 0.14)

Table 10. 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

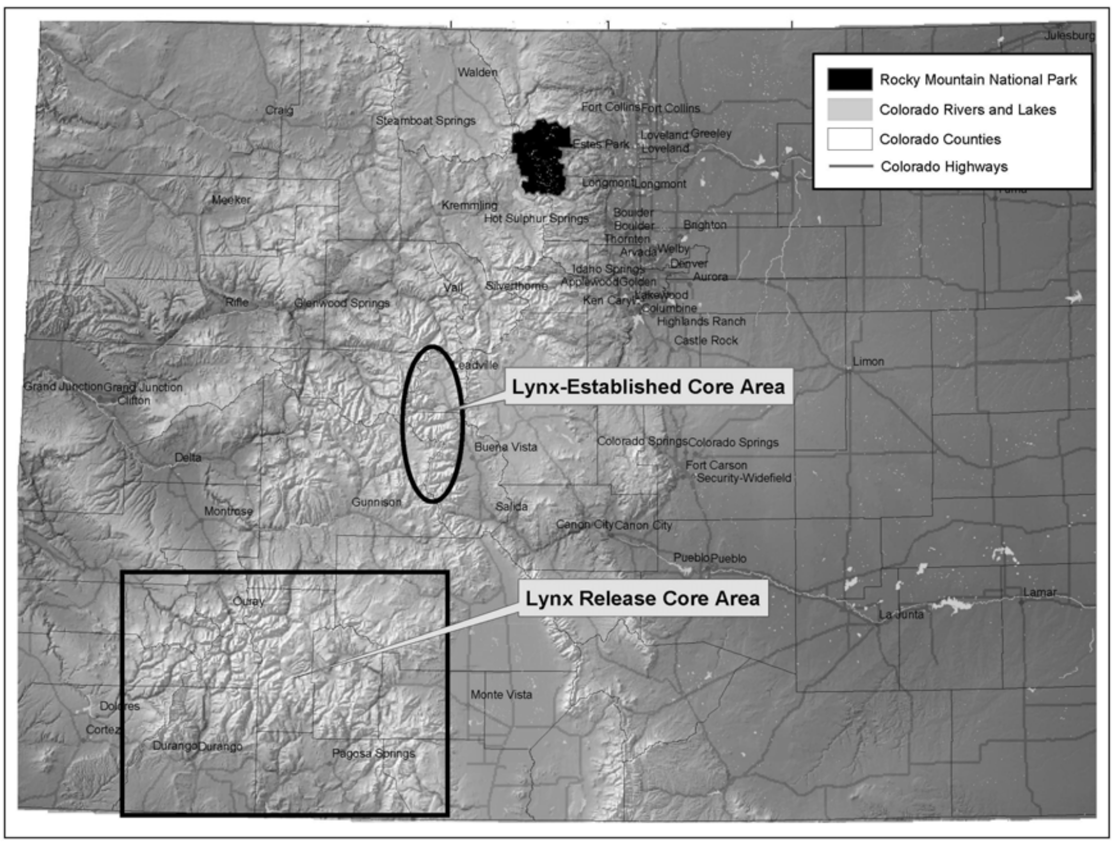

Figure 1. Lynx are monitored throughout Colorado and by satellite throughout the western United States. The lynx core release area, where all lynx were released, is located in southwestern Colorado. A lynx-established core use area has developed in the Taylor Park and Collegiate Peak area in central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

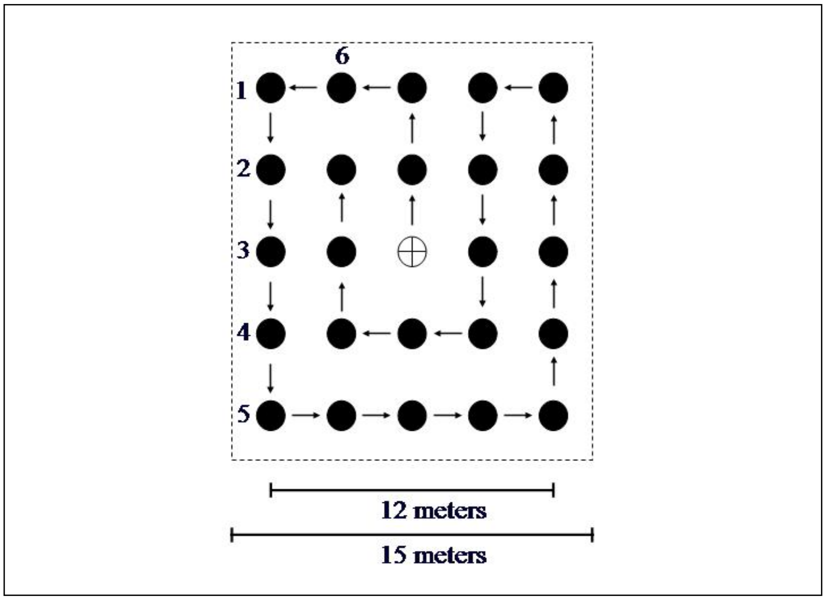

Figure 2. Design of site-scale habitat plot sampling plot. Each of the 25 points are 3 meters apart (the first 6 points are labeled 1-6). The object that triggered a habitat plot (e.g., kill) is the center point, depicted by the hollow circle. The actual pints encompass a 12 m x 12 m square but the understory and overstory data collected are influenced by vegetation occurring within a 15 m x 15 m square.

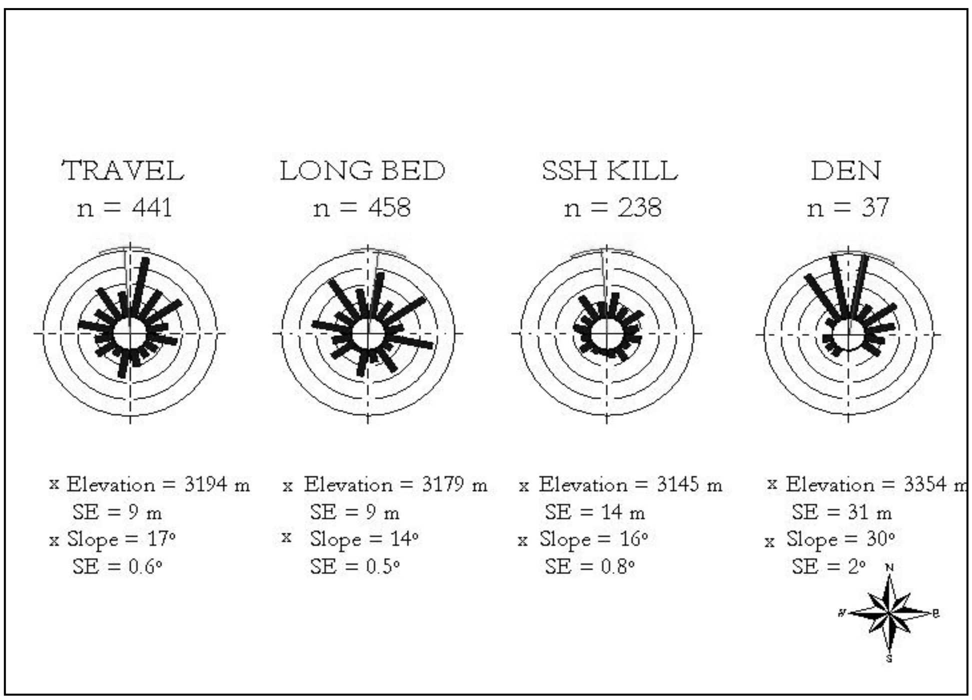

Figure 3. Frequency of aspect with mean vector and 95%confidence interval depicted as grey bars on graphs for 4 lynx use sites; dens, long beds, kills and travel as well as mean elevation and SE and mean slope and SE .

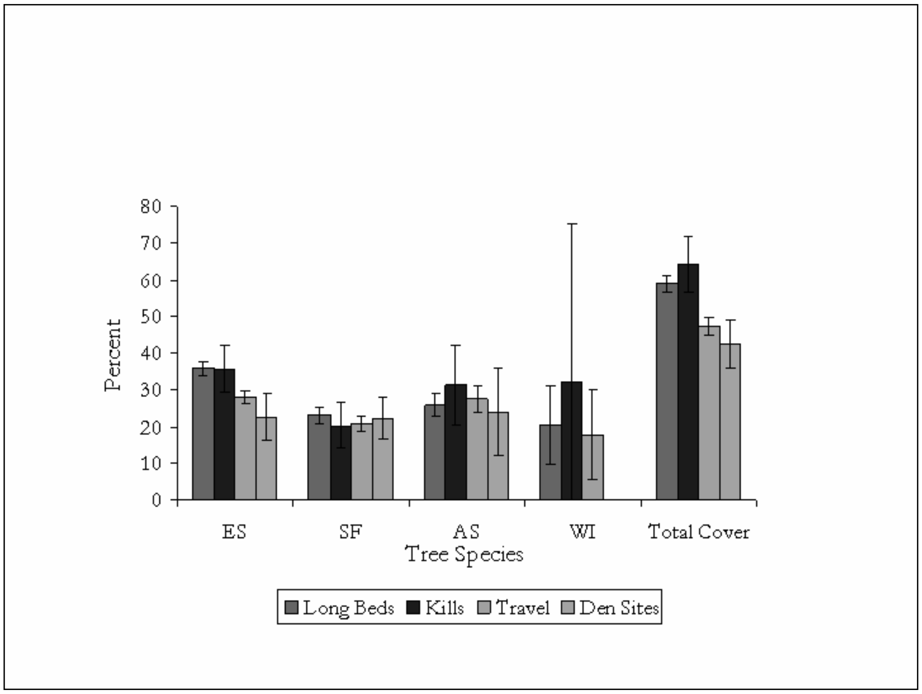

Figure 4. Mean percent overstory by tree species Engelmann spruce (ES), subalpine fir (SF), aspen (AS), willow (WI) and total cover for 4 different lynx use sites: long beds, kill sites, travel and den sites. Confidence intervals (95%) are depicted by error bars.

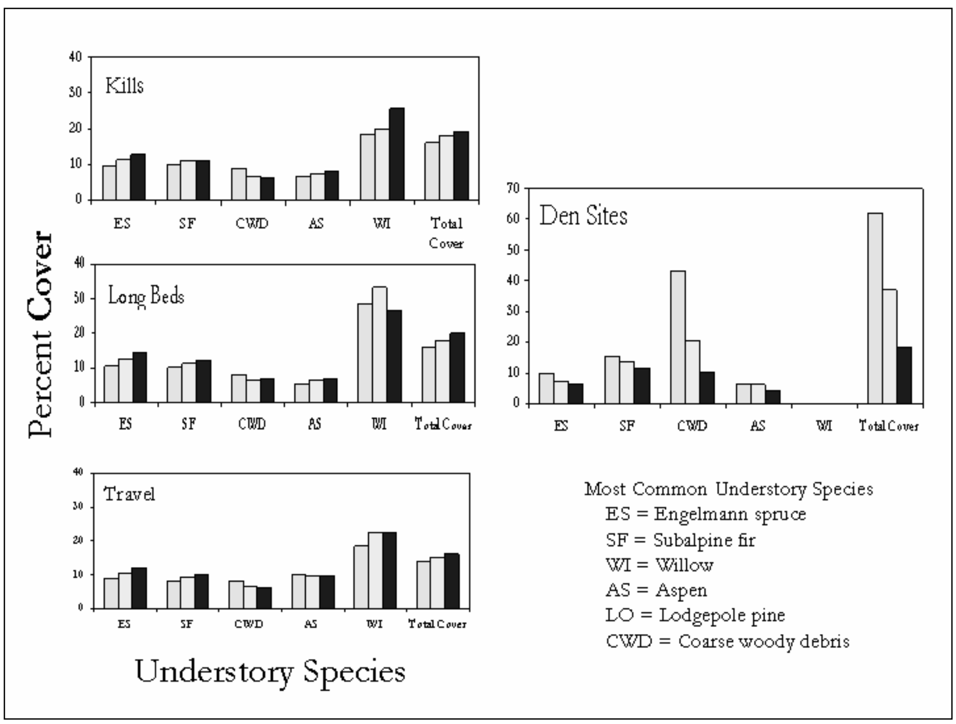

Figure 5. Mean percent understory by tree species Engelmann spruce (ES), subalpine fir (SF), coarse woody debris (CWD), aspen (AS), willow (WI), and total cover for 4 different lynx use sites: long beds, kill sites, travel, and den sites.

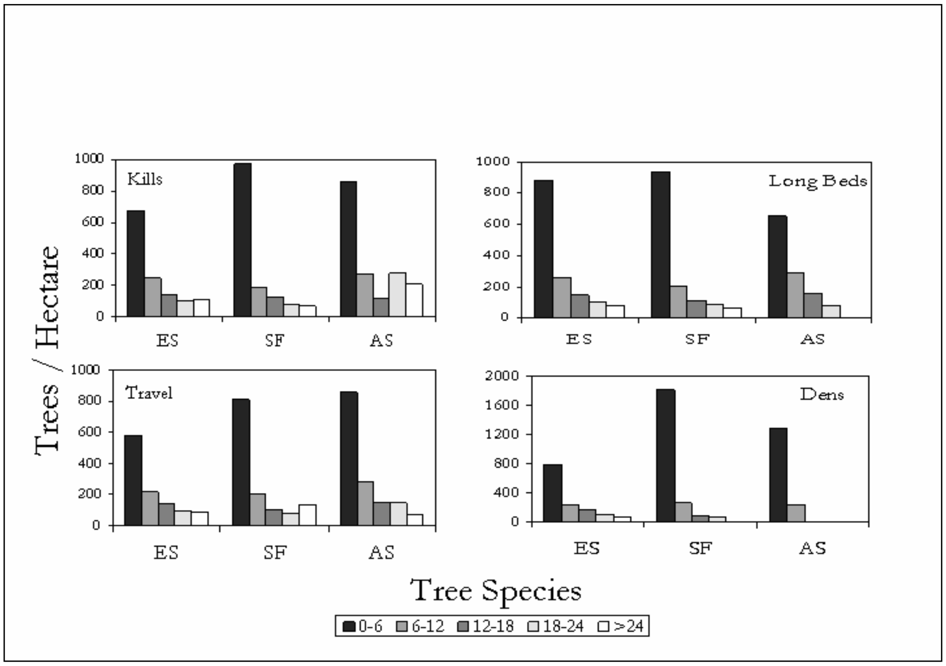

Figure 6. Mean tree density by species Engelmann spruce (ES), subalpine fir (SF), and aspen (AS) and dbh size class for 4 different lynx use sites**.**

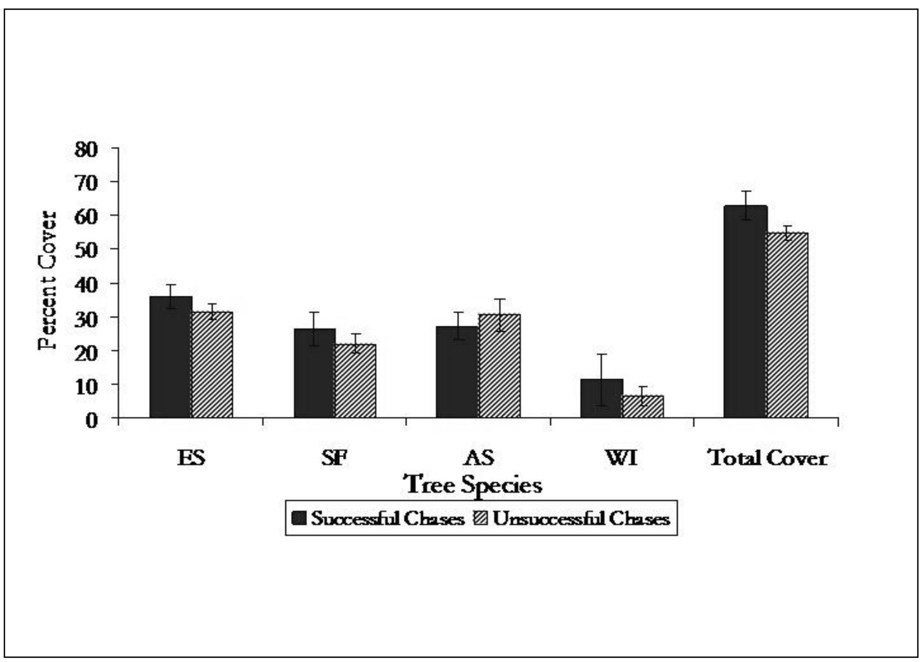

Figure 7. Mean percent overstory by tree species Engelmann spruce (ES), subalpine fir (SF), aspen (AS), willow (WI) and total cover for successful and unsuccessful snowshoe hare chases. Confidence intervals (95%) are depicted by error bars.

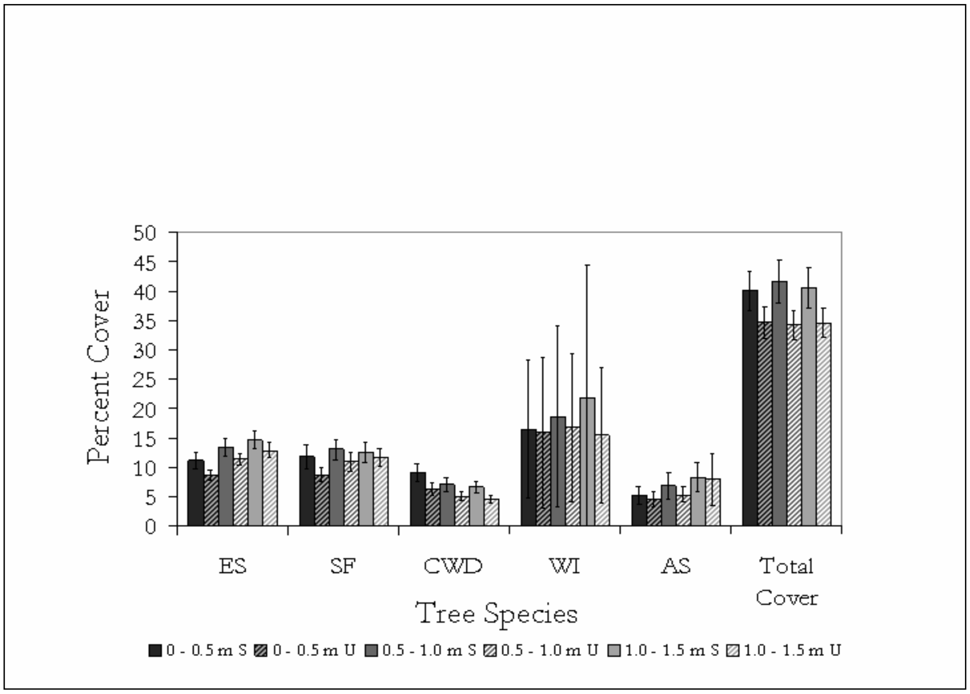

Figure 8. Mean percent understory by tree species Engelmann spruce (ES), subalpine fir (SF), apsen (AS), willow (WI), and total cover for 3 different understory height categories for successful and unsuccessful snowshoe hare chases. Confidence intervals (95%) are depicted by error bars.

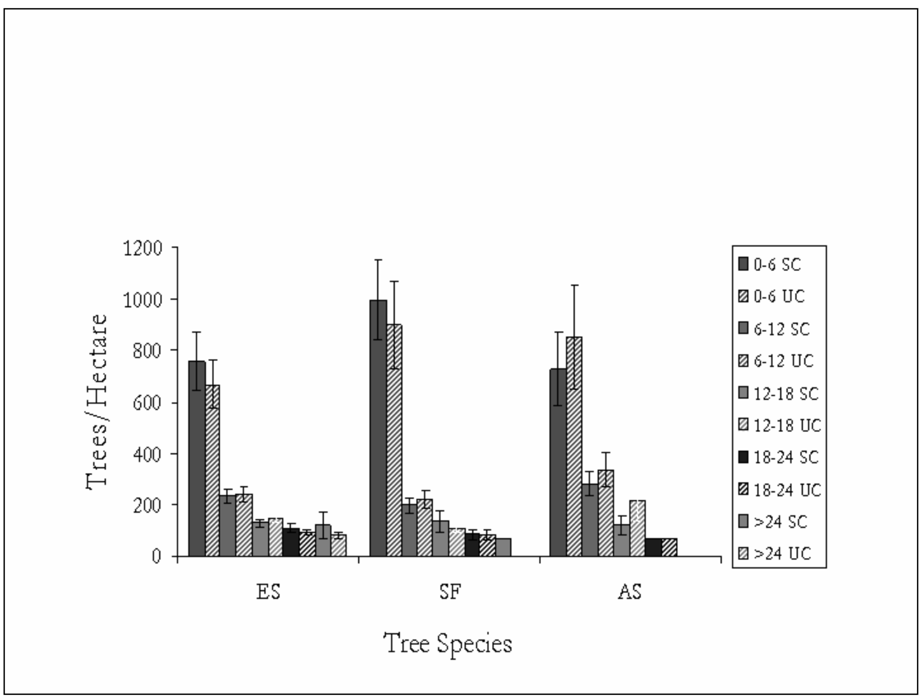

Figure 9. Mean tree density by species Engelmann spruce (ES), subalpine fir (SF), and aspen (AS) and 5 dbh size classes for successful chases (SC) and unsuccessful chases (UC) of snowshoe hares.

APPENDIX I

PROGRAM NARRATIVE STUDY PLAN
FOR MAMMALS RESEARCH
FY 2005-06 – FY 2009-10

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

Federal Aid Project No.: N/A :

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

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STUDY PLAN APPROVAL

Prepared by: ______________________________ Date: ___________________

Submitted by: ______________________________ Date: ___________________

Reviewed by: ______________________________ Date: ___________________

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Reviewed by: ______________________________ Date: ___________________
Biometrician

Approved by: ______________________________ Date: ___________________
Mammals Research Leader

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

NEED

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

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

Whereas extensive research on lynx-hare ecology has occurred in the boreal forests of Canada, literature regarding the ecology of these species in the southern portion of their range is relatively sparse. This scientific uncertainty is acknowledged in the "Canada Lynx Conservation Assessment and Strategy," a formal agreement between federal agencies intended to provide a consistent approach to lynx conservation on public lands in the lower 48 states (Ruediger et al. 2000). In fact, one of the explicit guiding principles of this document is to "retain future options…until more conclusive information concerning lynx management is developed." Thus, management recommendations in this agreement are decidedly conservative, especially with respect to timber management, and are applied broadly to cover all habitats thought to be of possible value to lynx and hare. 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, it 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 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). To maximize comparability, I will choose lodgepole stands so that all are generating from harvest or all are regenerating following fire. 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.

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.

OBJECTIVES

1) Compare telemetry-corrected estimates of density to those that would have been obtained from other commonly employed techniques used to convert population size estimated from a trapping grid to density (i.e., mean maximum distance moved, ½ mean maximum distance moved, ½ trap interval, nested grids, Program DENSITY). The purpose is to determine which common technique requiring less effort most consistently matches estimates from the intensive, telemetry-corrected approach.
2) Assess the relative value of the 3 stand types that purportedly provide high quality hare habitat by estimating and comparing survival, recruitment, finite population growth rate, and maximum (late summer) and minimum (late winter) snowshoe hare densities for each type.
3) Describe the timing, duration, and extent of broad-scale, seasonal movement patterns of snowshoe hares.
4) Relate specific vegetation, physical, and landscape characteristics of the 3 stand types to snowshoe hare density and demographics.

APPROACH

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.

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.

Location--.Identification of a suitable study area for this project and others that may follow is ongoing. The general study area must consist of an interspersion of young lodgepole pine and mature spruce/fir forest juxtaposed closely with open, seasonal habitats such as riparian willow. Within this general area, 3 sites will be selected such that 1) the 3 stand types of interest (small and medium lodgepole, large spruce/fir) occur within each site, 2) sites are close enough geographically to minimize differences due to climate, weather, and topography, but are far enough apart to be considered independent (e.g., 3 sites might occur in 3 different, but adjacent drainages), 3) each stand type within a site is adjacent to a riparian area, and 4) stand types of interest occur within 1 km of an access road (for logistical purposes). Such an arrangement often occurs in east-west drainages where spruce/fir grows on the north-facing slope, lodgepole pine covers the south-facing slope, and a riparian/willow area with road access separates the two (Figure 2). Additionally, sites must 1) include stands of suitable size and shape to admit a 16.5-ha trapping grid, 2) be consistent in their management history (i.e., all lodgepole pine stands in all sites must be either thinned or un-thinned, all regenerating after fire or all regenerating after harvest), and 3) be consistent in their intensity of use by lynx (core areas or not).

I recently obtained the U.S. Forest Service R2VEG GIS database (newest, most detailed stand inventory information available statewide) and am currently working to objectively select a suite of potential study sites that satisfy the above-stated conditions. Depending on the number of potential sites within this suite, I will choose a small set of provisional study areas to ground-truth based on logistical considerations (e.g, housing, access). I will randomly select the final study sites from among those that appeared qualitatively suitable during ground-truthing. Prior to data collection I will more intensively sample the vegetation characteristics of the various stand types within the selected study sites to ensure that they represent intended conditions.

Sampling.--All trapping and handling procedures will be 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 will begin data collection on site 1 immediately following the second birth pulse in late July. Along with a crew of 5 technicians, I will deploy one 7 × 12 trapping grid (50-m spacing between traps; grid covers 16.5 ha) in each of the 3 stand types of interest following Griffin (2004) and Zahratka (2004). Grid locations and orientation will be chosen randomly within each stand subject to the logistical constraint that they must be within 1 km of a road. Traps will be deployed in all 3 stands in a single day. As traps are deployed, they will be locked open and "pre-baited" with apple slices and commercial rabbit chow. On days 2-4, the crew will continue pre-baiting, replacing apples and rabbit chow as necessary. The purpose of this extended pre-baiting is to maximize capture rates when trapping begins. This will minimize the number of trap-nights needed to capture the desired number of animals which in turn will minimize trapping-related stress as well as the likelihood that American marten (*Martes americana*) will key into trap lines and prey 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.

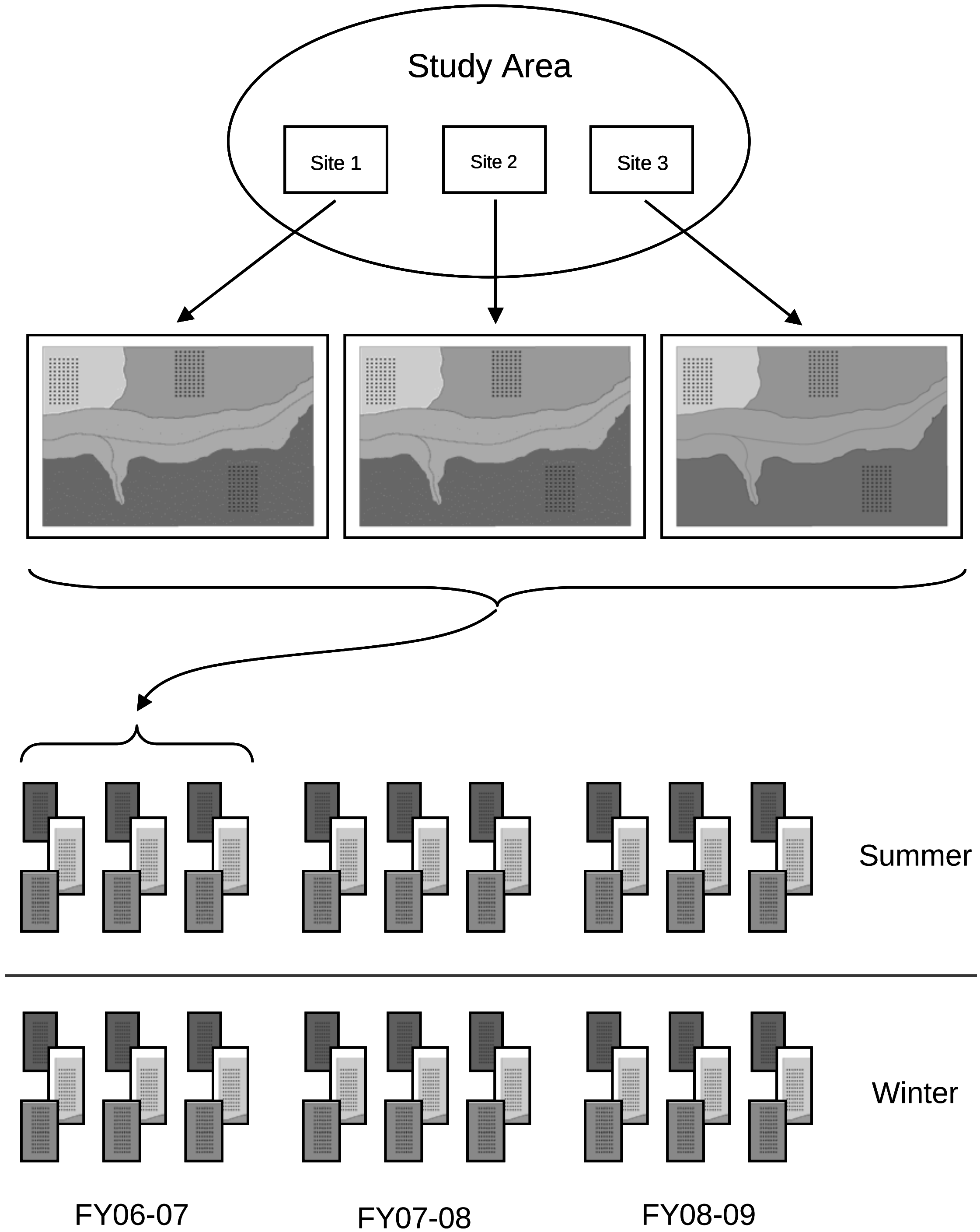

Figure 2. Experimental design for study of snowshoe hare density, demography, and movement. Within the study area, 3 sites, each consisting of 3 forest stand types (light to dark gray shades) and a riparian area (medium gray shade), will be sampled (dotted trapping grids) during late summer and late winter for 3 years.

Traps will be 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. Based on Zahratka (2004) and personal experience, I anticipate capturing up to 10–15 individual hares per grid. A crew of 2 people will work together on each grid to check traps and process captures as quickly as possible. All captured hares will be coaxed out of the trap and into a dark handling bag by blowing quick shots of air on them from behind. Hares will remain in the handling bag, physically restrained with their eyes covered, for the entire handling process. Each individual will be aged, sexed, marked with a passive integrated transponder (PIT) tag and temporary ear mark (to track PIT tag retention), then released. Aging will consist 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 will be scanned for a PIT tag prior to any handling and those already marked will be recorded and immediately released. Traps and bait will be completely removed from the grid on day 10.

In addition to PIT tags and ear marks, I will radio collar 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 expect 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 will randomly select a starting trap location each morning and run the grid systematically from that point. Thus, the first several hares encountered (and collared) will be 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 will refrain from deploying the final 3 collars until days 4 and 5 of the trapping session.

Immediately following the removal of traps, the field crew will begin work locating each radio-collared hare 1–2 times per day for 10 days. Locations will be obtained by "homing" on a signal (Samuel and Fuller 1996, Griffin 2004) taking care not to push hares while approaching them. Technicians will record their location with hand-held GPS units (Garmin model 12XL) as soon as a visual of the collared hare is obtained or if the signal can be picked up by the receiver without an antenna. Using the same make and model collars, Griffin (2004) found that hares are usually within ~15m when the signal came be received without an antenna (Griffin 2004). I will test this assumption with my telemetry equipment over a variety of transmitter locations and orientations. Because hares are largely nocturnal (Keith 1964, Mech et al. 1966, Foresman and Pearson 1999), an effort will be made 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 will gather telemetry locations for radio-collared hares on site 1 for 8–9 days. Then the 10–day trapping procedure and 8 to 9–day telemetry work will be repeated on the 3 grids comprising site 2 (Figure 3). The cycle will be repeated once more for grids on site 3 (Figure 3). The entire process will be repeated during the following winter when densities should be at a minimum.

In summary, for any given 9-week sampling period, I will collect data from 9 total grids, 1 grid in each of 3 habitat types (stand types) across 3 sites. 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 (Figure 2). During the interim between intensive trapping and telemetry work, a single technician and myself will attempt to gather 1–2 telemetry locations/hare/month in order to keep closer tabs on these individuals, determine more precisely when mortality occurs, and retrieve collars from dead hares. Telemetry work will also occur during "pre-baiting" days to determine which hares are still alive and immediately available to be sampled by the grid during the ensuing trapping period.

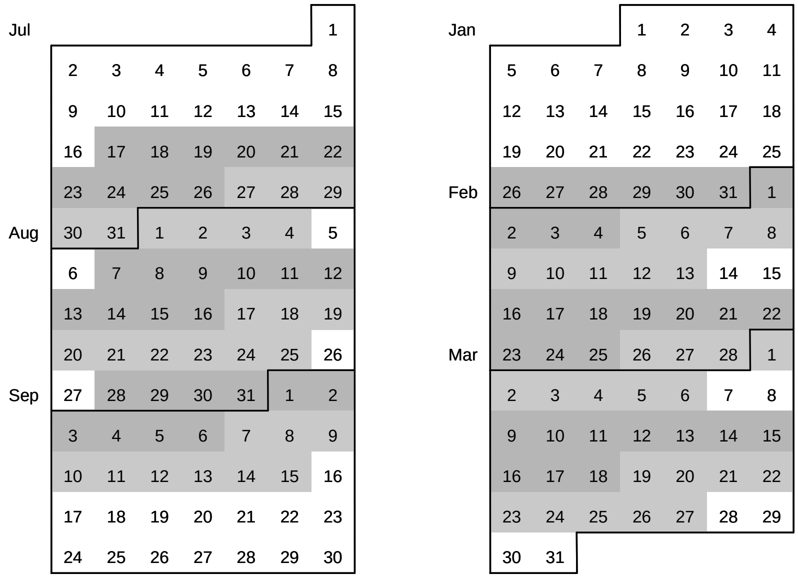

Figure 3. Approximate annual data collection schedule for trapping (■) and telemetry (■). Dates and weeks will change depending on calendar year and pay schedule. During telemetry work, the 6-person crew will be divided into 2 teams, only one of which will be working at any given time. Monthly locations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

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 9 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). 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.

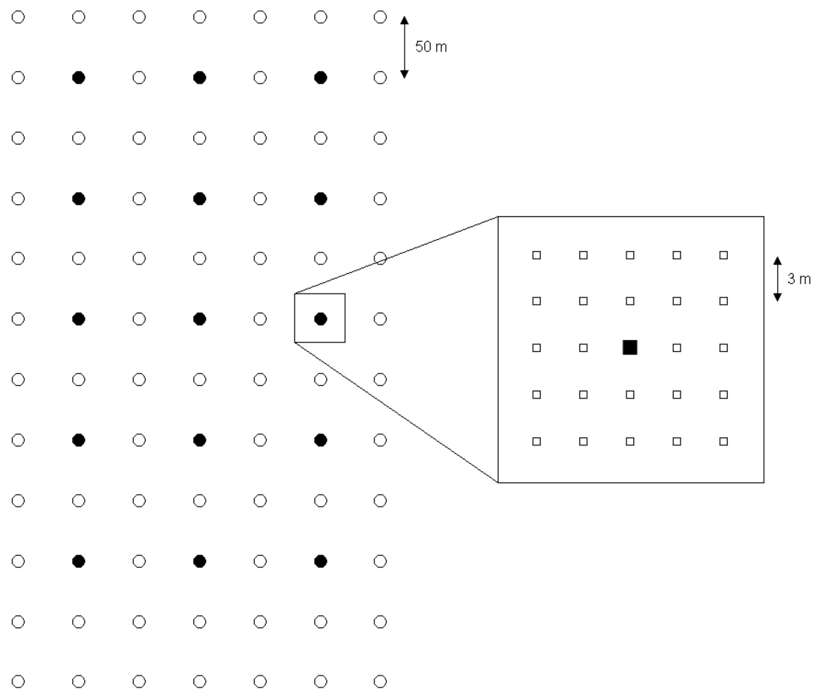

Figure 4. 15 trap locations (•) on 7 × 12 trapping grid where vegetation will be sampled by measuring stem density horizontal cover, and canopy cover at the 25 points on each 5 × 5 subgrid (inset). In addition, basal area will be measured at the trap location (■) on which each of the 15 subgrids are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

Data Analysis

Density.--I will assume that hare populations are demographically and geographically closed during the short 5-day mark-recapture sampling periods. To obtain a density estimate for each grid, I will use 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 will be 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 will take 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 will determine the proportion, $(\tilde{p}_k)$, of telemetry locations for each of the *k* = 1,…,10 radio-collared hares that fall within the "naïve grid area." By incorporating data from multiple grids, a logistic regression model will be 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 will compare hare density among seasons, years, 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).

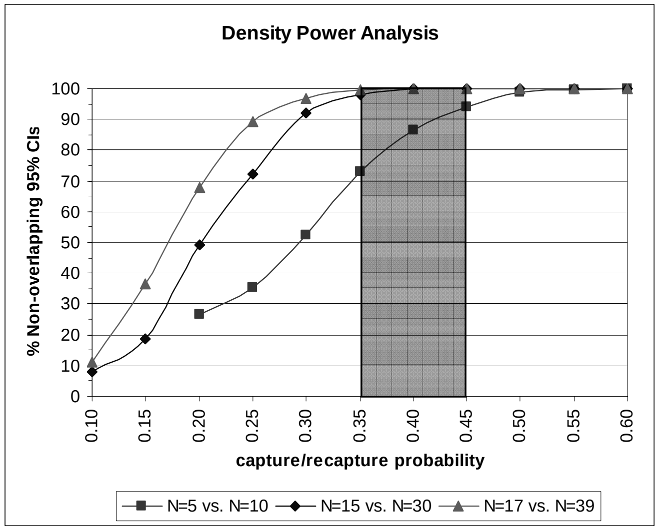

Figure 5. Power for distinguishing differences in snowshoe hare density between 2 habitat types when a difference actually exists. Gray area indicates the capture probability realized by the 3rd day of trapping during a pilot study in winter 2005. *N* indicates number of hares per grid, a range of roughly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

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.

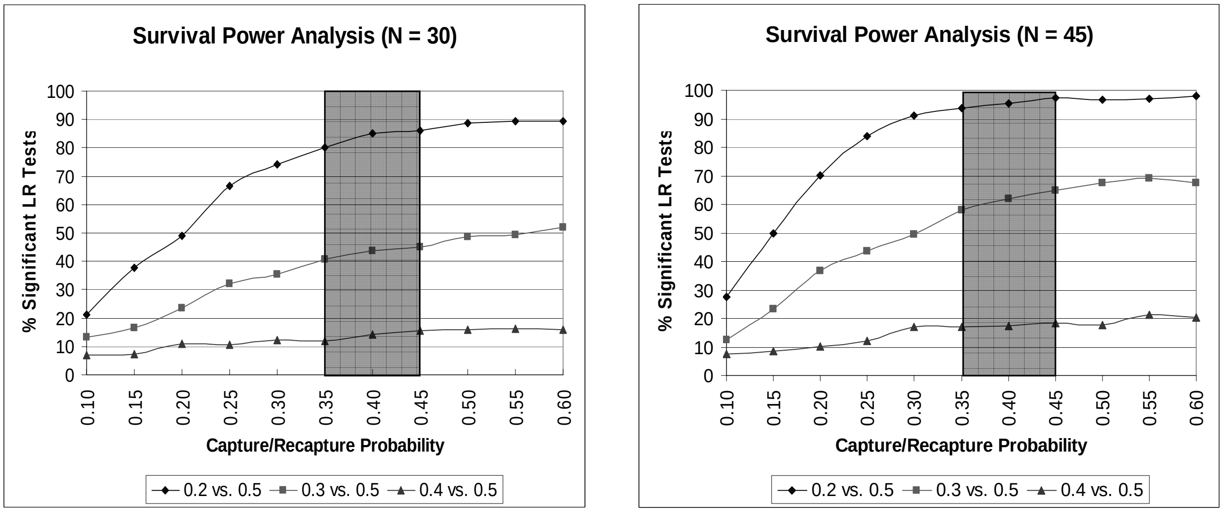

Figure 6. Power, or probability of distinguishing differences in snowshoe hare survival between 2 habitat types when differences actually exist. $N = 30$ (left) and $N = 45$ (right) correspond to reasonable estimates of the number of hares I expect to capture in each habitat type. Gray area indicates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

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.

Project Schedule

I will begin the first 9-week data collection period in mid July 2006. The first winter sampling period will begin in February 2007. Intensive sampling will occur across a total of 3 summer and 3 winter periods, with monthly telemetry work interspersed between the main sampling periods. All fieldwork will terminate with the winter 2009 sampling period. Analysis, write-up, and submission to journal outlets will occur during summer and Fall 2009. I plan to graduate during spring semester 2010.

Personnel

Jacob S. Ivan, Ph. D. student, Colorado State University will be the primary investigator responsible for the design and conduct of the study. Tanya M. Shenk, Mammals Research, Colorado Division of Wildlife, and Gary C. White, Professor, Colorado State University will serve as primary advisors. Also, as most lynx/hare habitat occurs on United States Forest Service (USFS) land, this project will require cooperation and coordination with USFS biologists and district rangers for permission and possibly logistical support (housing, campsites, trucks).

As presented here, this project will require an estimated minimum of 3,600 person-hours/year (5 technicians, 720 hours) in technician labor to complete the intensive 9-week sampling periods as well as 360 person-hours/year of technician labor to run the monthly telemetry operation. Thus, completion of the 3-year project will require an estimated minimum of 11,880 person-hours in addition to time spent by the primary investigator, advisors, and cooperators.

Estimated Annual Cost

	FY06-07	FY07-08	FY08-09
Personnel			
TFTE (5 techs, 360, $11.13/hr, 11.16% overhead)*	$ 22,270	$ 22,830	$ 23,410
TFTE (1 tech, 360 hours, $11.13/hr, 11.16% overhead)**	$ 4,454	$ 4,565	$ 4,679
Operating			
PURCHSERV (Ph.D. Stipend, tuition, minimal supplies)***	$ 27,500	$ 27,500	$ 27,500
SUPPLIES (bait, snowmobile repairs, handling supplies, etc.)	$ 4,000	$ 4,000	$ 4,000
EQUIPMENT (radio collars)	$ 11,500	$ 11,500	$ 11,500
Travel			
INSTTRAV	$ 1,500	$ 1,500	$ 1,500
VEHICLE LEASE/MILEAGE (3 vehicles, 5 months/year)**	$ 5,328	$ 5,328	$ 5,328
TOTAL COST	$76,552	$77,223	$77,917
TOTAL COST TO SSH BUDGET	$43,724	$44,395	$45,089

*Assumes 2.5% cost-of-living wage increase/year
**Telemetry work during interim between sampling periods
***Will be charged to budget centers other than lynx/snowshoe hare

EXPECTED RESULTS/BENEFITS

1) Seasonal density estimates and associated variability will help establish where Colorado lies on the continuum of hare densities reported in the literature. Whether densities are relatively high or low, stable or highly variable, or drastically different or roughly equal among cover types could influence future land management decisions as well as decisions regarding the lynx reintroduction process.
2) Combined with Zahratka (2004) and future research, density estimates from this project may elucidate the degree to which hare populations fluctuate or cycle in Colorado, a phenomenon of interest to wildlife ecologists and managers.
3) Comparison of "known" densities to those obtained from other commonly used methods will inform future research and monitoring programs which techniques are likely to produce results that are most consistently in agreement with the intensively derived estimates reported from this project. This knowledge will also enhance interpretation of previously reported hare densities in Colorado and elsewhere.
4) Assessment of density, demographic parameters, and their variability among habitat types will help identify which type(s) consistently support(s) high hare numbers and productivity. The current, conservative approach to lynx/hare conservation is to treat all potential habitat as equally and highly valuable, although this has not been substantiated scientifically, especially in Colorado. This project should determine if the current approach is justified or if there is a disparity in the value of different habitat types relative to lynx-hare conservation. If the latter is true, those charged with managing forests may be allowed more flexibility to accommodate competing resource uses while maintaining lynx/hare habitat.

5) Assessment of density and demographic parameters should help identify the general time period over which succession carries young, regenerating lodgepole pine stands into and then out of service as snowshoe hare habitat. It is apparent that stands in fresh clear cuts and mature lodgepole stands do not provide quality hare habitat (Zahratka 2004). The value of small and medium lodgepole stands to hares has not been quantified in Colorado and is of interest to resource managers.
6) Knowledge regarding the presence or absence of large-scale seasonal movements, and the extent to which this occurs will inform managers about the value of peripheral vegetation (other than conifer forest, such as riparian willow or aspen), will identify when and for how long peripheral vegetation is likely to be used, and will potentially identify other snowshoe hare management issues that have not received prior consideration.
7) A description and comparison of vegetation and landscape characteristics among the 3 stand types and their relationship to snowshoe hare demography and movement patterns should further aid land managers in creating and maintaining lynx/hare habitat.

RELATED FEDERAL PROJECTS

Given that the majority of lynx/hare habitat occurs on United States Forest Service land, this project will require cooperation with local ranger districts, regional biologists, and researchers within that agency. As soon as I have completed provisional study site selection, I will contact the appropriate collaborators to obtain permission, appropriate permits, etc.

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