



Research Article

Density and Demography of Snowshoe Hares in Central Colorado

JACOB S. IVAN,¹ *Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA*
 GARY C. WHITE, *Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA*
 TANYA M. SHENK, *Colorado Division of Wildlife, Fort Collins, CO 80526, USA*

ABSTRACT To improve understanding of snowshoe hare ecology in the Southern Rockies and enhance the ability of agency personnel to manage subalpine landscapes for snowshoe hares (*Lepus americanus*) and lynx (*Lynx canadensis*) in the region, we estimated snowshoe hare density, survival, and recruitment in west-central Colorado, USA from July 2006–March 2009. We sampled 3 types of forest stands that purportedly provide good habitat for hares: 1) mature Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*), 2) early seral, even-aged lodgepole pine (*Pinus contorta*), and 3) mid-seral, even-aged lodgepole pine that had been pre-commercially thinned. In all forest types and all seasons, snowshoe hare densities were <1.0 hares/ha. During summer, hare densities [\pm SE] were highest in early seral lodgepole pine (0.20 [0.01] to 0.66 [0.07] hares/ha), lowest in mid-seral lodgepole pine (0.01 [0.04] to 0.03 [0.03] hares/ha), and intermediate in mature spruce–fir (0.01 [0.002] to 0.26 [0.08] hares/ha). During winter, densities were more similar among the 3 stand types. Annual survival of hares was highest in mature spruce–fir (0.14 [0.05] to 0.20 [0.07]) and similar between the 2 lodgepole stand types (0.10 [0.03] to 0.16 [0.06]). Stand attributes indicative of dense cover were positively correlated with density estimates and explained relatively more spatial process variance in hare densities than other attributes. These same attributes were not positively correlated with hare survival. Both density and survival of hares in early seral lodgepole stands were positively correlated with the extent of similar stands in the surrounding landscape. Recruitment of juvenile hares occurred during all 3 summers in early seral lodgepole stands, 2 of 3 summers in mature spruce–fir stands, and in only 1 of 3 summers in mid-seral lodgepole. Based on estimates of density and demography specific to each forest type, we conclude that managers should maintain mature spruce–fir and early seral lodgepole stand types rather than thinned, mid-seral lodgepole stands to benefit snowshoe hares (and by association lynx) in central Colorado. Given the more persistent nature of spruce–fir compared to early seral lodgepole, and the fact that such stands cover considerably more area, mature spruce–fir may be the most valuable forest type for snowshoe hares in the region. © 2014 The Wildlife Society.

KEY WORDS Colorado, demography, density, forest management, *Lepus americanus*, recruitment, snowshoe hare, survival, telemetry.

Snowshoe hares (*Lepus americanus*), their famous 10-year population cycle, and close association with Canada lynx (*Lynx canadensis*) have been well studied in boreal Canada for decades (Hodges 2000a, Krebs et al. 2001a, b). However, hares range south into the Cascades and Sierra Nevada, Northern and Southern Rockies, Upper Lake states, and Appalachian Mountains (Hodges 2000b). Hare ecology in these areas is not as well understood (Hodges 2000b) but is critically important. In the Southern Rockies where an effort

to restore a viable population of the federally threatened Canada lynx has recently concluded (U.S. Fish and Wildlife Service 2000, Devineau et al. 2010), snow-tracking of reintroduced lynx and their progeny indicated that approximately 70% of the prey species in the lynx diet was snowshoe hares (Shenk 2009). Thus, existence of lynx in the region and long-term success of the reintroduction effort hinges, at least partly, on maintaining adequate and widespread populations of hares.

Over the past decade snowshoe hare research in the Rocky Mountains of the conterminous United States has accelerated. Much of this recent work has focused on estimating density of hares in various habitat types, and in all cases, stands with high hare density are characterized by dense understory vegetation that provides both browse and cover (Wirsing et al. 2002, Malaney and Frey 2006, Zahratka and Shenk 2008, Griffin and Mills 2009, Berg et al. 2012). Although animal density is often elevated in habitat patches

Received: 20 July 2012; Accepted: 21 January 2014
 Published: 16 April 2014

¹E-mail: jake.ivan@state.co.us

²Present address: Colorado Parks and Wildlife, 317 W Prospect Road, Fort Collins, CO 80526; Jake.Ivan@state.co.us

³Present address: National Park Service, 1201 Oakridge Drive, Suite 200, Fort Collins, CO 80525

that support high levels of individual fitness, it can be a misleading indicator of habitat quality because areas with high density may also function as population sinks (Van Horne 1983). Estimation of habitat-specific demographic rates in addition to density provides a more complete assessment of habitat quality.

Only a handful of studies have addressed both demography and density estimation of hares in the Rocky Mountains (Wirsing et al. 2002, Griffin and Mills 2009). Indeed, in some cases, forest types with high hare density are not necessarily the habitats where hares survive or recruit well (Griffin and Mills 2009). Thus, despite the growing body of literature relating hare density to forest types and forest structure, uncertainty still exists regarding the types of stands necessary for persistence of snowshoe hares at the southern extent of their range. Reducing this uncertainty is critical for those tasked with managing forests for snowshoe hares and Canada lynx. Our objective was to evaluate forest types that purportedly provide good hare habitat in the Southern Rockies to provide land managers in the region with local information about density and demography of snowshoe hares.

Based on the requisite association with dense understory cover noted above, we identified mature Engelmann spruce (*Picea engelmanni*)–subalpine fir (*Abies lasiocarpa*), and early seral lodgepole pine (*Pinus contorta*) as candidates of high quality hare habitat in the region. Additionally, we evaluated mid-seral, commercially thinned lodgepole pine because effects of this standard practice on hares inhabiting lodgepole stands has been shown to range from strongly negative (Griffin and Mills 2007, Homyack et al. 2007) to inconsequential (Thornton et al. 2012) or inconclusive (Ausband and Baty 2005) in other areas. Our evaluations used a combination of mark-recapture and radio telemetry sampling to estimate site- and season-specific (winter vs. summer) snowshoe hare density, survival, and recruitment in these forest types, which had not been done previously in the Southern Rockies. For parameter estimation, we combined the 2 sources of information into a single analysis, which should enhance rigor and precision compared to most previous approaches.

In montane regions of the western United States, highest densities of snowshoe hares are generally recorded in either young, even-aged conifer stands regenerating after stand-replacing fires or timber harvest (Koehler 1990, Wirsing et al. 2002, Griffin and Mills 2009, Berg et al. 2012) or in mature, uneven-aged conifer stands (Beauvais 1997, Zahratka and Shenk 2008, Griffin and Mills 2009, Hodges et al. 2009, Berg et al. 2012). Mid-successional stands rarely sustain high densities of hares but see Miller (2005) and Thornton et al. (2012) for exceptions. Given these results we expected hare densities in our study area to be highest in either mature spruce–fir or young lodgepole stands and lowest in mid-seral, pre-commercially thinned stands. Based on the only study to estimate density in both summer and winter (Griffin and Mills 2009), we also expected that the relative ranking of these forest types might change with season. Generally, we expected summer estimates taken after the second birth pulse to be higher than winter estimates.

Griffin and Mills (2009) found that weekly survival of hares using dense mature stands were highest, followed by dense young stands, then open young stands. Dolbeer and Clark (1975) found a similar pattern in survival for juvenile hares in Colorado, but adult survival was higher in sparse stands compared to densely forested stands. Wirsing et al. (2002) did not find differences in snowshoe hare predation rates between high and low cover sites. Given conflicting results from these previous studies, we had no a priori expectation with respect to snowshoe hare survival by forest type. Furthermore, the intervals over which we estimated survival were summer–winter and winter–summer. These intervals do not match well with seasonal estimates previously published (e.g., summer, winter, fall, spring); therefore, predicting results based on current literature is difficult. Given the diversity and abundance of food available to hares during mid-summer (e.g., grasses, forbs, and fungi in addition to conifer needles and small twigs), we postulated that during the summer hares would be on a higher nutritional plane than in winter, and this would enhance survival during the summer to winter interval. Others have found that 4-week survival rates covary with body mass, and that body mass is negatively correlated with accumulating snow (Hodges et al. 2006), which lends support to our hypothesis. However, the interplay between nutrition, predation, and survival likely is complex (Hodges et al. 2006).

Recruitment has rarely been estimated for snowshoe hare populations in the United States Rocky Mountains. Dolbeer and Clark (1975) reported annual natality rates and Wirsing et al. (2002) estimated recruitment based on immigration, but neither reported it by forest type. Only Griffin and Mills (2009) estimated fecundity (in situ recruitment) using ultrasound and they concluded that it was roughly equal among hares using different stand types. Therefore, we had no expectation that it would vary with forest type.

STUDY AREA

The study area encompassed roughly 1,200 km² around Taylor Park and Pitkin, Colorado, USA (39°50'N, 106°34'W; Fig. 1), and included a portion of the “Core Reintroduction Area” occupied by reintroduced Canada lynx (Shenk 2009). Open sagebrush (*Artemisia tridentata*) parks dissected by narrow riparian zones of willow (*Salix* spp.) and potentilla (*Potentilla* spp.) dominated the low elevation (approx. 2,800–3,000 m) parts of the study area. Extensive stands of lodgepole pine occupied mid-elevation slopes (approx. 3,000–3,300 m), giving way to bands of Engelmann spruce–subalpine fir in the sub-alpine zone (approx. 3,200–3,600 m). Alpine tundra topped the highest parts of the study area (approx. 3,300–4,200 m). Moist spruce–fir forests also occurred on north-facing slopes at mid-elevations. Patches of aspen occurred intermittently, usually associated with spruce–fir stands.

Climate was typical of continental, high-elevation zones with relatively short, mild summers and long, harsh winters. Mean July temperature was 14° C; mean January temperature was –11° C (Ivan 2011). Maximum snow depth on the study area averaged 80 cm but ranged from 22 cm to 163 cm

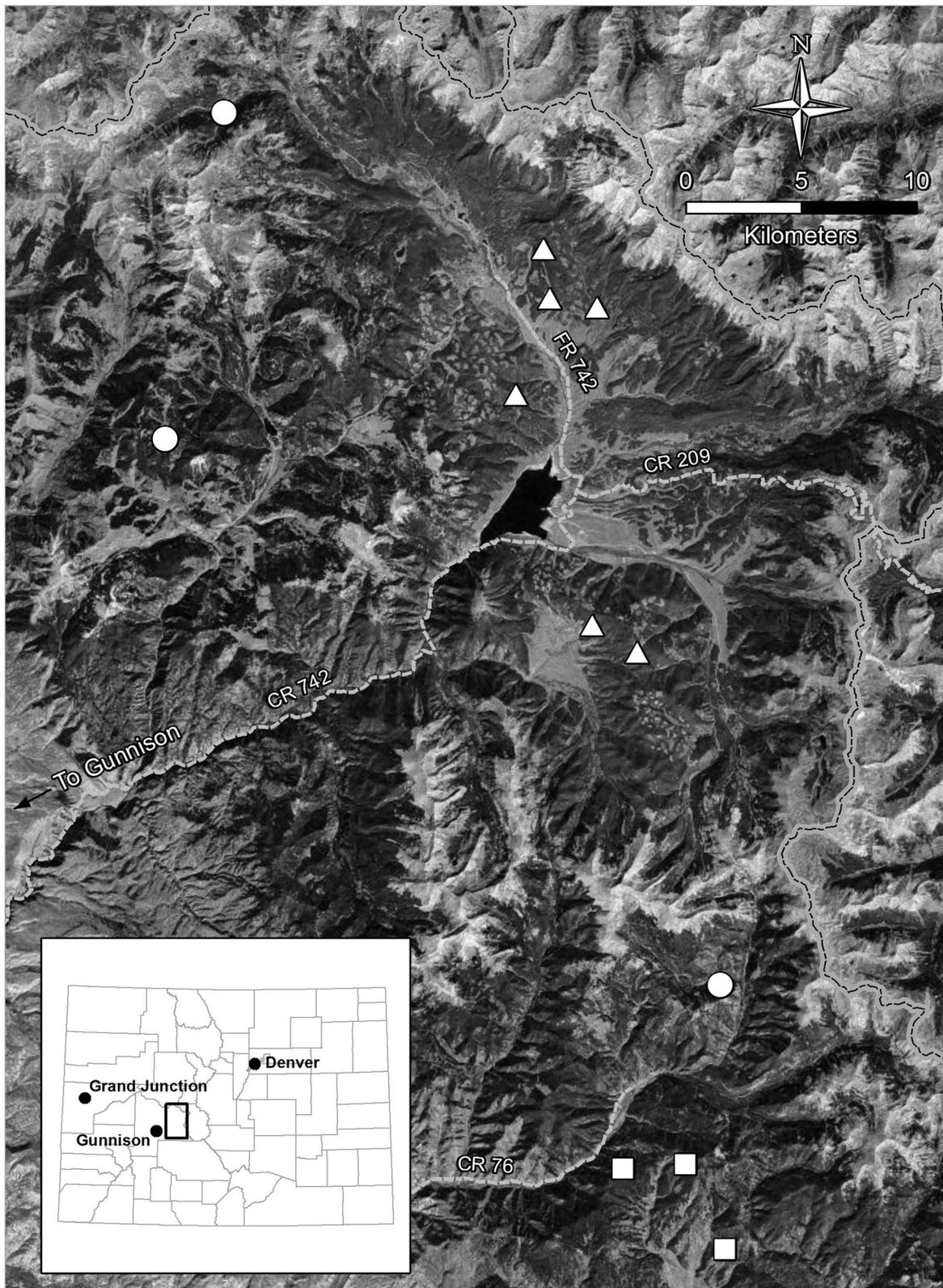


Figure 1. Study area near Taylor Park and Pitkin, central Colorado. We estimated snowshoe hare density and demography at 3 late-seral Engelmann spruce-subalpine fir sites (circles), 3 mid-seral lodgepole pine sites (squares), and 6 early-seral lodgepole pine sites (triangles) from summer 2006 through winter 2009.

depending on year, elevation, and aspect (Ivan 2011). Snowpack generally persisted from November through May (low elevations) or June (high elevations and north-facing slopes).

Some human habitation occurred in the study area, mostly in the form of seasonal residences. Considerable recreational use occurred during summer in the form of dispersed camping and off-highway vehicle traffic. A suite of native

predators were present within the study area including lynx, cougar (*Puma concolor*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), pine marten (*Martes Americana*), great horned owl (*Bubo virginianus*), and northern goshawk (*Accipiter gentilis*).

METHODS

Sampling

We subjectively selected 3 replicate stands of mature spruce-fir (22.86–40.64 cm diameter at breast height, dbh) and 3 replicates of mid-seral (12.70–22.85 cm dbh) lodgepole pine from within the study area to sample for snowshoe hare density and demography. Few early seral lodgepole stands were of sufficient size to hold a full trapping grid (see below) so we selected twice as many (6) of these stands and sampled them using half-sized grids. Spruce-fir stands had some evidence of historical logging but were largely unmanaged and structurally complex because of downed logs and uneven age. Mid-seral lodgepole stands were clear-cut 40–60 years prior to sampling and were thinned to 3-m spacing approximately 20 years pre-sampling. Trees in these stands were beginning to self-prune with lower branches approximately 0.8 m above ground. Early seral lodgepole sites were clear-cut 20–25 years prior to sampling and had regenerated into densely stocked stands (6,231 stems/ha, Appendix A). Trees in these stands had not started to self-prune and tree canopies generally extended to ground level.

We sampled in both summer (20 Jul–10 Sep) and winter (20 Jan–17 Mar) each year for 3 years (2006–2009) for a total of 6 sampling sessions (3 summer, 3 winter). For a given sampling session, we concurrently live-trapped for a 4–5 day period at 1 spruce-fir site, 1 mid-seral lodgepole site, and 2 early seral lodgepole sites. We then located hares within those 4 sites daily for 7–10 days post-trapping. Upon completion of both the trapping and telemetry sampling, we moved to the second and subsequently the third sets of 4 sites. We sampled the same 12 sites each season, but rotated the order in which they were sampled so that no set of sites was routinely sampled early or late within a sampling season. We computed density for each site during each sampling session and aggregated results by forest type (see below). We computed survival and recruitment across intervals between sessions.

We based estimates of hare density and demography on a combination of mark-recapture and telemetry data. Colorado State University and Colorado Parks and Wildlife Animal Care and Use Committees approved all methods (Colorado State University IACUC Protocol 06-062A-03). We used Tomahawk Model 204 live traps (Tomahawk Live Trap, Hazelhurst, WI) deployed on 7 × 12 (mid-seral lodgepole and mature spruce-fir) or 6 × 7 (early seral lodgepole) grids with 50-m spacing for mark-recapture sampling. We covered traps with pine boughs and bark to protect entrapped animals from elements. Additionally, during winter sampling sessions, we encased traps in several inches of snow to provide further protection. We baited traps with apple slices, commercial rabbit chow, and cubed

timothy hay (*Pbleum pratense*). During summer sampling sessions, we pre-baited traps for 3 nights, followed by 5 nights of trapping. However, during winter we locked traps open on the third night of each 5-night trapping effort to eliminate the possibility that hares could be trapped >2 nights in a row (i.e., traps were set for 2 nights, then locked open, then set again for 2 nights for a total of 4 trap nights during each winter trapping session). This altered schedule alleviated capture myopathy issues that we detected during the first winter trapping session. We aged, weighed, recorded sex, and individually marked captured hares with a passive-integrated transponder (PIT) tag (Biomark, Inc., Boise, ID), all without anesthesia.

We radio-marked up to 10 hares per study site using a 28-g collar (Model TW5SM, BioTrack, LTD, Wareham, Dorset, United Kingdom) equipped with a 6-hour mortality sensor. We expected individual heterogeneity in capture probability related to varying home range overlap with the trapping grid. We also expected varying behavioral response to the trapping process (we captured some hares early and often and others only once toward the end of a session). To account for these sources of heterogeneity and in an attempt to radiocollar a representative sample of hares at each site, we checked grids using random starting points each day (but checked traps in the same order) and collared hares as we encountered them so that hares captured near the edge were as likely to receive a collar as hares captured near the center. We also retained 2 of the allotted 10 collars per site for marking animals during the last 2 days of trapping. After trapping, we carefully removed all traps and bait from the site, so that post-trapping animal movements were not influenced by the trapping grid.

To correct density estimates (see below) we assessed snowshoe hare movements at a given site for a 7- to 10-day period beginning 1–3 days post-trapping. We located radiocollared hares using short-range triangulation (usually <250 m) or homing. Because hares are generally active during nighttime (Keith 1964, Foresman and Pearson 1999), we obtained an equal number of daytime and nighttime locations to locate hares during resting and active periods. We preferentially located hares that remained near the area formally occupied by the trapping grid because they were most important for correcting density estimates. We triangulated hares that strayed far from the grid after trapping at distances that were often >250 m. We estimated all triangulated locations using the maximum likelihood procedure (Lenth 1981) in Program LOAS (Version 4.0, Ecological Software Solutions LLC, Sacramento, CA). Sometimes homing in on individuals was more efficient, but we did this only during daytime when hares were inactive and holding tight to their hiding spots. We did not record a location if the signal indicated that the animal moved as we approached. We assessed accuracy of short-range locations by triangulating on hares during daytime when they were inactive, then immediately homing on them to obtain their true location.

In addition to the relatively short telemetry sampling periods that occurred post-trapping, we determined whether

collared hares were alive or dead from the air and/or ground 1–4 times between summer and winter trapping sessions. Because hares were capable of remaining still long enough to set off the mortality sensor in their collar, we did not consider animals dead until we observed signs of death in the field or until we obtained mortality signals on ≥ 3 consecutive checks. While working on the current sample of hares from a given site, we regularly located hares that we did not capture during that session but retained working transmitters from previous sessions.

Density Estimation

We estimated density using the “Density with Telemetry” data type in Program MARK (White and Burnham 1999), which makes use of auxiliary telemetry data to account for lack of geographic closure of sampling grids (Ivan et al. 2013a). Ivan et al. (2013b) suggested that for the range of densities and capture probabilities we encountered in the field, percent error should be minimized using this method compared to others available for addressing the closure issue. Ivan et al. (2013b) further suggested that if a logistical tradeoff were necessary, it was preferable to maximize the number of collars deployed on a study site at the expense of obtaining a large number of locations per collar. Therefore, we maximized collar deployment (10 at each site) and obtained approximately 10 locations per individual (approx. 1 location per day for 10 days).

We considered season (summer or winter), trapping session (1–6), forest type, site (1–12), and distance of the mean trap location for individual i to the edge of the trapping grid (DTE _{i}) as predictors of \tilde{p}_i , the parameter in the model that accounts for the proportion of time each animal spends on the study site. We defined the study site as the minimum convex polygon containing the trapping grid. We evaluated the same covariates, along with age, behavioral response to initial capture (Otis et al. 1978, White 2008), and minimum daily winter air temperature as potential predictors of the detection probability for each individual (p_i^*). Air temperature has been shown to influence capture probability for snowshoe hares in previous work (Zahratka and Shenk 2008); we measured it nightly at each site using a single HOBO Pro Series Temp datalogger (Onset Computer Corporation, Pocasset, MA).

Because the likelihoods for \tilde{p}_i and p_i^* are factorable and do not influence each other, we identified the best models for each parameter in 2 steps. First, we evaluated models in which we fixed p_i^* to be constant across sites and sessions, and considered all possible additive models using the 5 covariates for predicting \tilde{p}_i . We did not allow redundant variables in the same model. That is, a model with a site effect could not also include the nested effect of forest type. We identified the best structure for \tilde{p}_i using AIC_c (Burnham and Anderson 2002). Second, we fixed the best structure for \tilde{p}_i and built 60 models to estimate density using all additive combinations of covariates for p_i^* , again omitting combinations of variables that were redundant. We included individual heterogeneity (by modeling capture probability using 2 mixtures; Pledger 2000, White 2008) and DTE _{i} in every model for

p_i^* because our trapping experience and simulations indicated that both would substantially improve fit (Ivan et al. 2013b). We model-averaged (Burnham and Anderson 2002) site-specific density estimates from candidate models using AIC_c, then combined estimates and standard errors from each replicate to obtain average density estimates by forest type through time using the delta method (Seber 1982:7). For all estimates, we adjusted the nominal area of the study sites to account for topography (Surface Tools for Points, Lines, and Polygons Extension, ArcView 3.1, version 1.6b, Jenness Enterprises, <http://www.jennessent.com>).

Survival Estimation

We estimated survival of hares across intervals between trapping sessions using a Barker/Robust Design model (Kendall et al. 2013) as implemented in Program MARK (White and Burnham 1999). The Barker model (Barker 1997, 1999) incorporates information from multiple sources to estimate survival including recovery of dead animals, live resightings during mark-recapture sampling, and resightings of marked animals outside of mark-recapture sampling. These sources of information are combined into a single likelihood to improve survival estimates and precision. Here, live resightings during the interval between trapping sessions came in the form of live–dead data from telemetry signals.

The robust design (Pollock 1982, Kendall et al. 1995, 1997) is a sampling scheme in which >1 secondary sampling occasions (in our case, 4–5 days of trapping) occur within each primary sampling session (we had 6 primary sampling sessions: 3 summer and 3 winter). Intervals between the primary sessions over which survival is estimated are relatively long (in our case 131–204 days), whereas intervals between secondary occasions are short (in our case 24 hr), so populations can be assumed to be demographically closed across the secondary occasions. Such a sampling scheme allows estimation of more survival parameters than would be possible using traditional Cormack Jolly Seber models that lack secondary occasions, and it increases precision of estimates by incorporating information on capture probability from secondary, closed-capture occasions (Kendall et al. 1995). Parameters for the Barker/Robust design model include:

S_t = probability that an individual survives interval t , $t+1$ given that it was alive at t , where t is a primary sampling session.

r_t = probability that an animal that dies in the interval t , $t+1$ is found dead.

R_t = probability that an animal that survives t , $t+1$ is resighted alive during that interval.

R_t' = probability that an animal that dies in the interval t , $t+1$, without being found dead, is resighted alive in that interval before it died.

γ_t'' = probability of being on the study site and available for capture during primary session t , given that the animal was present during primary session $t-1$.

γ_t' = probability that an animal returns to the study site during primary session t given that the animal was not present on the site during $t - 1$.

F_t = probability an animal at risk of capture at time t does not permanently emigrate before $t + 1$.

p_t^* = probability that an individual is captured at least once during primary session t , given it was alive and on the study site. Note that this includes the usual closed capture parameters such as those representing mixtures (π), probability of initial capture during a secondary sampling occasion (p_i), and probability of recapture during a secondary sampling occasion (c_i).

We modeled survival using 2 groups: animals that were radiocollared and those that were not. For the radiocollared group, we specified r_t , R_t , and R_t' to be constant across sites and sessions because we fitted all hares with radio tags of the same make and model and we sampled under the same protocol (including attainment of locations from the air) during each session or interval. Thus, we had no reason to suspect that the probability of being seen alive (or dead), or being recovered, varied through time, across sites, with forest type, etc. Setting r_t constant across time also enabled us to estimate S_6 using dead animal recoveries collected during the 6-month interval after mark-recapture sampling ended in March 2009. This last winter-summer survival estimate would have been unidentifiable otherwise. For the group that did not receive radiocollars, we fixed r_t , R_t , and R_t' to zero because observing or recovering uncollared individuals was impossible during intervals between mark-recapture sampling. We modeled p_t^* using the best structure from the density estimation procedure.

We initially constructed survival models that allowed the probability of leaving or returning to a site within (γ_t'' , γ_t') or between (F_t) seasons to vary between large and small grids and between forest types. However, models incorporating such structures were not well supported, the parameters were not well estimated, and they were tangential to our goal of estimating survival. Therefore, we fixed γ_t'' , γ_t' , and F_t to be constant across sites and sessions for all models in the candidate set.

Given this base model structure (i.e., constant γ_t'' , γ_t' , and F_t ; constant r_t , R_t , and R_t' for the radiocollared group; $r_t = R_t = R_t' = 0$ for the group without radiocollars), we hypothesized that S_t might vary with hare age, interval, season, site, and forest type (specifically, survival may vary among all forest types, or more simply, spruce-fir may differ from lodgepole). Also, during the first 2 years of sampling, anecdotal field evidence indicated an apparent decline in hare numbers. Therefore, we postulated that individual survival may have been especially poor during those winters and we added such an effect (altered survival during the first 2 winter to summer intervals) to the list of explanatory variables. We constructed 56 models reflecting all additive combinations of these effects, avoiding redundancy as before. Because individual survival (S) is included in the likelihood in the Barker/Robust Design model (as opposed to density, which was a derived parameter), we were able to model it as a function of forest type, and thus it was not necessary to

aggregate estimates across sites post hoc to produce overall estimates for each forest type. We could estimate forest-specific survival directly from the model.

Variance Components

Initial candidate model sets included season and site as general predictors of survival and density. However, many other potentially important factors are nested within season and site (e.g., deviation from normal precipitation, understory cover), which may have explained variation as well. To avoid construction of thousands of models addressing all combinations of these nested factors, we assessed their influence on density and survival of hares using the variance components procedure in Program MARK (Burnham and White 2002). This approach allowed estimation of process variation in density or survival estimates (e.g., variation in density or survival due to differences in understory cover or some other covariate of interest) separate from sampling variation (e.g., if we sampled over and over again, we would find variation in the estimates due to the sample of animals obtained each time). Accordingly, we selected a general model from our initial set (i.e., fully session and-or site specific), extracted the temporally (or spatially) specific estimates from that model, and fit appropriate random effects models (see below) to those estimates (Franklin et al. 2002).

We sampled 12 sites across 6 primary sessions (or 6 intervals between the primary sessions in the case of survival), which under a general fixed effects model produced 72 estimates of density (or survival). However, these 72 estimates were not independent because we sampled multiple sites during the same primary session, and we sampled multiple primary sessions through time at each site. Thus, for the random effects portion of the procedure, we fit trapping session (or interval in the case of survival) as a fixed effect to estimate the process variation among the 72 estimates after accounting for the effect of session (σ_s^2). We then added habitat variables (see below) one at a time to this session model to estimate the spatial process variation left after accounting for both session and the habitat variable of interest (σ_{s+h}^2). The quantity $(\sigma_s^2 - \sigma_{s+h}^2 / \sigma_s^2)$ is an estimate of the percent variation in density or survival due to the habitat variable, after accounting for variation due to session. Similarly, we fit site as a fixed effect, then added session-specific variables (e.g., weather variables) one at a time to estimate the percent variation in density or survival due to the session variable, after accounting for variation among sites.

Density.—We considered 7 habitat covariates as potentially important predictors of process variation in snowshoe hare density from site to site (see Appendix A for detailed description). Because hares tend to be associated with thick cover, we expected density to be positively related to 1) horizontal cover 0–2 m above ground, 2) stem density for stems 1–7 cm in diameter, 3) percent tree canopy cover, 4) down wood, and 5) hectares of willow in the surrounding landscape; we expected a negative relationship between 6) crown height (measured as the distance from the ground to lowest live branch) and 7) distance (km) to the nearest willow

patch. We also conducted a separate variance components analysis only on the early seral lodgepole stands ($n = 36$) by fitting hectares of early seral lodgepole (see Appendix A) as well as distance to nearest early seral lodgepole patch as fixed effects. This sub-analysis reflected the idea that hare density in these isolated, small patches might be dependent on the amount of and distance to similar habitat in the surrounding landscape.

We considered 2 weather variables as potentially important predictors of variation in snowshoe hare density across sampling sessions. We evaluated the influence of total precipitation for the year (365-day window) immediately preceding a sampling session because increased precipitation should result in increased browse and cover, and accordingly survival and productivity, during the 12 months leading up to the year of interest. We also considered a 2-year lag (i.e., the 1-yr window beginning 730 days prior to the sampling session) in precipitation effects. Precipitation data were collected at a weather station 20 km west of the study area in Crested Butte, Colorado at 2,700 m elevation (National Climatic Data Center, Ashville, NC).

Survival.—We postulated similar relationships between habitat variables and hare survival. However, we hypothesized that precipitation could have an immediate effect on survival, so we included total precipitation during the interval of interest (rather than 1 yr prior) as well as a 6-month lag (rather than 2-yr lag). Because deviation from normal snowfall may influence survival by facilitating mismatches between seasonal hare pelage and the surrounding landscape, we also included departure from average days of snow cover for the interval of interest. We measured departure in days based on the 25-year average in Crested Butte, Colorado from 1985 to 2009 (National Climatic Data Center, Ashville, NC).

Recruitment

Because we sampled under a robust design framework and obtained age-specific (juvenile or adult) estimates of density and hare survival, we were able to estimate recruitment into each site during each sampling session following Nichols and Pollock (1990). Using their ad hoc approach, we estimated recruitment from in situ reproduction (B') as the product of the number of estimated juveniles alive at session t and the estimated proportion of those animals that survived to $t + 1$. We obtained recruitment of individuals of all ages from immigration (B'') by subtracting the estimated number of adult and juvenile survivors over the interval ($t, t + 1$) from the estimated number of adults at $t + 1$. We altered the equations of Nichols and Pollock (1990) by substituting density when their equations required N_i . Thus, estimates were standardized to reflect the number of hares recruited per hectare, rather than the total number of hares recruited per site, and estimates of recruitment were directly comparable to estimates of density. Because this approach is ad hoc, we could not compare various models of recruitment nor could we conduct any sort of variance components analysis as described above for density and survival. Instead, we aggregated site-specific recruitment estimates into estimates of average recruitment for each forest type in each interval. We derived density and survival estimates separately so we

could not directly estimate the covariance between them and assumed it to be 0. We calculated standard error for average recruitment by forest type using the delta method (Seber 1982:7).

RESULTS

We captured 305 hares (132 males, 151 females, 22 unknown sex; 246 adults, 59 juveniles) 740 times over the course of the study. We radiocollared 223 (73%) of these hares, and obtained 2,252 total locations, an average of 8.3 locations/hare/sampling session (range = 3–12). We obtained 91% of locations via triangulation and the remainder by homing. We obtained 54% of locations during daytime (approx. 1000 hours to 1 hour before official sunset) and 46% during nighttime (1 hour after official sunset to approx. 0200 hours). Based on 99 trials over the 6 sampling sessions, median estimated location error was 49 m (range 3–330), about 1 trap width.

Hares moved farther than we anticipated and individuals initially trapped in spruce-fir, mid-seral lodgepole, and early seral lodgepole stands often did not remain exclusively in those stands during sampling. We accounted for their movement when estimating density by incorporating telemetry data into the estimate, but we could not account for movement when estimating survival or recruitment across long intervals. Therefore, we redefined the area to which survival and recruitment estimates applied in the following manner. We identified the 90th percentile of the distance collared hares were located from the center of their grid of capture during each sampling session (range = 715–1175 m), buffered the trapping grids by these distances, and defined the area included in this buffer as the landscape in which collared hares lived. Thus, estimates for hares in spruce-fir sites reflected survival and/or recruitment of individuals that used a landscape comprised of approximately 85% mature spruce-fir, 7% mid-seral lodgepole, 6% willow, and 2% other. Estimates for mid-seral lodgepole reflected use of landscapes comprised of 64% thinned mid-seral lodgepole, 15% mature lodgepole, 13% aspen, and 8% other. Estimates for early seral lodgepole reflected landscapes comprised of 7% early seral lodgepole, 83% mature lodgepole, and 10% willow. Of note, early seral lodgepole landscapes contained little early seral lodgepole pine on a percentage basis because these stands occurred as small patches ($5.0 \text{ ha} \pm 2.2 \text{ SD}$) intermixed in a matrix of larger, unharvested lodgepole. However, these early seral stands were the signature component of these landscapes because mature lodgepole provided almost no hare habitat. Hares generally lived in 1 of the 3 landscape types and did not move between them. Any reference to mature spruce-fir, mid-seral lodgepole pine, and early seral lodgepole pine in survival or recruitment analysis from here forward refers to hares sampled in the original site plus its buffer.

Density

The top model for \tilde{p}_i was the general, additive structure in which \tilde{p}_i varied by trapping session, site, and DTE_i (AIC_c weight = 0.99). Capture probability (\hat{p}_i^*) was strongly influenced by behavioral effects (recapture probability was lower than initial capture probability), age (adults were more

Table 1. Model selection results for snowshoe hare density in mature spruce–fir, early seral lodgepole pine, and thinned, mid-seral lodgepole stands in central Colorado, USA, summer 2006–winter 2009. We compared 60 models and show the top 10 based on Akaike’s Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002). For all models, the structure indicated for capture probability (p) was paired with the best structure for \bar{p} (DTE + grid + session) as determined during a previous model selection step. Heterogeneity indicates a 2-point mixture model to account for individual heterogeneity in capture probability. DTE is an individual covariate representing distance to the edge of the site from the mean capture location. Age is an effect indicating juvenile (young of the year) or adult. Behavioral effects allow for recapture probabilities to differ from initial capture probabilities. K is the total number of parameters in the model and w_i is the Akaike weight. Density estimation was implemented in Program MARK using information from telemetry sampling to correct for lack of geographic closure.

Model	AIC_c	ΔAIC_c	w_i	K
p (heterogeneity + DTE + age + behavior + site + session)	3,482.2	0.0	0.73	41
p (heterogeneity + DTE + age + behavior + site + session + wintertemp)	3,484.3	2.0	0.26	42
p (heterogeneity + DTE + age + behavior + site + season)	3,492.5	10.3	0.00	37
p (heterogeneity + DTE + age + behavior + site + season + wintertemp)	3,494.2	11.9	0.00	38
p (heterogeneity + DTE + age + behavior + site)	3,494.8	12.6	0.00	36
p (heterogeneity + DTE + age + behavior + session + forest type)	3,500.9	18.7	0.00	32
p (heterogeneity + DTE + age + behavior + session)	3,501.9	19.7	0.00	30
p (heterogeneity + DTE + age + behavior + session + forest type + wintertemp)	3,502.4	20.2	0.00	33
p (heterogeneity + DTE + age + behavior + session + wintertemp)	3,503.1	20.8	0.00	31
p (heterogeneity + DTE + age + behavior + season + forest type)	3,504.5	22.3	0.00	28

difficult to capture than juveniles), trapping session, and site. These effects appeared in the only models that held any weight (Table 1), and slope parameters for these effects were strongly divergent from 0. Minimum daily temperature during winter trapping also appeared in the top models, but its inclusion increased AIC_c scores and the slope for this effect was 0, indicating that it is not an important variable. As we hypothesized, individual heterogeneity and DTE_i were important enough to include in every model because removing heterogeneity from the top model added 170 units to its AIC_c score and removing DTE_i added 50 units.

We estimated snowshoe hare densities in all forest types and all seasons to be <1.0 hares/ha (Fig. 2). During summer, densities [\pm SE] were generally highest in early seral lodgepole stands (0.20 [0.01] to 0.66 [0.07] hares/ha), lowest in mid-seral lodgepole (0.01 [0.04] to 0.03 [0.03] hares/ha), and intermediate in mature spruce–fir

stands (0.01 [0.002] to 0.26 [0.08] hares/ha). Summer 2008 was an exception in that density in spruce–fir was estimated near 0 because we did not capture many individuals. However, telemetry information and direct observation indicated that several hares were present in the spruce–fir sites but never captured. This phenomenon did not occur for other forest types or during other seasons and its cause was unclear. Regardless, we likely underestimated hare density in the mature spruce–fir stand type during summer 2008.

During winter, density estimates generally became more similar among forest types. Early seral lodgepole sites lost hares from summer to winter, mid-seral lodgepole stands gained hares (although inference is weak given the poor precision of these estimates), and mature spruce–fir stands retained nearly as many hares as during the previous summer (except during 2008 as noted above). The bulk of hares in the

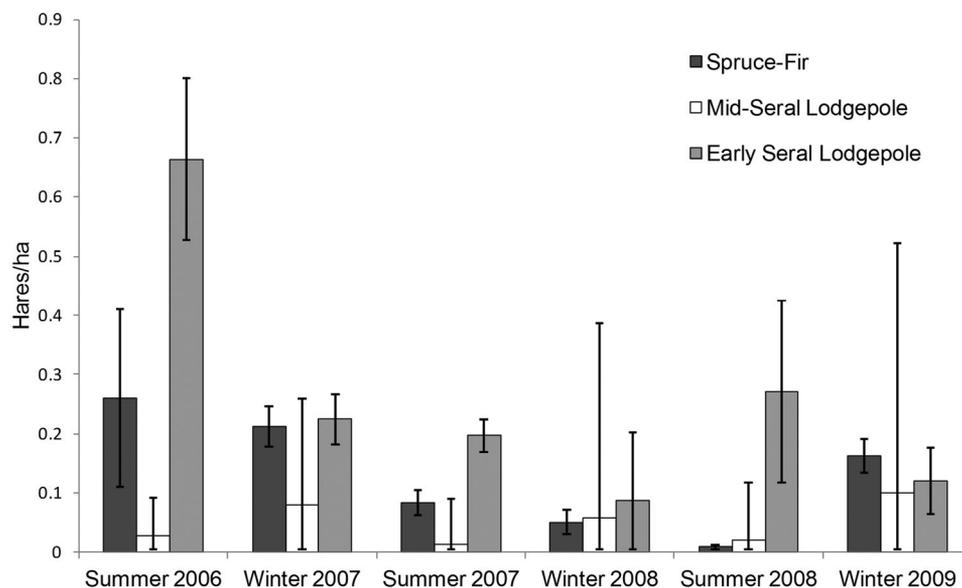


Figure 2. Snowshoe hare density and 95% confidence intervals in 3 forest types in central Colorado, summer 2006 through winter 2009. We derived estimates using a combination of mark-recapture and radiotelemetry to correct for lack of geographic closure during sampling periods.

Table 2. Table of model selection results for snowshoe hare survival in mature spruce-fir, early seral lodgepole, and thinned, mid-seral lodgepole pine stands in central Colorado, USA, summer 2006–summer 2009. We compared 56 models and show the top 10 based on Akaike's Information Criterion corrected for small sample size (AIC_c ; Burnham and Anderson 2002) are shown. For all models, the structure indicated for survival (S) was paired with the best structure for capture probability (P_i). Other model parameters were fixed to be constant (.) or 0. K is the total number of parameters in the model and w_i is the Akaike weight. Survival estimation was implemented via the Barker/Robust Design data type in Program MARK using telemetry sampling to improve precision over mark-recapture alone.

Model	AIC_c	ΔAIC_c	w_i	K
$S(\text{season} + \text{spruce-fir})$	2,631.9	0.0	0.09	32
$S(\text{season})$	2,631.9	0.0	0.09	31
$S(2\text{-winter decline})$	2,632.0	0.1	0.09	31
$S(2\text{-winter decline} + \text{spruce-fir})$	2,632.3	0.4	0.07	32
$S(\text{season} + \text{spruce-fir} + 2\text{-winter decline})$	2,632.7	0.8	0.06	33
$S(\text{season} + \text{spruce-fir} + 1\text{-winter decline})$	2,632.8	0.9	0.06	33
$S(\text{season} + 2\text{-winter decline})$	2,632.8	0.9	0.06	32
$S(\text{season} + 1\text{-winter decline})$	2,633.2	1.3	0.05	32
$S(\text{season} + \text{forest type})$	2,633.6	1.7	0.04	33
$S(\text{season} + \text{spruce-fir} + \text{age})$	2,634.1	2.2	0.03	33

system occurred in either early seral lodgepole or mature spruce-fir stands. Hares in these 2 forest types apparently underwent a decline that began in winter 2007 and ended in either summer 2008 (early seral lodgepole) or winter 2009 (spruce-fir; Fig. 2).

Survival

We found strong support for seasonal differences in hare survival and for depressed survival during the first 2 winters of the study (Table 2). These effects pervade the top models in the set (cumulative AIC_c weight for season = 0.66, cumulative AIC_c weight for 2-winter decline = 0.44) and parameter estimates were non-zero. The addition of spruce-fir improved model AIC_c scores (cumulative AIC_c weight for spruce-fir = 0.41) but the 95% confidence intervals on the coefficients overlapped 0. We found little evidence that hare age or forest type (considering all 3 forest types individually rather than simply spruce-fir or lodgepole pine) influenced survival; these effects appeared in some of the top models, but their addition generally increased AIC_c scores, cumulative AIC_c weights were low (0.17–0.25), and 95% confidence intervals on their coefficients included 0. Model-averaged estimates reflected that summer to winter survival was higher than winter to summer survival, winter survival early in the study was depressed, and survival was higher for animals in spruce-fir compared to the lodgepole forest types. Annual survival ranged from 0.10 (0.03) to 0.20 (0.07) depending on year and forest type (Table 3).

Variance Components

Density.—Horizontal cover explained the greatest portion of variation in hare densities after accounting for variation due to trapping session, followed by stem density, percent tree canopy cover, and down wood (Table 4). Hare density was positively associated with horizontal cover, stem density, canopy cover, and hectares of willow in the surrounding landscape, and negatively associated with distance to willow and height of tree crowns, but only the values of the

Table 3. Model-averaged adult survival estimates (SE) for snowshoe hares inhabiting mature spruce-fir forests, thinned mid-seral (MS) lodgepole pine, and early seral (ES) lodgepole pine in central Colorado, USA, summer 2006–summer 2009. Site-specific estimates and associated standard errors were averaged using the delta method (Seber 1982). Thirty-day survival estimates represent transformation of annual estimates into generic 30-day intervals.

	Year 1	Year 2	Year 3
Spruce-fir			
Summer–Winter	0.52 (0.08)	0.54 (0.07)	0.53 (0.08)
Winter–Summer	0.28 (0.05)	0.30 (0.05)	0.39 (0.05)
Annual	0.14 (0.05)	0.16 (0.05)	0.20 (0.07)
30-day	0.85 (0.02)	0.86 (0.02)	0.88 (0.03)
MS Lodgepole			
Summer–Winter	0.47 (0.07)	0.48 (0.07)	0.48 (0.07)
Winter–Summer	0.23 (0.05)	0.25 (0.05)	0.34 (0.10)
Annual	0.11 (0.03)	0.12 (0.03)	0.16 (0.06)
30-day	0.83 (0.02)	0.84 (0.02)	0.86 (0.02)
ES Lodgepole			
Summer–Winter	0.46 (0.004)	0.47 (0.004)	0.47 (0.003)
Winter–Summer	0.23 (0.002)	0.24 (0.003)	0.33 (0.01)
Annual	0.10 (0.03)	0.12 (0.03)	0.15 (0.05)
30-day	0.83 (0.02)	0.84 (0.02)	0.86 (0.02)

coefficients of horizontal cover and stem density differed from 0. For the analysis limited to early seral lodgepole sites, process variance could not be estimated, likely because it was swamped by large sampling variance. However, the coefficients and associated 95% confidence intervals in the random effects models indicated positive relationships between hare density and both the amount of early seral lodgepole surrounding the patch of interest and distance to the nearest early seral lodgepole patch. Total precipitation 1 year prior to sampling accounted for more trapping session to trapping session variation than total precipitation 2 years prior and it was positively correlated with density (Table 4).

Survival.—Habitat variables accounted for little of the variation in survival and no relationships were in the expected direction (Table 5). In the analysis limited to early seral lodgepole stands, we found evidence that survival was positively related to the amount of early seral lodgepole in the immediate landscape, and negatively related to distance to the nearest neighboring early seral lodgepole. Total precipitation in the current interval was positively associated with survival and explained a substantial portion of interval-to-interval variation in survival. Other weather variables explained little, if any variation, although the direction of the estimate for departure from normal snowfall was as predicted (Table 5).

Recruitment

In situ recruitment of juvenile hares was most consistent in early seral lodgepole sites (Fig. 3a). Juveniles were recruited into spruce-fir sites during 2 of the 3 years of the study, but were minimally recruited into mid-seral lodgepole in only 1 year (Fig. 3a). Hares immigrated into spruce-fir and mid-seral lodgepole sites during each summer to winter interval, but immigration estimates were 0 or slightly negative (i.e., emigration occurred) during winter to summer intervals (Fig. 3b). Conversely, hares tended to immigrate into early

Table 4. Variance components analysis for density estimates ($n=72$) of snowshoe hares from central Colorado, USA, summer 2006–winter 2009. Estimates were not independent of each other, so we examined effects that varied by site after fitting a fixed effect for trapping session; we examined effects that varied by session after fitting a fixed effect for site. Percentages represent estimated portion of the total process variation explained by the effect of interest, after accounting for site or session effects.

Effect	% Variation explained	Slope ($\hat{\beta}$)	95% LCL	95% UCL
After accounting for session				
Horizontal cover	60.4	0.000675	0.000232	0.001118
Stem density	34.1	0.000005	0.000001	0.000009
Canopy cover	22.6	0.043654	-0.005025	0.092333
Down wood	18.5	-0.000351	-0.000772	0.000070
Hectares of willow	8.3	0.001319	-0.000665	0.003303
Crown height	2.4	-0.013963	-0.039057	0.011131
Distance to willow	0.0	-0.000004	-0.000024	0.000016
Hectares of early seral lodgepole ^a	0.0	0.006527	0.003115	0.009939
Distance to early seral lodgepole ^a	0.0	0.000173	0.000022	0.000324
After accounting for site				
Total precipitation (1 yr prior)	58.0	0.000056	0.000021	0.000091
Total precipitation (2 yr prior)	25.5	0.000033	0.000000	0.000066

^a Random effects model run using data from early seral lodgepole stands only ($n=36$).

seral lodgepole from winter to summer. However, these inferences are very weak because of poor precision for all immigration estimates.

DISCUSSION

Snowshoe hare densities in the study area were <1.0 hares/ha and in most cases were <0.3 hares/ha. These densities correspond to those observed during the low phase of population cycles in boreal Canada (Hodges 2000*b*), but are within the usual range reported for other studies in the Rocky Mountains (e.g., Wirsing et al. 2002, Zahratka and Shenk 2008, Ellsworth and Reynolds 2009, Griffin and Mills 2009, Hodges et al. 2009) with the exception of western Wyoming where densities were higher (Berg et al. 2012). Our density estimates might have been higher had we used an abundance estimator in conjunction with a method for buffering the grid to account for lack of geographic closure, which is how other density estimates in the Rocky Mountains have been computed. Indeed, re-

calculating densities in this study area using popular $1/2$ mean maximum distance moved (MMDM) or full MMDM methods (Wilson and Anderson 1985, Parmenter et al. 2003), increased our estimates by an average of 100% and 33%, respectively. Simulations suggest, however, that such an approach is prone to positive errors, whereas the approach we used is not (Ivan et al. 2013*b*).

The generally higher hare densities we recorded in early seral lodgepole stands and mature spruce–fir compared to thinned, mid-seral lodgepole is consistent with our hypotheses and the results of other studies. Griffin and Mills (2009) reported that the highest summer densities of hares in Montana occurred in dense young stands followed by dense mature then open stands. Griffin and Mills (2007) and Homyack et al. (2007) also found that pre-commercial thinning had a negative impact on hare densities. Like Griffin and Mills (2009), we also observed lower hare densities in early seral lodgepole stands during winter compared to summer. Conversely, mid-seral lodgepole

Table 5. Variance components analysis for survival estimates ($n=72$) of snowshoe hares from central Colorado, USA, summer 2006–summer 2009. Estimates were not independent of each other, so we examined effects that varied by site after fitting a fixed effect for trapping session; we examined effects that varied by session after fitting a fixed effect for site. Percentages represent the estimated portion of the total process variation explained by the effect of interest, after accounting for site or session effects.

Effect	% Variation explained	Slope ($\hat{\beta}$)	95% LCL	95% UCL
After accounting for session				
Down wood	7.1	-0.000376	-0.000711	-0.000041
Canopy cover	3.5	-0.083534	-0.172465	0.005397
Horizontal cover	1.2	-0.000233	-0.000552	0.000086
Hectares of willow	1.2	-0.000064	-0.000156	0.000028
Distance to willow	1.2	0.000009	-0.000003	0.000021
Stem density	0.0	-0.000002	-0.000006	0.000002
Crown height	0.0	0.013311	-0.012057	0.038679
Hectares of early seral lodgepole ^a	55.6	0.001509	0.001001	0.002017
Distance to early seral lodgepole ^a	47.2	-0.000029	-0.000041	-0.000017
After accounting for site				
Total precipitation	82.0	0.000278	0.000217	0.000339
Depart normal days with snow	0.0	-0.000532	-0.002384	0.000132
Total precipitation (6-month lag)	0.0	-0.000017	-0.000070	0.000036

^a Random effects model run using data from early seral lodgepole stands only ($n=36$).

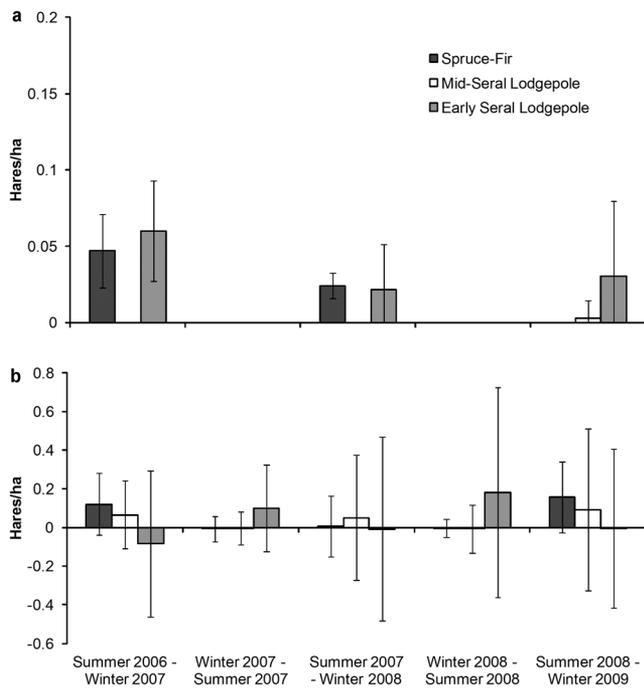


Figure 3. Recruitment of snowshoe hares (hares/ha) via in situ reproduction (a) and immigration (b) into 3 forest types in central Colorado, summer 2006–winter 2009. Negative immigration estimates indicate emigration of hares away from the forest type of interest.

stands had higher hare densities during winter. These patterns are consistent with our recruitment estimates, which indicate recruitment of hares into mid-seral lodgepole stands during the summer to winter interval, and movement into early seral lodgepole stands during the winter to summer interval.

The most obvious explanation for marked seasonal differences in density at lodgepole sites is the interaction between snow depth and tree canopy. Mid-seral lodgepole stands were mature enough that lower limbs were largely inaccessible to hares during summer, but during winter, snows brought those canopies within reach for use as browse and/or cover. Conversely, heavy winter snows exacerbated by a snow fence effect could have filled early seral lodgepole stands with snow making them less desirable. Hares in mature spruce–fir forests exhibited less dramatic seasonal changes in density, possibly because the complex structure of these stands provided cover and browse under a variety of conditions.

Beyond forest type, our analysis confirmed that variation in hare density was positively correlated with dense cover (e.g., horizontal cover, stem density), which has been shown consistently throughout the snowshoe hare literature (Hodges 2000b, Ellsworth and Reynolds 2009, Lewis et al. 2011). That precipitation during the 12 months preceding sampling explained a fair amount of variation in hare density may be related to high precipitation resulting in more herbaceous forage and cover, which promoted survival and reproduction. However, this correlation is tenuous given the short duration of the study.

In all forest types, snowshoe hare survival was highest during summer–winter and lowest during winter–summer, which we attribute to a nutritional advantage at the end of summer–winter that is reversed by the end of winter. The somewhat higher survival in spruce–fir stands than in either of the lodgepole types is consistent with higher survival for hares in dense mature forests compared to dense young or open young types described by Griffin and Mills (2009). Nutrition might partially explain the difference in survival between stands as well. Hodges et al. (2009) postulated that hares in the Yellowstone may be nutritionally stressed, especially over winter, because of the monotypic nature of lodgepole pine stands that lack a diversity of food items. We also observed that hares in early and mid-seral lodgepole stands made longer movements in all seasons compared to hares in spruce–fir, and many of these movements were through open patches with poor cover (J. Ivan, Colorado State University, unpublished data). Thus, lower survival in lodgepole pine stands could be a result poor nutrition, heavier predation, or some combination of the 2.

Survival and vegetation attributes were weakly related and largely opposite of the predictions based on previous work. We offer 2 explanations for this discrepancy. First, hares used larger areas than we anticipated at the onset of the study. Perhaps habitat measurements we made on relatively small trapping grids were not representative of the areas hares used during the study, which led to counterintuitive results. Second, we estimated survival over long time periods in which conditions covered a gradient from summer to winter. We measured habitat covariates at the endpoints of these intervals. Thus, our habitat covariates were not matched tightly to the interval we applied them. For instance, we simply used crown height as a covariate to try to explain variation in survival. However, crown height likely varied substantially as conditions changed from summer to winter, ranging from approximately 0.8 m to 0 m as snow accumulated. Had we sampled to estimate survival on a weekly basis, for example, and measured this covariate each week, the relationship may have been more meaningful.

We found both density and survival of hares in early lodgepole stands were positively associated with the amount of similar habitat in the surrounding landscape. Also, survival was negatively related to distance to the nearest similar patch. Lewis et al. (2011) also noted that hare density was positively related to the amount of good habitat in the landscape surrounding the patch of interest. Thus, in areas where early seral lodgepole is maintained for snowshoe hare and lynx conservation, juxtaposition may be an important consideration.

No combination of survival and recruitment estimates from any forest type in any year would result in a self-sustaining population. This is somewhat unsurprising given that we sampled during an apparent population decline, but it is not consistent with the partial recovery we observed, especially considering that we sampled purportedly good hare habitat. Annual and 30-day survival estimates were within the range of values reported elsewhere for hares (e.g., Hodges 2000b, Hodges et al. 2001, Griffin and Mills 2009); survival early in

the study was closer to rates reported for populations known to be in decline, whereas survival later in the study was consistent with rates reported for increasing populations (Hodges 2000*b*). This suggests that recruitment estimates, at least in the last year of the study when the population apparently began to recover, were too low. The first of our 3 summer sampling sessions started in mid-July each year, corresponding to the timing of the second birth pulse of hares in the area (Dolbeer and Clark 1975). Juveniles born during this pulse may have been unavailable for capture during initial summer sampling sessions. Given that second litters are often larger than first litters (Dolbeer and Clark 1975, Griffin and Mills 2009), and during recovery hares are more productive than usual (Krebs et al. 2001*a*), we may have missed a substantial number of juvenile hares. Furthermore, in some years, third litters are possible in Colorado (Dolbeer and Clark 1975). If third litters were produced in August, we likely under-sampled those juveniles to a greater degree than the second litter as sampling concluded a short time after they were born. However, given that we sampled replicates of each forest type evenly throughout the summer, relative differences in recruitment among forest types are probably representative even if overall recruitment was underestimated.

We observed a decline in hare densities at our spruce-fir and early seral lodgepole study sites, followed by a partial recovery. Coincidentally, research crews that were snow-tracking lynx throughout the Core Reintroduction Area in southwest Colorado noted apparent declines in snowshoe hare tracks at the same time. This seemingly widespread decline in hare density may have had important ramifications for Canada lynx ecology and management in Colorado. Colorado Parks and Wildlife documented reproduction by reintroduced lynx from 2003 to 2006, which included the first summer of snowshoe hare research presented here (Shenk 2009). Anecdotal information suggests that statewide hare populations were high during those years (T. Shenk, Colorado Division of Wildlife, unpublished data). No reproduction was recorded during the 2 summers of apparent hare decline during this study, but reproduction resumed following winter 2009 (Shenk 2009) when hare populations apparently began to recover. This association is purely correlative and suffers from the lack of a long time series. However, it has been shown elsewhere (e.g., Brand et al. 1976, Poole 1994) that snowshoe hares play a critical role in successful reproduction by lynx. Our results suggest that may be the case in Colorado as well.

This study is one of the first in the Southern Rockies in which site-specific density and demography of snowshoe hares were simultaneously quantified during both summer and winter across several forest types and across several years. We used multiple data sources simultaneously in the analysis to improve precision of estimates. Such an approach provides an accurate assessment of the full complement of vital rates necessary to properly evaluate forest types with respect to snowshoe hare ecology. We temper our findings with the recognition that sampling covered a relatively small area, and we did not choose sites randomly, which precludes any

statistical inference beyond those areas sampled. Despite these limitations, our results clearly show that snowshoe hare density and recruitment were uniformly low in thinned, mid-seral lodgepole pine. Hares reached their highest densities and recruited juveniles most consistently in early seral lodgepole stands, followed closely by spruce-fir. Survival was highest in spruce-fir stands. Thus, of the 3 forest types we sampled, early seral lodgepole pine and late seral spruce-fir provided the best habitat for snowshoe hares, and these stand types should be the priority for those charged with managing forests for snowshoe hares. We note, however, that early seral lodgepole stands occupied only 6,167 ha in the study area, whereas mature spruce-fir stands occupied 62,512 ha. Similarly, spruce-fir forests encompass twice the area of lodgepole pine forests statewide (Buskirk et al. 2000) and only a portion of statewide lodgepole pine stands are early seral. Furthermore, the complex structure of late-successional spruce-fir forests can potentially provide hare habitat for many decades, whereas the dense structure of early seral lodgepole stands is more ephemeral. Thus, although some metrics of snowshoe hare population performance favor early seral lodgepole, the sheer area covered by spruce-fir, combined with the longevity with which it may provide habitat, make it a priority resource for hares.

MANAGEMENT IMPLICATIONS

We conclude that timber management for snowshoe hares in central Colorado should focus on maintenance of mature spruce-fir forest on the landscape, as well as early seral lodgepole pine. In either case, management practices that encourage dense understory cover within these stands are likely to benefit snowshoe hares. Because early seral lodgepole pine often occurs as small (<5 ha) patches within a matrix of poor habitat, juxtaposition likely affects hare density. We found that both density and survival of hares inhabiting early seral lodgepole stands were related to the amount of similar stands in the adjacent landscape. Existence of only 1–2 early seral lodgepole patches in an area, or many patches that are far apart, may not provide good habitat for hares.

ACKNOWLEDGMENTS

K. Wilson, B. Romme, P. Doherty, D. Freddy, C. Bishop, and P. Lukacs provided helpful insight on the design of this study. We appreciate the invaluable logistical support provided by M. Jackson, A. Haines, J. Spritzer, K. Spetter, M. Michaels, G. Engler, D. Winkelman, B. Diamond, C. Parmeter, K. Dixon, L. Wolfe, L. Baeten, J. Gammonley, D. Freddy, C. Bishop, J. Vayhinger, and B. Bibles. The following hardy individuals collected the data presented here: B. Burkholder, M. Cuzzocreo, B. Gerber, B. Marine, A. Behney, P. Lundberg, K. Yale, B. Shielke, C. VanStratt, M. Watrobka, M. Goss, S. Blake, K. Rutz, R. Saltmarsh, J. Sinclair, E. Wilson, M. Levine, M. Strauser, G. Davidson, L. Yandow, R. Sattler, C. Cummins, D. Fraser, M. Ratchford, M. Petriello, C. Soria, R. Stitt, S. Ryan, E. Newkirk, K. Heinrick, M. Strauser, D. Miles, C. Brown, G.

Merrill, B. Dickman, B. Buckley, S. Murphy, C. Vanbianchi, and C. Nelson. K. Wilson, P. Doherty, W. Rommey, S. Mills, and an anonymous reviewer greatly improved early drafts of this manuscript. Funding was provided by Colorado Parks and Wildlife.

LITERATURE CITED

- Ausband, D. E., and G. R. Baty. 2005. Effects of precommercial thinning on snowshoe hare habitat use during winter in low-elevation montane forests. *Canadian Journal of Forest Research* 35:206–210.
- Barker, R. J. 1997. Joint modeling of live-recapture, tag-resight, and tag-recovery data. *Biometrics* 53:666–677.
- Barker, R. J. 1999. Joint analysis of mark-recapture, resighting and ring-recovery data with age-dependence and marking-effect. *Bird Study* 46:82–91.
- Beauvais, G. P. 1997. Mammalian responses to forest fragmentation in the central and southern Rocky Mountains. Pages 177–199 in R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker, editors. *Forest fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, USA.
- Berg, N. D., E. M. Gese, J. R. Squires, and L. M. Aubry. 2012. Influence of forest structure on the abundance of snowshoe hares in western Wyoming. *Journal of Wildlife Management* 76:1480–1488.
- Brand, C. J., L. B. Keith, and C. A. Fischer. 1976. Lynx responses to changing snowshoe hare densities in central Alberta. *Journal of Wildlife Management* 40:416–428.
- Brown, J. K. 1974. *Handbook for inventorying downed woody material*. United States Forest Service, Washington, D.C., USA.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second edition. Springer, New York, New York, USA.
- Burnham, K. P., and G. C. White. 2002. Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics* 29:245–264.
- Buskirk, S. W., W. H. Romme, F. W. Smith, and R. L. Knight. 2000. An overview of forest fragmentation in the southern Rocky Mountains. Pages 3–14 in R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W. L. Baker, editors. *Forest fragmentation in the Southern Rocky Mountains*. University Press of Colorado, Boulder, USA.
- Cottam, G., and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37:451–460.
- Devineau, O., T. M. Shenk, G. C. White, P. F. Doherty, P. M. Lukacs, and R. H. Kahn. 2010. Evaluating the Canada lynx reintroduction programme in Colorado: patterns in mortality. *Journal of Applied Ecology* 47:524–531.
- Dolbeer, R. A., and W. R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. *Journal of Wildlife Management* 39:535–549.
- Ellsworth, E., and T. D. Reynolds. 2009. Snowshoe hare (*Lepus americanus*): a technical conservation assessment. United States Department of Agriculture Forest Service, Rocky Mountain Region, Moscow, Idaho, USA.
- Foresman, K. R., and D. E. Pearson. 1999. Activity patterns of American martens, *Martes americana*, snowshoe hares, *Lepus americanus*, and red squirrels, *Tamiasciurus hudsonicus*, in westcentral Montana. *The Canadian Field-Naturalist* 113:386–389.
- Franklin, A. B., D. R. Anderson, and K. P. Burnham. 2002. Estimation of long-term trends and variation in avian survival probabilities using random effects models. *Journal of Applied Statistics* 29:267–287.
- Griffin, P. C., and L. S. Mills. 2007. Precommercial thinning reduces snowshoe hare abundance in the short term. *Journal of Wildlife Management* 71:559–564.
- Griffin, P. C., and L. S. Mills. 2009. Sinks without borders: snowshoe hare dynamics in a complex landscape. *Oikos* 118:1487–1498.
- Hodges, K. E. 2000a. The ecology of snowshoe hares in northern boreal forests. Pages 117–161 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, USA.
- Hodges, K. E. 2000b. Ecology of snowshoe hares in southern boreal and montane forests. Pages 163–206 in L. F., Ruggiero K. B., Aubry S. W., Buskirk G. M., Koehler C. J., Krebs K. S., McKelvey, and J. R., Squires, editors. *Ecology and conservation of lynx in the United States*. University Press of Colorado, Boulder, USA.
- Hodges, K. E., R. Boonstra, and C. J. Krebs. 2006. Overwinter mass loss of snowshoe hares in the Yukon: starvation, stress, adaptation or artefact? *Journal of Animal Ecology* 75:1–13.
- Hodges, K. E., C. J. Krebs, D. S. Hik, C. I. Stefan, E. A. Gillis, and C. E. Doyle. 2001. Snowshoe hare demography. Pages 141–178 in C. J. Krebs, S. Boutin, and R. Boonstra, editors. *Ecosystem dynamics of the boreal forest: the Kluane project*. Oxford University Press, New York, New York, USA.
- Hodges, K. E., L. S. Mills, and K. M. Murphy. 2009. Distribution and abundance of snowshoe hares in Yellowstone National Park. *Journal of Mammalogy* 90:870–878.
- Homyack, J. A., D. J. Harrison, and W. B. Krohn. 2007. Effects of precommercial thinning on snowshoe hares in Maine. *Journal of Wildlife Management* 71:4–13.
- Ivan, J. S. 2011. Density, demography, and seasonal movement of snowshoe hares in central Colorado. Dissertation, Colorado State University, Fort Collins, Colorado, USA.
- Ivan, J. S., G. C. White, and T. M. Shenk. 2013a. Using auxiliary telemetry information to estimate animal density from capture-recapture data. *Ecology* 94:809–816.
- Ivan, J. S., G. C. White, and T. M. Shenk. 2013b. Using simulation to compare methods for estimating density from capture-recapture data. *Ecology* 94:817–826.
- Keith, L. B. 1964. Daily activity pattern of snowshoe hares. *Journal of Mammalogy* 45:626–627.
- Kendall, W. L., R. J. Barker, G. C. White, M. S. Lindberg, C. A. Langtimm, and C. L. Peñaloza. 2013. Combining dead recovery, auxiliary observations and robust design data to estimate demographic parameters from marked individuals. *Methods in Ecology and Evolution* 4:828–835.
- Kendall, W. L., J. D. Nichols, and J. E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* 78:563–578.
- Kendall, W. L., K. H. Pollock, and C. Brownie. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* 51:293–308.
- Krebs, C. J., R. Boonstra, S. Boutin, and A. R. E. Sinclair. 2001a. What drives the 10-year cycle of snowshoe hares? *Bioscience* 51:25–35.
- Krebs, C. J., S. Boutin, and R. Boonstra. 2001b. *Ecosystem dynamics of the boreal forest*. Oxford University Press, New York, New York, USA.
- Koehler, G. M. 1990. Snowshoe hare, *Lepus americanus*, use of forest successional stages and population changes during 1985–1989 in North-central Washington. *Canadian Field-Naturalist* 105:291–293.
- Lenth, R. V. 1981. On finding the source of a signal. *Technometrics* 23:149–154.
- Lewis, C. W., K. E. Hodges, G. M. Koehler, and L. S. Mills. 2011. Influence of stand and landscape features on snowshoe hare abundance in fragmented forests. *Journal of Mammalogy* 92:561–567.
- Malaney, J. L., and J. K. Frey. 2006. Summer habitat use by snowshoe hare and mountain cottontail at their southern zone of sympatry. *Journal of Wildlife Management* 70:877–883.
- Miller, M. A. 2005. Snowshoe hare habitat relationships in northwest Colorado. Thesis, Colorado State University, Fort Collins, USA.
- Nichols, J. D., and K. H. Pollock. 1990. Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. *Ecology* 71:21–26.
- Nudds, T. D. 1977. Quantifying the vegetative structure of wildlife cover. *Wildlife Society Bulletin* 5:113–117.
- Otis, D. L., K. P. Burnham, G. C. White, and D. R. Anderson. 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monographs* 62:7–135.
- Parmenter, R. R., T. L. Yates, D. R. Anderson, K. P. Burnham, J. L. Dunnum, A. B. Franklin, M. T. Friggens, B. C. Lubow, M. Miller, G. S. Olson, C. A. Parmenter, J. Pollard, E. Rexstad, T. Shenk, T. R. Stanley, and G. C. White. 2003. Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. *Ecological Monographs* 73:1–26.
- Pledger, S. 2000. Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics* 56:434–442.

- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* 46:752–757.
- Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. *Journal of Wildlife Management* 58:608–618.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. Second edition. Charles Griffin & Company LTD, London, England.
- Shenk, T. M. 2006. Post-release monitoring of lynx (*Lynx canadensis*) reintroduced to Colorado. Colorado Division of Wildlife, Fort Collins, USA.
- Shenk, T. M. 2009. Post-release monitoring of lynx (*Lynx canadensis*) reintroduced to Colorado. Colorado Division of Wildlife, Fort Collins, USA.
- Thornton, D. H., J. W. Aaron, D. R. James, and L. M. Dennis. 2012. Complex effects of site preparation and harvest on snowshoe hare abundance across a patchy forest landscape. *Forest Ecology and Management* 280:132–139.
- U.S. Fish and Wildlife Service. 2000. Endangered and threatened wildlife and plants: determination of threatened status for the contiguous U. S. distinct population segment of the Canada lynx and related rule, final rule. *Federal Register* 65:16052–16086.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893–901.
- White, G. C. 2008. Closed population estimation models and their extensions in Program MARK. *Environmental & Ecological Statistics* 15:89–99.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* (46 Suppl):120–138.
- Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. *Journal of Mammalogy* 66:13–21.
- Wirsing, A. J., T. D. Steury, and D. L. Murray. 2002. A demographic analysis of a southern snowshoe hare population in a fragmented habitat: evaluating the refugium model. *Canadian Journal of Zoology* 80:169–177.
- Zahratka, J. L. 2004. The population and habitat ecology of snowshoe hares (*Lepus americanus*) in the southern Rocky Mountains. Thesis, The University of Wyoming, Laramie, USA.
- Zahratka, J. L., and T. M. Shenk. 2008. Population estimates of snowshoe hares in the southern Rocky Mountains. *Journal of Wildlife Management* 72:906–912.

Associate Editor: Amy Kuenzi.

APPENDIX A. VEGETATION SAMPLING

To characterize forest types and generate covariates for explaining variation in density or survival of hares, we systematically sampled structural attributes of each replicate site at 15 of the 84 trap locations (or 9 of the 42 trap locations for early seral lodgepole sites) using protocols developed from previous lynx and hare work in the region (Zahratka 2004, Shenk 2006). Specifically, at each sampled trap location we measured 1) stem density, 2) canopy cover, 3) horizontal cover, 4) crown height, and 5) down wood. We estimated stem density by measuring distance from the trap location to the nearest stem 1.0–7.0 cm diameter. We then applied the closest individual method of Cottam and Curtis (1956) to convert these measurements to density. We estimated canopy cover using vertical densitometer (Geographic Resource Solutions, Arcata, CA) readings from a subsample of 25 points centered at the trap location. We measured both canopy cover and stem density at heights of 0.1 m and 1.0 m above the ground to capture summer and winter conditions, respectively. We used a cover board (read from a distance of 6 m) to characterize horizontal cover in 0.5-m increments from 0 m to 2 m above ground (Nudds 1977). We measured crown height as the distance from the ground to the lowest live branch on the nearest tree. We estimated metric tons of down wood (≥ 2.54 cm in diameter) per hectare according to Brown (1974). We averaged all structural measurements across the 15 (or 9) trap sites to characterize the site.

In addition to these structural covariates, we also considered landscape attributes as potential explanatory variables as well. Thus, we quantified the hectares of willow and early seral lodgepole within the landscape around each site (landscape defined by a buffer around the trapping grid equal to the 90th percentile of the maximum movements of all hares from their respective grids during a given season; approx. 1,000 m) along with the distance to the nearest patch of each.

Table A. Structural characteristics of mature spruce-fir, even-aged small lodgepole, and thinned, even-aged mid-seral lodgepole stands that we sampled for snowshoe hare density and demography, central Colorado, summer 2006–winter 2009. Estimates represent means (SD) from $n = 3$ mature spruce-fir, $n = 3$ mid-seral lodgepole, and $n = 6$ early seral lodgepole sites. We obtained values for each site by averaging measurements from systematic subsampling at $n = 15$ (spruce-fir, mid-seral lodgepole) or $n = 9$ (early seral lodgepole) trap locations within each site. Note that all measurements are summarized here to give a complete picture of study site attributes. However, we used only a subset of these measurements as covariates for modeling density and/or survival.

Characteristic	Spruce-fir	Mid-seral lodgepole	Early seral lodgepole
Horizontal cover 0.0–0.5 ^a	69.7 (8.1)	37.1 (11.6)	53.7 (9.7)
Horizontal cover 0.5–1.0 ^a	37.4 (4.1)	25.3 (9.7)	56.6 (10.2)
Horizontal cover 1.0–1.5 ^a	24.4 (1.4)	22.3 (4.5)	56.6 (12.4)
Horizontal cover 1.5–2.0 ^a	31.3 (3.5)	27.9 (6.5)	65.6 (14.9)
Summer stem density 1–7 cm ^{b,c}	3,618 (1,046)	1,431 (912)	4,467 (1,808)
Summer stem density 7–10 cm ^{b,c}	577 (63)	151 (83)	1,117 (469)
Summer stem density >10 cm ^{b,c}	1,679 (401)	1,600 (198)	647 (317)
Winter stem density 1–7 cm ^{b,d}	1,366 (492)	332 (69)	2,966 (1,427)
Winter stem density 7–10 cm ^{b,d}	586 (129)	173 (79)	920 (621)
Winter stem density >10 cm ^{b,d}	1,465 (274)	1,447 (347)	527 (301)
Summer canopy cover (%) ^c	64.9 (2.7)	49.6 (8.0)	52.3 (5.8)
Winter canopy cover (%) ^d	56.6 (3.5)	45.3 (10.0)	46.2 (6.9)
Crown height (m) ^e	0.65 (0.21, 1.29)	0.83 (0.48, 1.16)	0.53 (0.23, 0.64)
Down wood ^f	57.7 (26.2)	47.7 (9.4)	24.5 (11)
Snow depth year 1 (m)	0.77 (0.31)	0.49 (0.13)	0.47 (0.14)
Snow depth year 2 (m)	1.37 (0.25)	1.07 (0.13)	0.97 (0.12)
Snow depth year 3 (m)	0.97 (0.12)	0.7 (0.13)	0.69 (0.14)

^a Percent of coverboard obstructed by vegetation in 0.5-m increments up to 2 m.

^b Stems/ha in 1–7, 7–10, and >10 cm diameter classes.

^c Summer measurement taken 0.1 m above ground.

^d Winter measurement taken 1.0 m above ground.

^e Median (25th percentile, 75th percentile) height from ground to lowest live branches. Median and percentiles were based on pooled data from all replicates within a stand type.

^f Metric tons/ha of down wood ≥ 2.54 cm in diameter.