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LANDSCAPE ECOLOGY OF SNOWSHOE HARES IN MONTANA

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For the degree of

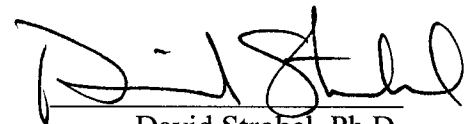Doctor of Philosophy, Fish and Wildlife Biology

The University of Montana

January 2004

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Landscape Ecology of snowshoe hares in Montana

Graduate Committee Chair: L. Scott Mills, Ph.D. _LSm_

This is an inquiry into landscape-level population dynamics in the snowshoe hare, *Lepus americanus*, using empirical field data to test ecological theory. We found evidence supporting a source-sink dynamic, the mechanism proposed to explain why snowshoe hare populations appear not to cycle in fragmented forests of the species southern range. We estimated birth, death, and movement rates for snowshoe hares that lived solely, or in mixtures of, 4 different categories of forest stand structure (FSS) type. We validated the use of ultrasonography as an effective tool to monitor fetal number and pregnancy rate. We sampled individual patterns of FSS type occupancy, which we used as covariates in survival and emigration models. Estimated survival rates decreased as individuals spent proportionally more time in the Open young and Open mature FSS types. The Dense young and Dense mature FSS types were potential "sources." Dense mature had positive expected population growth, which was lower in models that included movement. Open mature and Open young FSS types were "sinks." For a model landscape with a simplified model for succession, and where Dense mature forest was prevalent, snowshoe hare populations stayed higher when loss of high-quality patches was asynchronous.

We used an experiment to test for short-term effects of pre-commercial thinning (PCT) on snowshoe hare densities. Compared to control stands, snowshoe hare densities declined after standard prescription (100% of stand area) PCT; and in stands treated with pre-commercial thinning with reserves (PCT-R), where 20% of the total area was retained in uncut ¼ ha patches. Declines were prominent in the second winter after treatment. Snowshoe hares used retained patches more than thinned areas within PCT-R stands. Also, of 49 dead radio-collared snowshoe hare locations, none were in extremely densely vegetated microhabitats.

Predation risk influenced snowshoe hare movement behavior: snowshoe hares' responses to moonlight corresponded to seasonal variation in moonlight intensity. When the moon was more than half full and the ground snow-covered, predation rates were higher and snowshoe hare movement distances were lower than near new moons. Neither predation rate nor movement rate varied when the ground was snow-free.

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for Orion & Sue

for Scarlett & friends

Acknowledgements

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Chapter 1. Landscape ecology of snowshoe hares: motivations and directions

This dissertation is a research inquiry into landscape-level population dynamics in the snowshoe hare, *Lepus americanus*. Snowshoe hares are an attractive model organism for studies of demography because their generally short life cycle makes them tractable, and because they have been well studied in the north of the species range (reviewed in Hodges 2000). They are an attractive species for landscape ecology studies because their population dynamics are thought to be influenced by processes within single forest stands, and by routine movements or dispersal connecting separate forest stands. Snowshoe hares are also important for forest and wildlife management because of their central role in the diet of the threatened Canada lynx, *Lynx canadensis* (U. S. Fish and Wildlife Service 2000), and other forest carnivores.

The unifying question in this dissertation is, what are the relative impacts of intra-patch birth and death rates, and inter-patch immigration and emigration rates [vital rates], in multi-habitat landscapes? Snowshoe hare populations cycle regularly with high amplitude in the north, but may not cycle at all in the contiguous United States and southern Canada (Wolff 1980, Keith 1990, Hodges 2000). Long before metapopulation (Levins 1969, Gilpin and Hanski 1991) and source-sink (Pulliam 1988, Pulliam and Danielson 1991) theories were in vogue, the lack of regular, high-amplitude cycles in the southern range of the snowshoe hare was essentially explained as a result of source-sink processes in a heterogeneous landscape, with the prediction that low-quality habitats interspersed with high quality habitats prevent a synchronous buildup of hare populations over large areas (Howell 1923).

I tested these hypotheses by estimating differences in snowshoe hare habitat-specific fertility, survival, and movement rates in several forest stand structure [FSS] types. I then compared patterns of population growth against those predicted by various landscape-scale hypotheses of population dynamics. Experimental manipulation gave me additional insight into the effects of habitat heterogeneity as I asked what impact a sudden habitat change (via pre-commercial thinning) has on snowshoe hares. Finally, simulations that included a simplified model for succession indicated that habitat patch arrangement and the timing of habitat disturbance can influence population growth.

Overview of the dissertation

Estimating pregnancy rates and litter size in many animal species is difficult, but it was necessary for me to evaluate these components of fertility in different habitats. Newborn snowshoe hares (leverets) are nearly impossible to count after parturition because they are cryptic, and mothers attend to them only once per day (Rongstad and Tester 1971). In Chapter 2, I present and validate a new, relatively non-invasive, field technique for estimating snowshoe hare fertility rates: veterinary ultrasonography (Griffin et al. in press). This work resulted from close collaboration with Dr. Leslie Bienen.

My analysis of projected population growth rates in single forest stands and connected landscapes connected by movement is presented in Chapter 3 (Griffin and Mills, in preparation). For large or isolated local populations, intra-population birth and death rates may determine growth or decline, but when a landscape is made of patches that vary in quality and proximity, movements between patches can play a large role (Harrison 1994, Hanski and Simberloff 1997, Thrall et al. 2000). In support of the dominant paradigm that explains the apparent lack of cycles in southern snowshoe hare

populations (Howell 1923, Wolff 1980, 1981, Keith et al. 1993), I found that a source-sink dynamic does operate, such that low quality sink FSS types can prevent the population from growing to high densities over large areas. I also introduce a new framework for considering the relative value of different patch types in spatially structured populations, the "habitat rank" hypothesis.

In Chapter 4 I test for changes in density after experimental manipulation of vegetation structure, via pre-commercial thinning (Griffin and Mills in review). Pre-commercial thinning is a widespread practice in which the majority of small trees in a stand are cut in order to increase the growth rates of the young trees that remain (Daniel et al. 1979, Johnstone 1984), and to increase the frequency of favored tree species (Carey and Johnson 1995). I found that pre-commercial thinning does cause strong declines in snowshoe hare density in the 2 years after stand treatment, especially in winter. A modified prescription that leaves 20% of the stand in uncut 50 m x 50 m 'aggregate retention' patches maintained somewhat higher snowshoe hare density than prescription with uniform thinning; this modified prescription may be useful for areas where snowshoe hare retention is a management priority.

In chapter 5 I use spatially-explicit population simulation software (Akçakaya 2002) and a simple successional model to ask how the timing and distribution of vegetation structure change might influence snowshoe hare population dynamics (Griffin and Mills 2004). Landscape-level population growth was a function of processes within patches and movement between patches. I found that the arrangement and timing of vegetation structure change in the landscape did influence population trajectories, but the model for vegetation successional change may have driven the simulation outcomes.

Two topics related to my central research question are explored in appendices; for these, I motivated the research questions and study designs, and guided the field work, analysis and writing. In Appendix A (Griffin et al. in review) my coauthors and I tested and supported the predation risk hypothesis (Lima and Bednekoff 1999) by examining the influence of moonlight on snowshoe hare movement and predation rates. Only in winter was moonlight highly variable, and that was also when the moon modulated predation risk and hares correspondingly reduced movements. In Appendix C my coauthors and I show that no dead radio-collared hares were found in the densest of microhabitats available in the forested study site, while they were found with greater prevalence than available in extremely open habitats (Pouderoux et al. in preparation).

Considerations, and future directions for snowshoe hare studies in Montana

Any study of snowshoe hares must consider the possibility that observed demographic rates could result from large-scale population cycles, and not from proximate covariates such as vegetation structure. Over the course of studies at the Seeley Lake study sites I observed a regional decline in snowshoe hare density from 1999 – 2001 (Chapter 3, Figure 2). It is possible that the drought that started in 1999 (and which led to a disastrous fire seasons in 2000) contributed to the decline. Alternately, some undetermined cyclic mechanism may have played a role, but our data do not indicate a regionally synchronous increase in density in later years. Densities at the Spring Creek site had not increased by the end of my study, but they increased in 2002 at the Placid site and in 2003 at the Inez site. Five years is too short a period to determine whether or not snowshoe hare populations cycle in Montana. That conclusion can only be made after many years of monitoring. I look forward to the results.

Chapter 2. Estimating pregnancy rates and litter size in snowshoe hares using ultrasound

Abstract: Accurate estimates of pregnancy rate and litter size are essential to many studies of population dynamics. We examined the use of ultrasound for estimating pregnancy rate (the proportion of pregnant females in a population) and litter size and for monitoring fetal development and survival in snowshoe hares (*Lepus americanus*). We compared ultrasound-based estimates of fetal number in 16 females to either radiographic estimates of fetal number for the same females, or to the number of newborn hares counted after parturition. With ultrasound we detected fetuses as small as 4 mm and at least 25 days before parturition. Ultrasound-based estimates of fetal number were correct for 8 hares, low by 1 fetus for 6 hares, and high by 1 fetus for 2 hares. Sequential ultrasound examinations detected change in fetal size and position, and detected ceased or abnormal fetal development in 2 hares. Ultrasonography is an effective, minimally invasive tool to monitor fetal number and pregnancy rate. Application of the technique to other species would require familiarity with internal anatomy and training in operation of the ultrasound machine.

Key words: *Lepus americanus,* litter size, pregnancy rate, snowshoe hare, wildlife ultrasonography

Ultrasonography is widely used in zoo and traditional veterinary medicine but is less often used in wildlife field studies, despite its potential as a valuable tool. Because fat and intestinal contents are the main confounding factors when counting fetuses with ultrasound, estimates should be more accurate in wild animals than pets or livestock because wild animals generally have less body fat. Obtaining an estimate of minimum

fetal number in wild animals allows comparison of pregnancy rates and minimum litter sizes across different habitats, years, and management treatments.

Population dynamics of snowshoe hares (*Lepus americanus*) are the focus of recent attention in the southern part of their range because they are the primary prey of the Canada lynx (*Lynx canadensis*), listed as threatened in the contiguous 48 states (United States Fish and Wildlife Service 2000). Snowshoe hares give birth to as many as 4 litters per summer (Severaid 1942, Keith 1990). In the northern range, the number of offspring per female per breeding season varies from 7.5 in the decline phase of the cycle to 17.9 in the late increase phase (Cary and Keith 1979). Conception occurs immediately post-parturition (Severaid 1942, Bookhout 1964, Keith 1990) in a synchronous birth pulse (Hodges 2000*a*), with a gestation period of 34–37 days (Keith 1990).

Traditionally, litter sizes were estimated using methods such as abdominal palpation (Cary and Keith 1979), holding females in captivity until parturition (O'Donoghue and Krebs 1992), and necropsy of sacrificed pregnant females to count corpora lutea scars (corpora albicans; Bookhout 1964, Cary and Keith 1979). Each technique has advantages and disadvantages. Abdominal palpation requires no expensive equipment and reliable detection of pregnancy with palpation has been reported 8 or 10 days after coitus (Bookhout 1964, Kieth et al. 1968), but we have not found publications validating its accuracy in assessing litter size in snowshoe hares. Palpation has the potential to damage or dislodge fetuses, particularly if performed at critical stages of placental development (Harkness and Wagner 1995); it requires a gentle technique (Short 1967), and early in gestation it can be difficult to distinguish fetuses from digestive organs (Tainturier 1988). Holding females in captivity for prolonged periods can produce significant, chronic stress

levels, which can affect observed litter size at birth (Hillyer and Quesenberry 1997). Necropsy can not provide information about changes in fetal number or viability during the course of a pregnancy, is not acceptable in long-term studies at low population size when survival and density parameters are estimated from marked animals, and poses ethical conflicts. Radiography with X-rays yields precise estimates of litter size but is not practical for widespread diagnosis of pregnancy and fetal number unless gestational stage of the females are known because fetuses can only be visualized late in gestation, after the fetal skeleton has mineralized.

In domestic rabbits the use of ultrasound to diagnose pregnancy is now widespread (Cubberly et al. 1982, Inaba et al. 1986, Tainturier 1988, Beregi et al. 2000) and minimally invasive (Beregi et al. 2000), although it does require specialized equipment, training, and anesthesia. To complement long-term demographic studies of snowshoe hares in western Montana, we assessed the accuracy of abdominal ultrasound in determining litter size by comparing ultrasound estimates of fetal number to estimates using late-term radiographs and to counts of newborn hares born to females held in captivity for short periods of time.

Methods

In the summers of 2000 and 2001, we live-trapped adult female snowshoe hares in the Seeley Lake region of western Montana. We limited this research to the second and third birth pulses; litter size in the first birth pulse is consistently small (Keith 1990). We housed captive hares in 76 x 76 x 41 cm hutches on a forest litter substrate. We fed captive hares apple, common wild plants, and commercial pellets. We shaded cages with cloth and branches and hung an interior curtain for hare cover (Carol Stefan, University

of British Columbia, personal communication). We released animals that met objective stress indications (weight loss, self-injury, hair pulling, or pacing) or subjective criteria (inappetence or aggression).

In 2000, we held seven females in captivity 15–23 days, and held 3 captive at a forested site 6–9 days. Of these, we could use 6 to test ultrasound-based litter size estimates via comparison to X-ray radiography (5 hares) or necropsy (1 hare); we released the other 4. In 2001, we held captive in forested sites 12 females that were identified as likely within 10 days of parturition via ultrasonography, until they gave birth; we released 2 of these after 7 days to minimize stress to the mother. Thus, sample size for evaluation of ultrasound was 16 hares for 2000 and 2001 combined.

We anesthetized hares prior to all ultrasound and radiologic exams. Five of 33 exams in 2000 were performed using isoflurane gas (Isoflurane USP, Schein Pharmaceutical, Phoenix, Ariz.) administered with a mask but no regulated delivery system; all other exams followed intramuscular injections of 9.4 mg/kg ketamine (Ketalar, Parke-Davis Pharmaceutical, Morris Plains, N.J.) and 1.75 mg/kg xylazine (Rompun, Bayer Pharmaceutical, New Haven, Conn.) given in the epaxial muscles. These low doses provided sedation for 30–50 min. We were concerned with potential effects of injectable drugs on fetal development, so in 2001 we used only regulated isoflurane gas. Isoflurane has the advantage over nonreversible injectable drugs in that, when applied at low flow rates, the animal regains consciousness < 5 min after the gas is turned off (Thurmonn et al. 1996). We placed each hare in an anesthesia box with 3–4% isoflurane flow rate until the hare was sedate, then applied a mask connected to a

vaporizer and flow meter (Ohmeda, Madison, Wisc.; $900 used), maintaining 1–2 % flow of anesthetic gas.

We shaved anesthetized hares on the ventral abdomen from pubic bone to the most caudal rib prior to ultrasound examinations. We performed examinations with hares in dorsal recumbency, using a Universal SonoVet 600 veterinary ultrasound machine and a 6.5 MHz microconvex probe (Universal Medical Systems, Bedford Hills, N.Y.; $12,000 new). We obtained estimates of fetal number by counting separate echogenic masses inside the body and horns of the uterus (Figure 1), following each horn craniolaterally until the lumen was no longer visible. We measured each fetal mass in cross-section at its largest diameter, by measuring from the dorsal edge of the fetus to the junction of the fetus and the uterine wall on the ventral aspect of the uterus. This method provided consistent measurements within each exam and allowed us to monitor fetal growth between ultrasound exams. Later in gestation we measured longitudinal spine lengths and cranial diameter of fetuses to estimate both fetal number and gestational stage (Figure 2). Only 1 ultrasound operator (L. B.) measured fetuses and estimated litter size in all examinations.

For ventrodorsal radiologic exams in 2000, we used high-speed, high-contrast film with a rare earth detail cassette and a MinXRay 803G portable x-ray machine (MinXRay Inc., Northbrook, Ill.; $3,200 used), at settings of 70kVp, 30mA, and 0.06 sec with a focal distance of 76 cm. For 5 hares, radiographic estimates of fetal number were made in the radiology program at Tufts University School of Veterinary Medicine by counting individual fetal skulls. Fetal number also was determined by necropsy in a sixth hare in 2000 after she died, most likely due to unregulated isoflurane anesthesia.

To minimize the length of time females were held captive in 2001, we used ultrasound to approximate gestational stage of all females captured. Later-term fetuses were distinguished with ultrasound by their size and the relative development of skull, limbs, and vertebral column. Only females with very late-term fetuses were put into captivity. We recorded total litter size born to captive females within 24 hr of parturition. We estimated the earliest point in gestation when fetuses were visible based on females that gave birth in captivity and were examined early in pregnancy.

We assessed the bias of ultrasound-based litter size estimates by comparing ultrasound estimates to the observed number of fetuses visualized on late-term radiographs, counted after parturition or in necropsy. We examined 1 female that gave birth to 5 leverets with ultrasound twice, with ultrasound-based estimated litter sizes of 4 and 5; to be conservative when analyzing the accuracy of ultrasound as a technique, we used the incorrect ultrasound estimate.

We used Akaike's Information Criterion (AIC; Akaike 1973, 1974; Burnham and Anderson 1998) to compare 4 models against the data to assess fit. Models differed only in the expected values of litter size; observed litter size was the number of fetuses or newborns counted by radiography or after birth of the litter. Three models, "Accurate," "Negative bias," and "Positive bias" had expected values of litter size that were, respectively, the number seen on ultrasound examinations, one fetus higher, or one fetus lower. A fourth model, "Average," had only 1 expected value that was the mean litter size recorded for all hares in the study, using radiography or observed litter size at birth. The AIC value for each model was 2 X the number of parameters plus 2 X the negative

log likelihood. We calculated model likelihood as a product of the likelihood of all 16 pairs of expected and observed values, given a Poisson distribution.

Results

We correctly determined the pregnancy status (pregnant or nonpregnant) of all females examined, as evidenced by fetal development detected with radiography or by parturition. We successfully detected fetuses of known gestational stages 25 d before parturition (9–12 d after coitus); these were 8, 9, 11, and 13 mm in cross-sectional diameter. The smallest measured fetus in a female of unknown gestation stage was 4 mm; by comparison, Bookhout's (1964) 9-day old embryos were 3.5 mm on average in necropsy. Sibling fetuses measured with ultrasound varied in size, as has been noted in previous studies (Bookhout 1964). Growth curves for fetuses of known age (Figure 2) indicated that, based on our small sample size, fetal cross-sectional diameter was a more reliable indicator of gestation stage early in pregnancy; this measure was also the most reliable of fetal age in small companion animals (Mattoon and Nyland 1995). Late in gestation spinal length had a more predictable relationship to age than did head circumference.

Ultrasonography was a reliable technique for estimating minimum litter size; differences between estimated litter size and observed litter size did not exceed 1 fetus. Mean bias of ultrasonography for the 16 females was –0.375 because our predictions were low by 1 fetus for 8 hares, were correct for 6 hares, and were high by 1 fetus for 2 hares. The estimated bias was not the same at 3 realized litter sizes, but there was not a systematic pattern of greater bias at more extreme litter sizes. The average bias for litter size 3 was +0.4, at litter size 4 it was –0.71, and at litter size 5 it was –0.2. Practically,

this means the most common mistake was for females actually carrying 4 fetuses; they often were estimated to have only 3 with ultrasound.

The best model to explain the relationship between our estimates and the observed values of litter size was 1 where estimates equal litter size ("Accurate" model). A model where our estimates were low by 1 fetus ("Negative bias") fit our data well, with differences in AIC (ΔAIC) of 0.0209. The model for litter size that used the mean of litter sizes counted by radiography or at birth ("Average") also fit the data well (ΔAIC = 1.54); models with ΔAIC < 2 are considered to have roughly comparable levels of parsimonious fit to the data (Burnham and Anderson 1998). The comparable fit of these 3 models to our data indicated that ultrasound was generally accurate or biased low by 1 fetus; simply guessing that each female had litter size identical to the average observed (via radiography, necropsy, or at birth) would have been comparably accurate to ultrasound. This last estimation procedure, though, presupposed knowledge about the average litter size (such data require some means of observation).

We obtained reliable estimates of fetal number from diagnostic-quality X-ray radiographs for 5 hares and from necropsy for 1 hare. In the necropsy true diameters of 3 fetuses were within 1.4 mm of diameters estimated by ultrasound, and their locations within the uterus corresponded to the positions estimated from the ultrasound exam. A fourth fetus present in the right uterine horn was not detected on ultrasound exam due to its extremely distal position, where it was more likely to be confused with intestinal contents.

Discussion

Ultrasonography can provide detailed, safe, and demographically useful information about the parameters of female fertility that potentially affect population dynamics of snowshoe hares. These parameters are pregnancy rate in a particular geographic area, habitat, or time span, the number of fetuses in early pregnancy, and the development of fetuses in late pregnancy.

All females with fetuses visible by radiology or evidenced by parturition were correctly diagnosed as pregnant by ultrasonography. Ultrasonography in particular is a good choice of technique if the pregnancy status or gestational stage of the animal is not known because ultrasound can reliably identify and measure fetuses at small sizes; in snowshoe hares we identified fetuses as small as 4 mm. Predictive growth curves for fetuses visualized with ultrasound (Figure 2) can be improved in the future as more studies record fetal size in litters with known parturition dates.

Measurements made with ultrasound can be used to identify late-term pregnant females, to minimize time in captivity until parturition. If parturition in rabbits is delayed 3 days beyond the mean gestation interval, fetuses can grow abnormally large and may die (Harkness and Wagner 1995). In 2001, 10 of 12 pregnant females identified as late-term gave live birth in captivity, with all 40 leverets born surviving to detection.

It is easier to determine pregnancy status of an animal than to count the precise fetal number. Identifying pregnancy rate alone answers some research questions. Interestingly, in 2001 we noted low pregnancy rates in the third birth pulse period across a large region of western Montana (Griffin, Bienen and Mills, unpublished data), a

pattern that parallels pregnancy rates during the low phase of the 10-year cycle in the north (Cary and Keith 1979).

As long as ultrasonographic examinations are carried out by a trained individual, ultrasound-based estimates of litter size can be used as highly reliable estimates of the minimum values and reasonable estimates of true values. The "Accurate" and "Negative Bias" models both fit our data better than the "Positive Bias" model, suggesting that our ultrasound-based estimates were generally either correct or low by 1 fetus. Although overestimation of litter size can occur with ultrasonography, it was clearly not a source of systematic bias. The other model that had an equally good fit to the data, "Average" assumed that litter size was equal for all females and required accurate knowledge of the true value for mean litter size that could only be accurately obtained by widespread sacrifice or late-term radiography of many hares in a study site. Because litter size can vary so widely (Cary and Keith 1979), average values for litter size can not be assumed to stay constant among years or habitats. As a result, using the "Average" model would not allow for comparison of fecundity across birth pulses or habitats.

Identifying fetuses using ultrasound requires correct identification of the uterus and careful examination of the contents of the uterine horns from the caudal to cranial ends. For this reason, researchers applying ultrasound to any wildlife species must be familiar with the internal anatomy of their study organism and should be trained in the recognition of other echogenic structures that might be confused with fetuses, such as fecal material and kidneys. The training period for L. B. included 10 days of training in the ultrasound department of a university hospital with no particular emphasis on diagnosing pregnancy and 5 hours of training from an equipment salesperson. We expect the training period

would be short for other practicing veterinarians who have some experience with ultrasonography. For other users, veterinary schools and ultrasound machine manufacturers offer 2–3 day short training courses in the use of ultrasound for abdominal examinations, including pregnancy diagnosis, for $800–1500. Following such a course the operator should practice with captive pregnant hares or rabbits until competency before use in the field.

Both ultrasonography and palpation can potentially be used to estimate litter size in animals captured at various stages of gestation, thus allowing for estimates of fetal resorption rates in animals captured and examined more than once. In contrast to palpation, ultrasound potentially provides more detailed information about gestational stage via precise measurement of fetal anatomical structures, verification of fetal viability by detecting heartbeats, and is considered less invasive. The high costs of equipment, the specialized training required to differentiate internal anatomical structures, and the need to administer anesthetics to pregnant animals are all disadvantages to the use of ultrasound. Ultimately, the choice of technique for a given study may depend on the level of acceptable risk to fetuses, the need for assessing the viability of fetuses counted, and the confidence of individual researchers in manual versus visual estimation.

In the southern part of the snowshoe hare range, where habitat may be more varied than in the north (Howell 1923, Dolbeer and Clark 1975, Wolff 1980), the existence of a cycle is controversial (Hodges 2000b) and there is little information about litter size variation across habitats or years. Along with more traditional methods, ultrasonography is 1 more tool that wildlife biologists could use to establish or refute the existence of regular cycles of fecundity corresponding to those observed in the northern range. The

ability to compare litter sizes across habitats could help to identify the habitat features associated with high and low reproductive rates for a variety of wildlife species.

Figure captions

Figure 1. View from an ultrasound examination showing cross-sectional width of a snowshoe hare fetus in the left uterine horn of a snowshoe hare. The measured diameters between both pairs of "+" cursors and "x" cursors were 9 mm.

Figure 2. Three different measures of fetal size made with ultrasound (y-axis) are regressed against days before parturition (x-axis) for fetuses in 10 hares that gave birth in captivity. Squares and the lowest regression line represent cross-sectional diameter of individual embryos ($r^2 = 0.68$; $P = 0.00029$). Triangles and the middle line represent measures of head circumference ($r^2 = 0.02$; $P = 0.42$). Diamonds and the highest line represent measured spinal length ($r^2 = 0.19$; $P = 0.031$).

Figure 1.
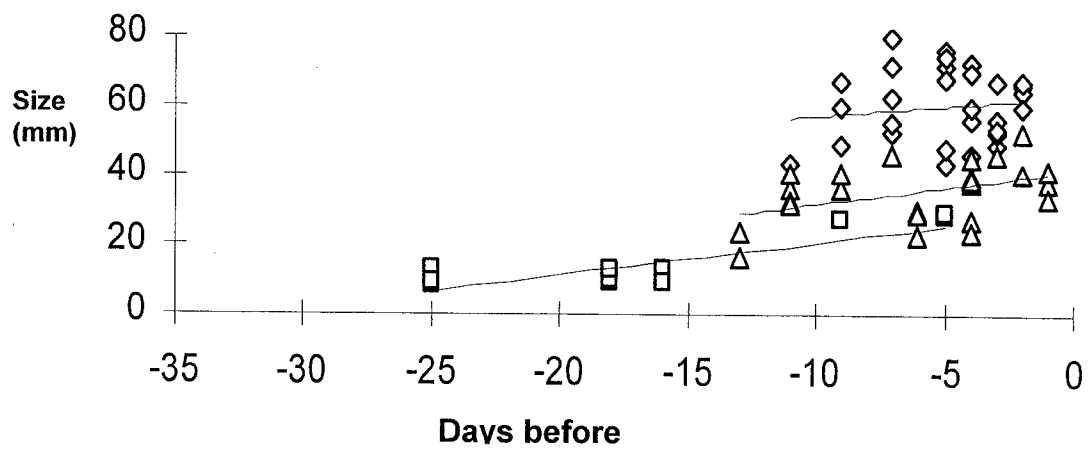
Figure 2.

Chapter 3. Snowshoe hare demography in heterogeneous southern landscapes

Abstract

We tested predictions of the source-sink, pseudosink, balanced dispersal, and habitat rank hypotheses, evaluating the effects of spatial structure on patch-level and landscape-level dynamics in the snowshoe hare, *Lepus americanus*. Differences in estimated survival rates supported a source-sink dynamic, which has been proposed to explain why snowshoe hare populations appear not to cycle in the fragmented forests of the species southern range. We estimated birth, death, and movement rates for snowshoe hares that lived solely in, or in mixtures of 4 different categories of forest stand structure (FSS) type. We monitored radio-collared snowshoe hare movements and sampled individual patterns of FSS type occupancy, which were used as covariates in survival and emigration models. Estimated emigration rate was highest during fall and winter. Estimated survival rates were lowest in Open young and Open mature FSS types, and were higher in Dense young and Dense mature FSS types. Post-weaning juveniles had slightly lower estimated survival rates than adults, and all hares had lower estimated survival in spring and fall than in summer and winter. Based on our samples; fertility rates may have been slightly lower in the Dense mature FSS type, but both newborn survival and fertility rates from the four FSS types had overlapping confidence limits. Population growth projection models without dispersal indicate that the Open young and Open mature FSS types had negative expected population growth. Survival rates in the Open mature and Open young FSS types were so low that these types appear to be permanent sinks. When emigration and immigration were included in a simple landscape, population growth projections followed predictions of the source-sink model. The FSS type with positive projected

growth in the absence of dispersal had decreased projected growth when dispersal was included, while the FSS types with strongly negative projected growth in the absence of dispersal had increased projected growth when dispersal was included. Our results indicate that movement between patches of different quality could indeed depress density and prevent the widespread and synchronous buildup of snowshoe hare density associated with cycles.

Key words: balanced dispersal, demography, habitat rank, habitat use, landscape ecology, Montana, pseudo-sink, refugium model, source-sink, survival

Introduction

The realization that spatial arrangement of natural habitats can have widespread impacts on local and regional population dynamics, genetics, and community structure has emerged from metapopulation theories and empirical studies (Hanski and Simberloff 1997, Thrall et al. 2000). Understanding the relative influences of intra-patch and inter-patch processes on overall population dynamics can yield insights for conservation and management (Harrison 1994, Hanski and Simberloff 1997, Tilman and Lehman 1997, Davies et al. 2001, Mills and Lindberg 2002).

Across multiple spatial scales, the discrete time measure of expected population change, λ, is the best indicator of spatial structuring of population dynamics. $\lambda_{Individual}$ is an index to the expected fitness of that individual when compared to the average $\lambda_{Individual}$ in the population (McGraw and Caswell 1996). When landscapes are composed of multiple patch types (e.g. Levins 1969, Gilpin and Hanskii 1991, Noon and McKelvey 1996, Thomas and Kunin 1999) λ_{Patch} is an indicator of patch quality. If the population of each patch is closed to movements to and from each patch, then $\lambda_{Single\ Patch}$ depends

only on local birth and death rates. If emigration and immigration rates are specified then $\lambda_{Multiple\ patch}$ can be estimated for patch types when movement between patches is allowed, and $\lambda_{Landscape}$ can be estimated for landscapes composed of connected patches (Caswell 1989, Wooton and Bell 1992, Burgman et al. 1993, Gyllenburg et al. 1997).

Several theoretical models make predictions about the influences of intra-patch and inter-patch processes on the overall dynamics of spatially-structured populations, but tests comparing these models against empirical data have been rare (Diffendorfer 1998). Under the source-sink hypothesis (Pulliam 1988, Pulliam and Danielson 1991), sources are defined as patches in which reproduction exceeds mortality, so that $\lambda_{Single\ Patch} > 1$ in the absence of dispersal (Table 1). Mortality exceeds reproduction in sinks, so that in the absence of dispersal, $\lambda_{Single\ Patch} < 1$. A prediction of the source-sink hypothesis is that the population in the overall landscape is stabilized by the flow of individuals from sources to sinks, such that $\lambda_{Single\ Patch} > \lambda_{Multiple\ Patch}$ for sources and $\lambda_{Single\ Patch} < \lambda_{Multiple\ Patch}$ for sinks. Thus, dispersal rates must be estimated to assess patch-level dynamics, because a patch with stable abundance measures may be a sink, maintained solely because of an influx of immigrants (Holt 1985, Dias 1996, Diffendorfer 1998). The pseudo-sink hypothesis (Watkinson and Sutherland 1992) predicts that a third kind of local patch dynamic could exist in pseudo-sinks, which could persist without immigrants at low density, but which appear to be sinks when immigration elevates the abundance above carrying capacity. The balanced dispersal hypothesis (McPeek and Holt 1992) contrasts with the source-sink and pseudo-sink hypothesis because it posits that $\lambda_{Multiple\ Patch}$ is equivalent across all patches. Two critical predictions of this hypothesis are that: the emigration rates for multiple patches are inversely proportional to the ratio of their

carrying capacities; and that sinks do not exist. Differentiating the source – sink and psuedo-sink hypotheses from each other and from the balanced dispersal hypothesis is difficult because it requires estimates of patch-specific birth, death, emigration and immigration rates (Diffendorfer 1998).

One important process often missing from analyses of the dynamics of spatially structured populations is temporal variation in growth rates, which implies that $\lambda_{Single\ Patch}$ will generally not be static for a given patch (Dias 1996, Thomas and Kunin 1999, White 2000). For example, $\lambda_{Single\ Patch}$ might exceed one for all habitats in 'good' years, or be less than one in all habitats in 'bad' years. Even if this is the case, some patches may be consistently more favorable than others. To explain systems with systematic differences in the rank of $\lambda_{Single\ Patch}$ we propose a fourth hypothesis for spatially structured populations, 'habitat rank.' This hypothesis predicts that, despite temporal variation in λ, the same habitat type will always have the highest relative $\lambda_{Single\ Patch}$ among a set of patch types (Table 1).

Snowshoe hares in the southern geographic range

Snowshoe hares – whose regular 9 – 11 year cycles in the northern range (north of the U.S. – Canada border) make them the 'poster child' for population studies (Elton 1924, Elton and Nicholson 1942, Moran 1953, Keith 1983, Keith 1990, Krebs et al. 1995, Krebs et al. 2001) – are an ideal species for testing for the effects of spatial structure on population dynamics. The montane and subalpine forests of the southern range are fragmented by elevation and moisture gradients, fire, insect outbreaks and, more recently, industrial forest management. Populations appear either not to cycle in the southern range, or to cycle irregularly, or with only low amplitude (Keith 1990, Hodges 2000a,

Murray 2000). Long before metapopulation (Levins 1969) and source-sink (Pulliam 1988, Pulliam and Danielson 1991) theories were formalized, Howell (1923) proposed that source-sink dynamics prevent snowshoe hare populations in the fragmented forests of the southern range from cycling. The proposed mechanism, also later suggested by Dolbeer and Clark (1975), Wolff (1980, 1981), and Keith et al. (1993), predicts that source habitats consistently produce a net surplus of hares, but low reproduction and / or high mortality in sink habitats prevents the landscape-level population from synchronously building in density over large regions. Predictions of this dominant paradigm connecting snowshoe hare spatial structure to regional population dynamics, dubbed the 'refugium model' by Wolff (1980, 1981), have remained untested because no studies to date have simultaneously examined all the vital rates necessary to evaluate the existence of sources and sinks in the snowshoe hare's southern range.

Most formulations of population structure invoke discrete patches separated by a hostile matrix (Levins 1969, Noon and McKelvey 1996, Hanski 1997, Bjørnstad et al. 1998) but snowshoe hare behavior in a fragmented landscape requires consideration of a second important process not often addressed in studies of spatial dynamics: individuals repeatedly move between and use adjacent patches over short time periods. Attempts to synthesize the effects of multiple patch use on individual, patch, and population dynamics have been rare (Weins 1997). For species that do move frequently between different patch types, the simplifying assumption that observed vital rates are specific to one patch type could yield misleading conclusions about the effects of spatial pattern on population dynamics. If survival and reproduction are partially functions of the risks and resources

found in multiple habitats, then demographic models should incorporate the effects of using multiple patches at the spatial scale of individuals, patches, and landscapes.

We collected data to test whether any of the four hypotheses linking spatial structure to population dynamics (Table 1) operate and could potentially explain the dampened cycles in southern snowshoe hare populations. We used birth and death rate estimates to test whether $\lambda_{Single\ Patch}$ varies across discrete forest stand structure (FSS) types ($\lambda_{Single\ FSS}$), or when individuals use mixed proportions of different FSS types. We then included emigration and immigration rate estimates in a simple model to test whether movement between discrete patches influences $\lambda_{Multiple\ Patch}$ (or $\lambda_{Multiple\ FSS}$)and depresses $\lambda_{Landscape}$.

Methods

Forest Stand Structure types, study sites, and seasons

To simplify the diversity of stand histories, successional stages, stem densities, and species compositional mixes typical of montane coniferous forests in Montana, we chose a subset of 4 distinct FSS types from opposing ends of the ranges of age and tree stem density (Table 2; Dense mature, Dense young, Open young, and Open mature FSS types). Snowshoe hares are often considered to be early-successional species because they seem most abundant in young (20-45 years), dense stands providing ample cover and conifer needle forage (Adams 1959, Wolfe et al. 1982, Buehler and Keith 1982, Litvaitas et al. 1985a). It has also been suggested, however, that mature stands (>150 years old and with average DBH > 30 cm) that have dense forest understories may also be important for local hare populations (Beauvais 2000, Buskirk et al. 2000). In contrast to the dense young and dense mature FSS types, open young and open mature FSS types with less

horizontal and / or vertical cover have generally lower recorded hare density (Dolbeer and Clark 1975, Wolff 1980, Wolfe et al. 1982, Hodges 2000b). In the field we classified stands that fit into these 4 types based on sampled vegetation structure for sapling density, basal area, horizontal cover, and overhead canopy cover (Appendix 1). Stands not fitting in one of the 4 FSS categories were not targeted for study.

Long-term study site selection was based on the presence of large stands (over ~30 ha) from each of the 4 target FSS types in close proximity (within 1.5 km of one another). For logistical reasons we further constrained site selection so that all stands were within 1 km of a forest road. We used air photos of the Seeley-Swan region to choose three study sites: Inez (~ 4,600 m el.), Placid (~ 4,000 m el.), and Spring Creek (~ 5,400 m el.) (Figure 1). We sampled vegetation structures to confirm that stands at each site fit into the 4 FSS categories. The 3 sites were 22 - 30 km from each other. At these distances, local processes at 1 site should not have influenced the others, but weather patterns could have influenced all three simultaneously.

We differentiated four seasons which varied in duration according to our understanding of snowshoe hares and weather in the region. For survival analyses we considered winter to be 16 weeks (~13 December to ~2 April), a time when snow was likely to cover the ground completely. Spring (~3 April to ~25 June), summer (~26 June to ~17 September) and fall (~18 September to ~ 12 December) were each 12 weeks long.

Trapping and density estimation

We used live traps (Tomahawk Trap Co., Tomahawk, WI) to capture snowshoe hares for 3 purposes: density estimation, radio-collar placement, and fertility rate estimation. When trapping to estimate density in a particular FSS type stand (Mills et al.

in review), we arranged 50 live traps in a 5 by 10 grid, with traps 50 m apart. The resulting 200 m by 450 m rectangular trapping grid fit within each stand with a buffer of 50 m or more. We trapped 4-6 days on all FSS sites at a site simultaneously, checking traps every morning. We baited traps with apple, alfalfa, and horse pellets. Hares were ear tagged (National Band and Tag Co., KY), weighed, and sexed.

In the summers of 1998 and 1999 we trapped at each grid in three primary sessions, each composed of 5 or more secondary sessions. We trapped twice at each grid in the summer of 2000. In summer 2001, 2002, and 2003 we trapped for density estimation during a single 5-day session at each grid. Winter trapping with 5-day primary sessions began at Inez and Spring Creek in the winter of 1999-2000, and included all three sites in 2000-2001 and 2001-2002. We used the Lincoln-Petersen estimator with small sample size correction (Chapman 1951) for abundance estimation because in many cases we had low capture rates and because we could increase the number of individuals per sample by pooling trap nights into two sample periods (Mills et al. in review). We estimated the effective trapping area for each trapping grid based on the mean maximum distances moved (Wilson and Anderson 1985, Litvaitis et al. 1985b, Karanth and Nichols 1998) by individual hares recaptured during single trapping periods (Mills et al. in review).

We used the time series of density estimates to estimate the observed mean growth rate for snowshoe hares inhabiting each trapping grid, $\lambda_{FSS\ Observed}$. This was a measure that complemented the detailed vital rate estimation necessary for projecting population growth in each FSS type; the estimated $\lambda_{FSS\ Observed}$ values for each FSS type, and the corresponding $\lambda_{Site\ Observed}$ values for the composite growth at each site, could be

compared to those from a projection model for $\lambda_{\text{Multiple FSS}}$ and $\lambda_{\text{Landscape}}$ that included

movement between FSS types. $\lambda_{\text{FSS Observed}}$ for each trapping grid was evaluated as the

geometric mean of the observed annual growth rate in population density, (D_{t+1}/D_t). We

used only the first estimated density value from every summer, because only adult

snowshoe hares were caught in these trapping sessions. In calculating $\lambda_{\text{Site Observed}}$, which

reflected the average overall annual population growth rates at each site, the estimated

site density for each summer was the summed total of estimated hare abundance in the 4

FSS types, divided by the summed total of the effective trapping areas for the 4 trapping

grids.

Telemetry

The Inez site was selected for intensive study with radio telemetry after

simulations indicated that high sample sizes would be necessary to detect survival

differences between FSS types, even at one site. Of the 3 sites, the Inez site had highest

observed snowshoe hare abundance. To increase the sample of radio-collared hares we

trapped extensively and repeatedly on permanent trapping grids and on auxiliary trap

lines over ~ 5.3 km^2 of the site and throughout the study period. Juvenile and adult hares

over 500g were radio-collared with 30 g (Biotrack Ltd., U.K.) or 40 g (AVM Instrument,

CA; Holohil Ltd., Canada) transmitters. Transmitters were equipped with motion-

sensitive 'mortality switches' that took effect after 6-10 hours of motionlessness. The 4

target FSS types occupied most of the Inez study site, but early successional riparian

vegetation structures were found in small patches over ~ 4 % of the site. We pooled hare

locations from these stands structures with the dense young FSS type because they were

dominated by young aspen trees and alder shrubs less than 10 cm DBH.

Snowshoe hares are generally crepuscular or nocturnal (Keith 1964, Mech, Heezen and Siniff 1966, Foresman and Pearson 1999, Hodges 1999), so in addition to locating radio-collared hares in their daytime hiding locations, we located hares as often as possible between dusk and dawn. We did not record a location if radio signals indicated a hare was moving away from us as we approached. UTM coordinates for all locations were recorded with handheld GPS recorders (<10 m inaccuracy). GPS data collected before April 2000 were differentially corrected, using GeoExplorer (Trimble Navigation Ltd., CA). If it was not recorded at the time when a hare was located in the field, we used GIS to specify the FSS type for each hare location point (Appendix 2).

We determined the majority of snowshoe hare locations by sight (n > 1664), or heard transmitter signals without an antenna (n > 1050), indicating location error of <15 m (N. Olson and P. C. Griffin, unpublished data). Because of the high accuracy, relative to the distances snowshoe hares typically move, we preferred the walk-in method of locating hares. However, we triangulated 204 snowshoe hare locations from June - August 2000; coordinate positions were estimated using program TelLoc7 (G. McDaniel, U.S. Forest Service, Missoula, MT, unpublished). For the 204 triangulated locations, mean location uncertainty was 46 m (S.E. = 2.0 m), based on the location error method (Zimmerman & Powell 1995) using data from a field trial with 43 triangulations of known-location radio-collars (Griffin and Waroquiers, unpublished data).

Movement, Emigration, and Immigration

We calculated the maximum displacements between all points where each individual was located within a given season, and over all dates monitored. These displacements were an index to the total area spanned by each hare, including movements

within home ranges and dispersal events. We tested for variation in the maximum displacement distances that hares moved, according to season and animal age, and used the distribution of observed displacements to estimate the spatial scale of the population. A second measure of movements, home range size, is an indication of the area covered by an animal's routine movements. If home ranges are smaller in a particular FSS type, then that might indicate that that is a relatively more productive habitat, where essential food, cover, and water resources are available in a smaller area. We estimated the home range size of every radio-collared hare with 3 or more recorded locations using the minimum convex polygon (MCP) estimator (Mohr and Stumpf 1966). Because MCP home range estimates are sensitive to the number of locations (Jennrich and Turner 1969), we controlled for the number of locations when testing for correlations between the proportion of locations in each FSS type and estimated home range area.

Season, age, sex, and cover type are biologically reasonable covariates to include in models for snowshoe hare emigration (Dolbeer and Clark 1975, Boutin et al 1985, Wirsing et al. 2002, Gillis and Krebs 2000). We used program MARK (White and Burnham 1999) to test a suite of models that either did or did not include effects of these covariates on emigration rate for each FSS type (E_{FSS}), the annual proportion of individuals permanently dispersing from a FSS type. We used known fate data from 141 radio-marked adult and juvenile hares compiled in 36 4-week periods, during which each monitored hare was recorded as having stayed or having emigrated. We only wanted to estimate emigration rate based on the animals being monitored in any given 4-week period, so individuals were recoded as emigrated during the period when they emigrated, and were right-censored if the animal died or was lost from telemetry. We diagnosed

emigrants as radio-collared hares that permanently dispersed greater than 500 m in one direction, a distance more than 2 times the diameter of a reasonably large (20 ha) home range (Hodges 1999). For adults, because natal location was not known, to be operational our criterion required 5 or more locations prior to dispersal to detect a > 500 m shift in home range. The same locations provided individual covariate values for each hare's proportional use of each FSS type, based on the assumption that the locations were reliable samples from the individual's trajectory of habitat use.

Known fate models usually estimate survival rate, but our models were estimating (1 − emigration) for 4 -week periods, so we converted these parameter estimates to annual emigration rates. Emigration rates for 4-week intervals in each FSS type (E_{FSS}) were estimated by model averaging the parameter estimates from models with $\Delta AICc$ (Burnham and Anderson 1998) values less than 4 (Table 4). Model averaging weights the parameter estimates coming from each model by the relative likelihood of the model, given the data (Burnham and Anderson 1998). We did not include covariates with model-averaged covariates that had 95% confidence intervals overlapping zero. For projection models where landscapes included the 4 FSS types, emigration rate for the total population ($E_{Landscape}$) was estimated as the average of the E_{FSS} values (Table 5), weighted by the density of hares in each FSS type.

Because a majority of hares on our study site remained unmarked, it was not possible to distinguish reliably immigrants from unmarked resident hares. Therefore, for landscape projection models we made the simplifying assumptions that the overall immigration rate ($I_{Landscape}$) for a population is the same as the overall emigration rate ($E_{Landscape}$), and that the FSS type in which dispersers settle was random. The first

assumption implies that dispersers do not suffer mortality rates higher than the population at large either during or after dispersal; neither Gillis and Krebs (2000) nor Wirsing et al. (2002) found increased mortality in emigrant snowshoe hares. The second assumption implies that dispersers do not differentially select their final destinations, e.g., on the basis of habitat quality or density. We tested this second assumption against the frequencies at which emigrants settled in each FSS type, compared to the frequencies of FSS types from which they originated, using a contingency table.

Under our assumptions, the expected rate of immigration into an FSS type (I_{FSS}), can be expressed as $I_{FSS} = E_{Landscape} \times (N_{Landscape}/ N_{FSS}) \times (Area_{FSS} / Area_{Landscape})$. If E_{FSS} were equal across all FSS types one would expect stands with high hare density to lose more hares from emigration than they gain from immigration because, for the same area, low-density stands do not generate the same number of emigrants as high density stands.

Reproductive rates

Adult females at our study area could have bred in each of three synchronous pulses per summer. Fertility, defined as the number of female offspring in each birth pulse per reproductive age female, is the product of pregnancy rate and litter size. Fertility in snowshoe hares varies between birth pulses; for example in southern populations, the 1st birth pulse almost always has high pregnancy rates and litter sizes yielding between 1.1 – 1.8 female leverets in southern populations, while the 2nd and 3rd birth pulses can have lower pregnancy rates but potentially higher litter sizes (Murray 2000). Summed across the entire breeding season, fertilities range between 3.5 to 9.5 in cyclic populations (Cary and Keith 1979, Stefan and Krebs 2001) and between 3.2 to 5.8 in non-cyclic populations (Murray 2000).

We estimated pregnancy rates and litter sizes using ultrasound in 2000 and 2001 (Griffin et al. WSB in Press), based on examinations of adult females at all sites. We trapped females at each site for 3 days corresponding to the middle of each gestation period. The timing of birth pulses was determined by ultrasound examinations and observation of trapped females during the first gestation period and birth pulse, and by counting days until the next roughly synchronous birth pulses (Keith 1990). To capture additional females for fertility estimates we also trapped at 2 auxiliary sites within the Seeley-Swan region known for relatively high snowshoe hare density (sites 36 and 102; Mills et al. in review).

All adult females trapped were carried to a central examination area in the field, anesthetized and examined with a portable veterinary ultrasound imaging system (Universal Medical Systems, NY). If fetuses were detected, then the female was considered pregnant, and the litter size was the number of fetuses counted in the uterus; fetuses at least 9 – 12 days old were reliably detected (Griffin et al. in press). Additional measures of litter size came from for females held in captivity until parturition as part of a validation study (Griffin et al. in press); we counted the number of late-term fetuses counted with X-ray radiography, or the number of leverets on the morning after parturition.

To test for potential effects of site or FSS type on reproductive output, we used 95% confidence intervals to compare fertility rate estimates, using groups of females pooled by site or by FSS type. Females from the auxiliary trapping grids were included only in overall means for all sites and FSS types.

Survival rates of Leverets

Snowshoe hares wean after 4 to 5 weeks (Keith 1990). We estimated newborn snowshoe hare (leveret) survival rate up to weaning at 35 days old based on the Kaplan-Meier method and the survival histories of 41 radio-monitored newborns born to 15 females in captivity at the Inez site (Sterling et al., in prep.). That sample size of mothers was too low to test reasonably for an effect of the mother's use of different FSS types on leveret survival; estimates for each FSS type had overlapping 95% confidence intervals, but we could not assess whether this was due to a lack of difference between FSS types or due to a small sample size. For projections we applied the estimates for leveret survival rates to weaning (mean = 0.563; 95% C.I. {0.403, 0.722}) to all FSS types.

Survival rates and habitat use of adults and post-weaning juveniles

We estimated the survival rate of post-weaning juveniles (> 500g) and of adults based on the known fates of radio-collared individuals. We attempted to monitor the location and survival status of all radio-collared hares once per week, though this was not always possible (for example, we only monitored survival once, by airplane, from mid-August through September 2000 because fire precluded all access to all forest lands regionally). There were 144 7-day time periods included in the survival analysis, corresponding to dates from July 26, 1999 to April 28, 2002.

The frequent monitoring of live hares allowed us to estimate the proportion of time each hare spent in each FSS for each 7-day time period. If we located an animal twice or more in a given 7-day period, then we assumed that the animal was found in each FSS type in proportion to the fraction of locations observed (i.e., an animal observed twice in 1 type and once in a second would have estimated use of 0.67 for the first and 0.33 for the second). If no location was recorded for an animal in a 7-day period then we

assumed that it remained in the same FSS type as its last observed location. When a radio-collared hare's remains were found in a given FSS, that was also recorded as one location in that FSS. For each 7-day period, the proportion of each hare's estimated use in each FSS type was recorded as an individual covariate. With 144 7-day time periods and 5 FSS types, each animal had a vector of 720 individual covariates that represented time-specific habitat use.

For each dead hare, in addition to the UTM coordinate location of the remains and the FSS type in which they were found, we recorded the date of mortality or (if the date of mortality was not known) the date when the mortality signal was first discovered. In some cases we were able to assess the exact mortality date, based on snow accumulations or other sign at the site of the remains.

Because telemetry allowed us to determine the survival status of every animal with a radio-collar, we used known-fate model structure (Cox and Oakes 1984) analysis in program MARK (White and Burnham 1999) to estimate survival rates, with survival rates in different models potentially influenced by individual covariates. Hares were added to the data set for each time period from the first date when they were monitored with telemetry, and were right-censored if we lost their signal (e.g., due to collar failure or dispersal outside of the range of radio reception). Juveniles that survive to spring are reproductive adults, so each individual's age was coded as a dummy variable for three different time periods: June 1999 - April 2000, May 2000 - April 2001, and May 2001 - April 2002. Hare ages were coded as juvenile for all weeks in their first summer, fall, winter and spring of life. The survival input and individual covariates for each hare represented whether the animal was alive or dead in each of the 144 week-long

observation periods, sex, age, and 720 proportional use estimates for each week in each of the 5 FSS types at the Inez site.

We developed a candidate suite of models to represent competing hypotheses about the effects of season, habitat, age, and sex on survival. Each of these models potentially had survival rate estimates influenced by up to the four different seasons, the 4 FSS types, sex, and hare age. Simpler model structures pooled or omitted effects of season, sex, age, or FSS type. Any seasonal effects parameters applied across all FSS types. Some models included an effect of 2 season-groups, where spring and fall were combined and compared to summer and winter. This reflected the biological hypothesis that spring and fall could have different mortality rates than summer and winter. Several mechanisms may reduce survival in spring and fall: in both seasons hare pelage may not match background colors in the environment (Litvaitis 1991); in the fall herbaceous foliage has senesced, yet no snow gives access to higher conifer branches; in the spring nutritional may be poor while energy demands prior to reproduction increase. Sex was modeled as either having an effect throughout the year, or only during the potential reproductive and nursing season (~ 21 April to ~ 30 September). Age was modeled as an effect throughout the year.

FSS type effects applied across all seasons and were included in a variety of models. First, each FSS was modeled as its own effect, with all others pooled. Second, open FSS types were pooled and compared to dense FSS types; similarly, mature FSS types were pooled and compared to young FSS types. All survival models that included effects of FSS type included logit link functions with parameters that are multiplied by the time-specific covariates that specify use in each FSS type (Schwartz et al., in review).

In models with such parameters, the estimated survival rate for each time period is partially a function of the proportion of time spent in a given FSS type.

We used AICc to select the most parsimonious models relative to the survival data and used models with ΔAICc < 4 to estimate the weekly survival rates and the associated 95% confidence intervals for snowshoe hares living in different FSS types. Because bootstrap goodness-of-fit testing is not possible in program MARK for known fate models with individual covariates, we tested the goodness-of-fit of the most parsimonious model (Table 6, Model 1) by assuming that the deviance of the model was chi-square distributed, where deviance is –2 times the natural log of the model likelihood. For this test the degrees of freedom are equal to the number of parameters in the saturated model (with 144 time steps, 2 sexes, 2 ages, and 2 FSS types compared in any one model) minus the number of parameters in the model being tested (White and Burnham 1999).

The multiple models used to generate values for expected weekly survival included coefficients in the logit link functions that are multiplied by the proportional use of different FSS types. After model averaging, expected weekly survival could be estimated for an individual in any season, of either sex, either age, and occupying any proportion of different FSS type. Projected seasonal survival rates were weekly survival rates raised to the 12th power for spring, summer and fall, and to the 16th power for winter.

Projected growth rates for individuals, FSS types, and landscapes

We modeled expected individual growth rates for groups of snowshoe hares that varied only in the proportions of different FSS types they occupied, λ_{FSS}. The projection equation was a function of expected fertility (f), newborn survival ($S_{Leveret}$), juvenile

survival in every season ($S_{\text{Juv Summer}}$, $S_{\text{Juv Fall}}$, $S_{\text{Juv Winter}}$, and $S_{\text{Juv Spring}}$), and adult survival in every season ($S_{\text{Ad Summer}}$, $S_{\text{Ad Fall}}$, $S_{\text{Ad Winter}}$, and $S_{\text{Ad Spring}}$).

The simple model for population growth in the absence of movement did not include emigration or immigration, so it reflects the growth rate of a closed population composed only of individuals that all have the same proportional use of different FSS types.

The projection equation is the change in abundance of adults from the end of one spring to the end of the next spring. It sums the annual survival of adults and the product of adult fecundity (F_{FSS}) and annual juvenile survival.

$$\lambda_{\text{Single FSS}} =$$

$$(S_{\text{Ad Summer}} \times S_{\text{Ad Fall}} \times S_{\text{Ad Winter}} \times S_{\text{Ad Spring}}) + (F_{\text{FSS}} \times S_{\text{Juv Fall}} \times S_{\text{Juv Winter}} \times S_{\text{Juv Spring}})$$

Fecundity in the above equation is the expected number of juvenile female snowshoe hares that survive to the end of summer per adult female present at the beginning of summer. In addition to fertility in each birth pulse (f_{bp1}, f_{bp2}, f_{bp3}) the fecundity term incorporates the survival of mothers up to the birth of leverets in each birth pulse, the survival of leverets to weaning 5 weeks later (S_{Leveret}), and the survival of weaned juveniles up to the end of summer. Parturition for the 1$^{\text{st}}$ birth pulse occurs 3 weeks before the end of spring, so because the projection interval is from the end of one spring until the end of the next spring, the number of adult females alive at the start of the 1$^{\text{st}}$ birth pulse is actually greater than the number counted at the end of spring. Therefore, the adult female survival term multiplied by 1$^{\text{st}}$ birth pulse fertility is the cubed inverse of the spring weekly survival rate. Adult females must survive through 2 weeks of summer before parturition for the 2$^{\text{nd}}$ birth pulse, and through 7 weeks of summer before the 3$^{\text{rd}}$

birth pulse. Leverets born in the 1st birth pulse must survive through 10 weeks of summer after weaning, those born in the 2nd birth pulse must survive through 5 weeks of summer after weaning, and those born in the 3rd birth pulse need only survive to weaning. Thus, annual fecundity can be expressed in terms of fertility, weekly adult survival, leveret survival, and weekly juvenile survival.

$$F_{FSS} = \{ \, [\, f_{bp1} \times (1/ S_{Ad\ Spring\ Week})^3 \times (S_{Leveret}) \times (S_{Juv\ Summer\ Week})^{10} \,] \, +$$

$$[\, f_{bp2} \times (S_{Ad\ Summer\ Week})^2 \times (S_{Leveret}) \times (S_{Juv\ Summer\ Week})^5 \,] \, +$$

$$[\, f_{bp3} \times (1/ S_{Ad\ Spring\ Week})^7 \times (S_{Leveret}) \,] \, \}$$

The weekly survival values for adults and juveniles in the equation for Fecundity are potentially a function of the proportion of different FSS types used by the hares. We calculated $\lambda_{Single\ FSS}$ for each FSS type using expected survival rate and F_{FSS} values for individuals occupying only single FSS types. Noting that the fertility rates we observed in 2000 and 2001 were low, relative to other published values, we also used iterations of the projection equation to ask what increase in fertility rates would lead to stable population growth rates for a single FSS type, e.g., $\lambda_{Single\ FSS} = 1.0$. We used the same equation for $\lambda_{Single\ FSS}$ to describe the expected individual growth rate for a snowshoe hare that occupies specified proportions of different FSS types, $\lambda_{individual}$ (McGraw and Caswell 1996). The average value of $\lambda_{individual}$ across all hares in a population should be a measure of λ for the landscape at large, because individuals in the population contribute to the overall growth rate.

Projected growth in a simple heterogeneous landscape

In contrast to projections of $\lambda_{Single\ FSS}$, which rely only on survival and reproductive rates, projections of growth for one FSS type connected by movement to

other FSS types ($\lambda_{\text{Multiple FSS}}$) also require emigration and immigration rate estimates. We explored the effects of emigration and immigration on projected population growth rates for connected FSS types because: some predictions about the influence of spatial structure (Table 1) are the result of movements between patches; and because we wanted to compare projections to the $\lambda_{\text{FSS Observed}}$ and $\lambda_{\text{Site Observed}}$ values, which were estimated from real populations where movement was possible. In projecting $\lambda_{\text{Multiple FSS}}$ and $\lambda_{\text{Landscape}}$ we made a number of simplifying assumptions. First, and in contrast to our field observations, we assumed that all hares in the model population only used one FSS type during any given season, although individuals could change FSS type if they emigrated in the fall. This assumption allows the model to give insights into the effects of movement on population growth within FSS types and in the overall landscape, but limits the utility of the model because it ignores our field observations of routine movement between stands, and ignores the impact that using multiple FSS types can have on expected $\lambda_{\text{Individual}}$. Second, overall immigration rate for each FSS type (I_{FSS}) was assumed to be the total number of emigrants from the landscape, divided by the area of the FSS type; in effect, all emigrants settled back randomly in the population. Finally, we assumed that all 4 FSS types had equal areas, so that the number of immigrants was distributed equally to all FSS types.

Conceptually, the projection model yields expected number of adults at the start of the summer at time t+1, based on the number of females that occupy each of the 4 FSS types at the start of the summer in time t. All emigration and immigration was modeled to occur at the start of fall, so individuals from each FSS type had to survive through the summer before the emigration probability was applied. The projected number of adults in

a particular FSS type at time t+1 is the sum of surviving adults starting in that FSS type

that do not emigrate; their surviving offspring that do not emigrate; and adults and

juveniles from the entire population who have survived the summer in the FSS type

where they started, emigrated, and settled in that FSS type. The total number of emigrants

from each FSS type that are summed from all FSS types, distributed equally across the

FSS types at the beginning of the fall season, and who must then survive through the

spring in the FSS type of their destination is:

$$N_{emigrants\ FSS} = E \times N_{FSS} \times [(S_{Ad\ Summer}) + F_{FSS} \times (S_{Juv\ Summer})]$$

Here, E is the Emigration rate assumed to be common to all FSS types. We started our

projections with densities in the 4 FSS types in proportion to the average observed across

all 3 sites in 1998. At years 5, 10, and 15 we recorded values for $\lambda_{Multiple\ FSS}$ for each of

the FSS types and for the overall $\lambda_{Landscape}$.

Results

Snowshoe hare density

There were consistent differences in snowshoe hare density according to FSS type

at the three site replicates. The highest summer densities at each site were generally in the

dense young FSS type, and the next highest in most years and sites was in the dense

mature FSS type (Figure 2). Only stands of Dense mature FSS types consistently had

winter densities that were as high or higher than in the preceding summer. Density in

almost all trapping grids decreased from summer 1999 to summer 2003, although some

trapping grids had increased density in the summer of 2002 or 2003. Estimated average

$\lambda_{FSS\ Observed}$ in these short time series for summer densities on each trapping grid varied

according to site and FSS type (Table 3). At the Placid and Spring Creek sites, the

highest average $\lambda_{FSS\ Observed}$ estimates were in the Dense young type, while the average

$\lambda_{FSS\ Observed}$ estimate was highest in the Dense mature type at the Inez site.

Telemetry

We monitored 175 snowshoe hares with radio-telemetry at the Inez site from 26

July 1999 to 26 April 2002, recording 3240 locations. Because of staggered entry into the

study, mortality, and transmitter loss, individuals varied in the number of locations. The

median number of locations per hare at the Inez site was 10.

Movement distances, emigration, immigration

We found greater maximum movement distances for hares in the fall (730 m, S.E.

= 150 m) than in spring (430 m, S.E. = 50 m), summer (440 m, S.E. = 50 m), or winter

(420 m, S.E. = 40 m), though 95% confidence intervals of these means overlap. From the

observed distribution of annual displacements (Figure 3), 50% of maximum

displacements were < 470 m, 75% of maximum displacements were < 780 m, and 90% of

maximum displacements were < 1800 m. Therefore, the spatial scale of trapping at the ~

5.3 km^2 Inez site corresponded roughly to the scale of snowshoe hare movements.

The majority of hares monitored were located within more than 1 FSS type

(Figure 4), and movement between FSS types was common over small spatial scales. The

average proportional occupancy across all hares was 37.1% Dense mature, 29.6% Dense

young, 20.8% Open young, and 12.5% Open mature. 118 of 128 hares located 5 or more

times were recorded in more than 1 FSS type. After controlling for number of locations,

the only biologically significant correlation between MCP home range size and the

proportion of locations in an FSS type was in the Dense young FSS type (ρ = -0.227; P =

0.027). As snowshoe hares' proportional use of the Dense young FSS type increased, their observed MCP home range sizes declined.

We recorded emigration in 13 of 34 radio-collared juveniles and 7 of 107 adults with enough locations to distinguish emigration from other movement. Of these 20 emigrants, the number originating from and settling in each FSS type was: Dense mature (7 originated, 11 settled); Dense young (10 originated, 5 settled); Open young (3 originated, 2 settled); and Open mature (0 originated, 2 settled). The distribution of destinations does not differ from that of the origins (Chi-square = 4.75; d.f. = 3; P = 0.191), suggesting that at this sample size we can not discern a preferred destination for emigrants. There were 23 emigration models with AICc < 4, all of which included an effect of season, with higher estimated emigration rates in fall and winter than spring and summer. The seasonal increase in emigration rate during fall and winter was the only effect with an estimate that did not overlap zero after model-averaging. Compared to spring and summer 4-week emigration rates of 0.007 {95% C.I.: 0.002, 0.020}, 4-week emigration rate was higher by 0.020 in the fall and winter {95% C.I.: 0.016, 0.043}. Although effects of each FSS type, age, and sex were included in some of these 23 models, the beta parameter estimates for all of the FSS, age, and sex covariates implied minimal effect sizes, and all had 95% confidence intervals that overlapped zero. This meant that with our data we could not discern an influence of FSS type usage on propensity to emigrate, and we only included the effects of fall and winter on annual emigration rate in projection models. The resulting annual emigration rate was 0.205 {95% C.I. = 0.121, 0.351}. Based on the assumption that deviance was chi-square distributed, with the degrees of freedom equal to the number of parameters in a saturated

model minus the number in the model being tested, the most parsimonious emigration model had acceptable goodness-of-fit (chi-square = 183.4, d.f. = 575, P = 1.0).

Reproduction

As expected, litter sizes and pregnancy rates from 2000 and 2001 varied according to birth pulse, but 95% confidence intervals for litter size and pregnancy rate estimates overlapped across all FSS types and sites within any given birth pulse. Fertility in the first birth pulse was close to values observed in most other snowshoe hare populations that have been studied: nearly all reproductive age females were pregnant with a litter size of 3 either-sex offspring. We did not find a statistical difference in fertility rate according to FSS type for the combined second and third birth pulses (t-test, P = 0.098), although a higher sample size may have shown that fertility in Dense mature FSS type for birth pulses 2 and 3 (n = 14, mean = 2.0, S. E. = 0.49) was actually lower than in the 3 other FSS types (n = 40, mean = 2.9, S. E. = 0265). Fertility rates in birth pulses 2 and 3 at the 2 auxiliary sites (n = 25, mean = 2.56, S. E. = 0.432) seemed comparable to the 3 main study sites. Unable as we were to exclude that variation in fertility according to FSS type was a result of sampling alone, we pooled fertility rate estimates for each of the 3 birth pulses across all sites and FSS types (Table 4). The low fertility rates we observed in the 2nd and 3rd birth pulses of 2000 and 2001, and the resulting overall low fertility rates, are lower than those recorded in a previous study in Montana (Adams 1959), but similar to those recorded during the prolonged low phase of the snowshoe hare cycle in the northern range (Cary and Keith 1979; Stefan and Krebs 2001).

Adult and post-weaning juvenile survival

163 radio-collared snowshoe hares at the Inez site provided data for survival analyses. Model selection indicated that weekly snowshoe hare survival was heavily influenced by season and the FSS type occupied, and was less influenced by individual age and sex. The 12 models with the lowest AICc values all included parameters representing effects of season and FSS type (Table 5). Goodness-of-fit testing for the most parsimonious model, based on model deviance, was adequate (Chi-square = 964.4; d.f. = 1148, P = 1.0). In all cases, spring and fall were seasons with the lowest estimated weekly survival rates. Overall, the Open young and Open mature FSS types had the lowest estimated weekly, seasonal, and annual survival rates. The mean and 95% confidence interval for the weekly estimated effect of age were negative, which translated to a ~2.5 % lower annual survival rates for post-weaning juveniles than adults. Confidence intervals overlapped zero for the estimated effect of sex, indicating that sex did not greatly influence seasonal or annual survival rate.

Over the course of a season the weekly effect sizes of season and FSS on survival (Table 6) led to sizable differences in expected survival rates (Table 7). Expected spring and fall survival rates increased with the proportional use of the Dense young and Dense mature FSS types, as compared to the Open young or Open mature FSS types. Hares living exclusively within the Dense mature FSS type have survival rates with 95% confidence intervals that overlap that of hares in the Dense young FSS type, whose 95% confidence intervals overlap both other FSS types. Although survival point estimates were higher in Dense mature, comparable emigration and immigration rates across all FSS types, coupled with high hare densities that were generally observed during trapping

in the Dense young FSS type throughout the study indicate that survival in the Dense young FSS type is also relatively high.

Population projections

Variation in weekly survival rates led to large differences in the expected fecundity values and population growth rates for animals living exclusively in single FSS type in the absence of dispersal ($\lambda_{Single\,FSS}$, Table 7). Because the survival models that best fit our data did not include parameters to differentiate Open young and Open mature FSS types, several estimates (survival, fecundity, and $\lambda_{Single\,FSS}$) were the same for these 2 FSS types. Hares inhabiting multiple FSS types were also predicted to have variable $\lambda_{Individual}$ values according to their proportional occupancy of different FSS types (Figure 5). Because our estimates of survival rate were highest in the Dense young and Dense mature FSS types, $\lambda_{Individual}$ was predicted to be the highest for hares inhabiting these FSS types exclusively or in some combination. In contrast, as an individual's proportional use of either the Open young or Open mature FSS type increased, predicted $\lambda_{Individual}$ declined `markedly. The differences in projected $\lambda_{Individual}$, as a function of the proportional use of different FSS types, implicated routine movement between favorable and unfavorable FSS types as a potential cause of depressed growth rates in the overall population.

Based on the fertility rates that we observed in 2000 and 2001, only the Dense mature FSS type was predicted to have a mean positive population growth for hares living in it exclusively. Mean population growth rate projections for the Dense young FSS type would also be > 1.0 if fertility were ~ 50% higher than the observed rate – such higher estimates were recorded in an earlier snowshoe hare study in Montana (Adams 1959) – or if annual survival rates there had been modestly higher (130% of observed

rates). In contrast, for population growth rate to exceed 1.0 for hares exclusively inhabiting the Open FSS types, fertility would need to increase by 320% over the observed rate, or survival increase to 140% greater than the rate observed there.

Simple landscape model projections led to expected values of $\lambda_{\text{Multiple FSS}}$ (Table 8) that were roughly comparable to estimates of $\lambda_{\text{FSS Observed}}$ from the 1999 – 2003 time series at the Inez site (Table 3). The asymptotic value of $\lambda_{\text{Landscape}}$ predicted with the simple landscape model (0.967) were slightly lower than to the $\lambda_{\text{Site Observed}}$ average observed across the 4 FSS types at the Inez site (1.03). However, the predicted $\lambda_{\text{Multiple FSS}}$ and $\lambda_{\text{Landscape}}$ estimates from the model did not match the observed $\lambda_{\text{FSS Observed}}$ or $\lambda_{\text{Site Observed}}$ values observed at the Placid or Spring Creek sites. Not surprisingly for a model where the point estimate for projected survival was highest in the Dense mature FSS type, the proportional hare densities projected by the simple landscape model were markedly highest there (Table 8). This projection contrasted to density measures from all sites, where highest summer snowshoe hare densities were generally observed in the Dense young FSS type. The mismatch between the projected proportional densities and $\lambda_{\text{Multiple FSS}}$ growth rates under the simple landscape model (Table 8), as compared to the observed densities (Figure 2) and $\lambda_{\text{FSS Observed}}$ population growth estimates (Table 3) indicate that the Dense young FSS type is probably more valuable for snowshoe hares in reality than our rate estimates and projection models suggest.

Discussion

The central predictions (Table 1) of the source-sink model (Pulliam 1990, Pulliam and Danielson 1991) were observed in our study of snowshoe hares. The Dense mature and Dense young FSS types had high enough projected growth rates that they appeared to

be potential sources, providing a net supply of snowshoe hares that moved through and into neighboring patches. Compared to the projected $\lambda_{Single\ FSS}$ values for the Dense mature FSS type, we recorded lower $\lambda_{FSS\ Observed}$ values from density time series and also lower projected $\lambda_{Multiple\ FSS}$ values. These results suggested that 'surplus' hares from Dense mature sources were absorbed by less optimal Open FSS types. At the other extreme, the Open young and Open Mature FSS types were projected to be sinks; annual survival or fertility would need to increase dramatically for populations of hares living exclusively in these FSS types to increase in the absence of immigration.

We observed the highest densities of snowshoe hares in the Dense young FSS type, but based on the vital rates estimated, the projected point estimate for $\lambda_{Single\ FSS}$ for this FSS type was < 1. Although we can not label this FSS type a source with that result, we still conclude that this FSS type is quite valuable for snowshoe hares because of the relatively high observed survival rates there, the high observed densities and $\lambda_{FSS\ Observed}$ growth rates. With only slight increases in either fertility or survival rate, the Dense young type would have behaved as a source in projection models. We can not evaluate whether the observed low survival in the Dense young type was a result of the relatively high observed densities. If this was the case then Dense young FSS type would match the definition of pseudo-sink (Watkinson and Sutherland 1995), a habitat with low expected λ values when density is maintained at high levels by immigration. Alternately, the fertilities observed in 2000 and 2001 may have been anomalously low because of severe drought; hot summers and low-snowfall winters have been associated with low fertility rates (Keith and Meslow 1971, Cary and Keith 1979). Higher fertility rates in the 2nd and

3rd birth pulses, such as might occur after winters with heavier snowfall, could cause the Dense young FSS type to be a source.

Of the 4 models for spatial population dynamics, we can reject only the balanced dispersal hypothesis (McPeek and Holt 1992) for snowshoe hares in our study because we found that individual fitness is not equal for hares inhabiting different FSS types. Moreover, we found that $\lambda_{Individual}$ varies for hares occupying different mixtures of FSS types. Predictions of the habitat-rank hypothesis (Table 1) could not be fairly tested with our data because no models with inter-annual variation had good fit to our data for emigration or survival. The estimated vital rates for each FSS type did not vary over time, so the relative ranks of $\lambda_{Single\ FSS}$ could not change. There must be temporal variation in vital rates for FSS type ranks to potentially change; our 3 year study was apparently too short, relative to the data needed to test the habitat rank hypothesis.

Snowshoe hares in fragmented southern landscapes

A source-sink dynamic appears to exist for this southern snowshoe hare population. Our results indicate that spatial patterns of patch distribution and size can strongly influence snowshoe hare population dynamics. If the area of a landscape is dominated by sink FSS types, then dispersing hares may not survive long enough to elevate densities in nearby forest stands.

Observed snowshoe hare displacements were an index to the spatial scale of the population; of 144 observed maximum displacements, 90% were less than 1.8 km. Our analyses of survival and movement at the ~ 5.3 km^2 Inez site, therefore, matched the approximate spatial scale of an operating population. We infer, based on this fairly small spatial scale, that habitat heterogeneity in the southern range could lead to asynchronous

local dynamics if barriers more than a few km effectively separate potentially interacting groups of hares.

Do vital rates for intra-patch processes (death and birth) or for inter-patch processes (emigration and immigration) play the most significant role in the source-sink dynamic depressing $\lambda_{Landscape}$? Haydon et al. (1999) used elasticity analysis (Caswell 1989) to examine the relative importance of survival and reproductive rates on projected λ values, and found highest sensitivity for juvenile survival rates, followed by adult survival, then by fertility. For $\lambda_{Single\ FSS}$ our results suggest a similar pattern: 2nd and 3rd litter fertility rates in Open FSS types would have had to increase ~320% to cause $\lambda_{Single\ FSS} = 1$, while annual survival would have needed to increase by only ~140% for the same effect. Our simple landscape model suggests that emigration rates in all FSS types (and the corresponding immigration rates) would need to decrease by ~20% to raise $\lambda_{Landscape}$ to 1.

In assessing the relative impacts of different vital rates on landscape-scale population dynamics, one should assess the range of variability of the rates, and the possibility that multiple rates will vary (Wisdom et al. 2000). Even though changes in fertility have lower relative impact on population growth than survival, its wide variability means that even the Open young and Open mature FSS types could realize positive $\lambda_{Single\ FSS}$ when reproduction is extremely high. The fertility rates we observed are as low as those observed during the decline and prolonged low phase of the northern population cycles, and the high fertility necessary to affect population growth in Open FSS types has been recorded only during increase phases in the northern range (Cary and Keith 1979, Stefan and Krebs 2001). In contrast to fertility, we can not assess whether the

smaller increase in annual survival necessary to give Open FSS types stable $\lambda_{Single\,FSS}$ values is plausible. It may be that the vegetation structure in Open FSS types, lacking sufficient hiding cover, dooms its resident hares to chronically low survival. In a study at the Inez site examining their spatial distribution of snowshoe hare mortality sites, no dead radio-collared snowshoe hares were found in the densest of microhabitats available, but they were found with greater than available prevalence in extremely open habitats (Pouderoux et al. in preparation).

Factors influencing inference scope of these results

Our projection models used vital rate projection rates that, with the exception of weekly survival rates and monthly emigration rates, were the same for snowshoe hares inhabiting all FSS types monitored. It is worth considering whether the similar vital rates were actually are the same across FSS types, or whether we had inadequate sampling to detect differences that existed. First, our estimates of survival and emigration rate were based on observations of 163 radio-collared hares at only the Inez site, Although we can not test whether our survival and emigration estimates are a reflection of only the Inez site, we point out that the influences of FSS type were spatially replicated within the ~5.3 km^2 Inez site; each FSS type was represented by 2 or more discrete stands. Second, sample sizes in some FSS type – birth pulse combinations were low for fertility estimates. The same limitation occurred in the study that we relied on for estimates of leveret survival to weaning (Sterling et al. in prep), which had an inadequate sample for robust evaluation of FSS type effects. Nonetheless, the salient differences in $\lambda_{Single\,FSS}$ would not have been changed by slight differences in fertility or leveret survival, because $\lambda_{Single\,FSS}$

was dominated by the very low annual survival rates in Open young and Open mature FSS types.

We are cautious about the estimates of precision associated with the vital rate estimates and with the λ values that result in projection models. For example, the 95% confidence intervals of weekly and seasonal survival for Dense mature and the Open FSS types do not overlap, but in closed population projection models the confidence intervals around $\lambda_{Single\ FSS}$ estimates do overlap for all FSS types. We recognize that the estimates of precision for vital rate estimates reflect some combination of sampling and process variation, but without a longer time series or further spatial replication these sources of variation would be difficult to separate (Burnham et al. 1987, Thompson et al. 1998, Gould and Nichols 1998, Ludwig 1999, White 2000).

Empirical conclusions and implications for snowshoe hares

We used empirical data to evaluate whether survival, fertility, and emigration rates were the same or different in 4 different FSS types. Besides their usefulness for testing theoretical models that address spatial structure, our results yield some practical insights for management and conservation of snowshoe hares in their southern range.

In theory, the frequency of favorable habitats in a landscape can influence local and regional population sizes (Pulliam 1988, Pulliam and Sutherland 1991, Watkinson and Sutherland 1995, Gyllenburg et al. 1997), because of differences in local intra-population birth and death rates. Given the spatial scale of snowshoe hare populations that we observed, one strategy for maintaining some dense local populations of snowshoe hares could be to conserve clusters of favorable FSS type forest stands within $5 - 10$ km^2. Also, recognizing that an individual's proportionate use of different habitats

influences $\lambda_{Individual}$, the adjacency of Dense mature with Dense young FSS type stands would be more valuable than adjacency of either with Open FSS type stands.

The high estimated juvenile and adult survival rates yield high $\lambda_{Single\ FSS}$ for hares in Dense mature and Dense young FSS types. These also were the FSS types where we observed the highest density of snowshoe hares based on trapping and mark-recapture estimation. The high winter densities we observed in Dense mature FSS types may reflect the relatively high estimated fall survival rates there. Dense mature FSS type stands also appear valuable for long-term stability of snowshoe hares in a landscape because of their temporal stability. There are several reasons why we do not necessarily recommend that landscapes be composed entirely of Dense mature FSS type stands if a goal is achieving high snowshoe hare densities. First, we found a trend suggesting lower fertility rates for females captured in the Dense mature FSS type. Second, ~68% of radio-collared hares who were ever located in Dense mature FSS type routinely used other FSS types, indicating that some aspect of adjacent stands complements the food and cover resources available to hares in the Dense mature FSS type. For example, it is possible that herbaceous plants and conifer needles in the Dense mature FSS type may be less nutritious than in FSS types where levels of sunlight in the understory and available soil nutrients are higher. Despite these caveats, our results indicate that Dense mature forest stands may be as favorable for snowshoe hares as stands of the Dense young FSS type; indeed, point estimates of $\lambda_{Single\ FSS}$ were actually higher for Dense mature. Because Dense mature stands have longer residence time than early forest successional stages, they could play a role as "refugia" of high-quality habitat over longer time periods than Dense young stands.

Stands of the Dense young FSS type should continue to be considered important for snowshoe hare population dynamics because they appear to have high snowshoe hare carrying capacity and abundant food and cover resources. The highest observed snowshoe hare densities at all sites were generally in the Dense young FSS type. Survival rates were high, and fertility may have been higher than in the Dense mature type. As further indication of the high productivity of Dense young stands, home ranges were smaller in the Dense young FSS type than in any other FSS type. In efforts to maintain high prey densities for Canada lynx, stands of the Dense young FSS type have rightly been targeted for conservation, because highest snowshoe hare densities have been observed there (U.S. Fish and Wildlife Service 1999). Regenerating forest stands are in young successional stages for only a short time, however, while Dense mature FSS type stands are presumably closer to an ecological steady state (McKelvey et al. 2000). We conclude that both Dense young and Dense mature FSS types are valuable for elevating snowshoe hare density in the landscapes of the southern range. Future studies should evaluate whether landscapes dominated by these favorable FSS types sustain snowshoe hare densities high enough to trigger the complex cyclic dynamics observe in the north.

Acknowledgements

Chapter 3 Appendix 1. Vegetation measurements

We estimated the vegetation measures for each stand in the study using 6 or more

systematically-located vegetation plots per stand. In each vegetation plot basal area of

trees was estimated with variable radii, using Relaskops (Speigel, Germany). Overhead

canopy was estimated at 25 points arranged at 5 m intervals in a 20 m x 20 m square

around the plot center, using a point densiometer that indicated canopy cover directly

over the observer. Sapling density estimates were based on complete counts within a 5-m

radius plot of all conifer trees over 0.5 m tall and < 10 cm DBH. Horizontal cover was

measured across four lines of sight per plot using a horizontal cover board (Wolfe et al.

1982). The 2 m tall cover board had four 0.5 m-tall sections. An observer 11.2 m away

from the cover board estimated the proportion of each 0.5 m section obstructed by

intervening vegetation.

Chapter 3 Appendix 2. Designating FSS using GIS

We entered locations for all radio-collared snowshoe hares in a GIS that also had spatial data layers for elevation, forest stand boundaries, roads, and LandSat 7 satellite imagery recorded August 3, 1999 with 15 m pixel resolution. FSS type was relatively homogeneous within stand boundaries because these were the borders of recent human or natural disturbance. In stands where we sampled vegetation structure, our designations of FSS type (Table 2) corresponded to distinct stand age and stocking density categories on U.S. Forest Service and Plum Creek Timber Co. spatial data layers. Therefore, we used U..S. F. S. and P. C. T. C. forest stand categories to assign 1 of our 4 FSS types to each stand that matched our criteria. We visited each stand and used our experience in the 12 stands that were formally sampled with vegetation plots to judge whether the vegetation structures in the unsampled stands matched the FSS type designations made via GIS.

Table 1. Hypotheses of spatial population dynamics make predictions that are testable with different estimates of the discrete rate of growth, λ, based on survival, reproduction, and movement rate estimates specific to patch types of potentially varying quality.

Hypothesis	Predictions
Balanced dispersal	$\lambda_{\text{Multiple Patch}}$ is equivalent across all patch types; $\lambda_{\text{Individual}}$ is equivalent across all patch types.
Source-sink	Sources always have $\lambda_{\text{Single Patch}} > 1$, and net emigration; sinks always have $\lambda_{\text{Single Patch}} < 1$, and require net immigration to persist; $\lambda_{\text{Single Patch}} > \lambda_{\text{Multiple Patch}}$ for sources; $\lambda_{\text{Single Patch}} < \lambda_{\text{Multiple Patch}}$ for sinks.
Pseudo-sink	Sources exist; other patch types, pseudo-sinks, have $\lambda_{\text{Single Patch}} > 1$ at low density, and $\lambda_{\text{Multiple Patch}} < 1$ at high densities above carrying capacity.
Habitat Rank	$\lambda_{\text{Single Patch}}$ is always greater in certain patch types than in others, although values could vary above or below 1 in all patches.

Table 2. The criteria defining the 4 FSS types and distinguishing them from other types relied on observed sapling densities, large tree basal areas, and overhead canopy cover. These categories were predominant at the Inez study site, but leave out a large number of vegetation structure types found in the study region. Saplings are defined here as trees over 0.5 m tall, but less than 10 cm diameter at 1.4 m height.

FSS type	Structural attributes
Dense mature	Uncut forest stands with > 40% overhead canopy cover and basal area > 13.8 m^2 / ha
Dense young	Dense stands of regenerating conifers with > 5600 saplings / ha
Open young	Open stands of regenerating conifers, with < 3360 saplings / ha
Open mature	Partially harvested forest with < 30% overhead canopy cover and basal area > 13. 8 m^2 / ha

Table 3. The observed geometric mean $\lambda_{FSS\ Observed}$ values estimated from annual changes in estimated summer densities on individual trapping grids from 1999 – 2003 varied from site to site. The same was true of overall values for λ_{Site}, based on annual changes in average estimated density across all trapping grids at a site. The average proportional densities ($D_{proportion}$) observed in each of the four FSS types did not vary greatly from site to site in 1999, the year of the study with the highest average observed hare densities. Standard errors of the means are in parentheses.

	$\lambda_{FSS\ Observed}$ Placid	$\lambda_{FSS\ Observed}$ Inez	$\lambda_{FSS\ Observed}$ Spring Ck.	$D_{Proportion}$
Dense mature	0.58 (0.40)	1.34 (1.33)	0.23 (0.39)	0.340 (0.113)
Dense young	1.04 (1.26)	1.01 (0.31)	0.54 (0.17)	0.528 (0.084)
Open young	*	0.76 (0.25)	*	0.043 (0.043)
Open mature	*	0.94 (0.49)	*	0.089 (0.089)
$\lambda_{Site\ Observed}$	0.85 (0.63)	1.09 (0.45)	0.63 (0.10)	

* No values for these trapping grids could be estimated because densities were zero.

Table 4. Parameter estimates for fertility in each of three birth pulses (f_1, f_2, f_3), leveret survival rate (S_{Lev}), and annual emigration rate (E) were common to all FSS types. Fertility in each birth pulse, the number of female leverets per adult female, is the expected product of pregnancy rate and litter size divided by 2. Brackets indicate the 95% confidence intervals associated with each estimate.

f_1	f_2	f_3	S_{Lev}	E
1.40	1.87	0.89	0.563	0.205
{1.20, 1.58}	{1.70, 2.04}	{0.59, 1.14}	{0.403, 0.722}	{0.121, 0.352}

Table 5. The best-fitting known fate models tested against survival data for 175 radio-collared hares at Inez included effects of FSS, season, age and sex on weekly survival rates. The "Summer and Winter" effect had one pooled parameter describing the effect those seasons on survival, in contrast to pooled survival rates in Fall and Spring. The models shown here had ΔAICc values within 4 units of the best fitting model, indicating relatively good fit to the data compared to other models considered. For estimation of survival rates with model averaging, we used AICc weights from these models only.

Model rank, and effects included in the model	ΔAICc	AICc weight
1. Summer and Winter; Open FSS types; Sex in summer	0.000	0.169
2. Summer and Winter; Dense Mature FSS type; Sex in summer	0.297	0.146
3. Summer and Winter; Open FSS types; Sex in summer; Age	0.642	0.123
4. Summer and Winter; Open FSS types	0.658	0.122
5. Summer and Winter; Open FSS types; Age	0.853	0.111
6. Summer and Winter; Dense Mature FSS type	1.49	0.0804
7. Summer and Winter; Dense Mature FSS type; Sex in summer; Age	1.93	0.0645
8. Summer and Winter; Open FSS types; Sex year round	2.36	0.0521
9. Summer and Winter; Dense Mature FSS type; Age	2.93	0.0391
10. Summer and Winter; Dense Mature FSS type; Sex year round	2.93	0.0391
11. 4 different seasons; Dense Mature FSS type; Sex in summer	3.53	0.0290
12. 4 different seasons; Open FSS types; Sex in summer	3.87	0.0244

Table 6. The magnitude of different effects included in known fate models for weekly snowshoe hare survival, averaged by the AICc weights of the models, indicate that summer and winter are periods with higher weekly survival rates, and that the Open young and Open mature are the least favorable FSS types. Spring, Dense young, and adult females are the season, FSS type, age and sex against which other seasons, FSS types, age, and sex were contrasted. 95% confidence intervals for the effect sizes are in brackets.

Effect Name	Effect Size	95% C.I.
Summer	+ 0.0222	{+ 0.0114, +0.0288}
Fall	+ 0.000287	{- 0.000647, + 0.000949}
Winter	+ 0.0220	{+ 0.0123, + 0.0277}
Dense mature FSS type	+ 0.009	{+ 0.0136, + 0.0277}
Open young and Open mature FSS types	- 0.0189	{- 0.0380, - 0.00584}
Juvenile	- 0.00186	{- 0.000935, - 0.00205}
Male, from 21 April – 30 September	+ 0.00829	{- 0.00616, + 0.0165}
Male, from 31 September – 20 April	- 0.000438	{- 0.00200, + 0.000675}

Table 7. Seasonal survival (S) and annual fecundity (F) for female snowshoe hares vary by age, season and FSS type. Fecundity (F), the expected number of female leverets per female adult, is the sum of fertilities rates in each birth pulse discounted by mothers' expected survival and the leverets' expected survival until the beginning of fall. Projected annual growth rates for closed populations ($\lambda_{single\ FSS}$) vary as a result of both S and F. Seasonal survival rates for the 12 week spring, summer, and fall, and 16 week winter, are based on model-averaged weekly survival rates for each FSS type. 95% confidence intervals are below each estimate.

JUVENILES	$S_{Juv\ Spring}$	$S_{Juv\ Summer}$	$S_{Juv\ Fall}$	$S_{Juv\ Winter}$
Dense Mature	0.683	0.841	0.688	0.787
	{0.591, 0.756}	{0.757, 0.897}	{0.498, 0.759}	{0.683, 0.860}
Dense young	0.604	0.795	0.610	0.730
	{0.506, 0.686}	{0.697, 0.863}	{0.430, 0.690}	{0.611, 0.816}
Open Young	0.476	0.712	0.483	0.626
	{0.361, 0.579}	{0.580, 0.807}	{0.308, 0.584}	{0.475, 0.743}
Open Mature	0.476	0.712	0.483	0.626
	{0.361, 0.579}	{0.580, 0.807}	{0.308, 0.584}	{0.475, 0.743}

Table 7, cont.

Adult survivals, fecundities and expected λ for individuals inhabiting the listed FSS types exclusively

ADULTS	$S_{Ad\ Spring}$	$S_{Ad\ Summer}$	$S_{Ad\ Fall}$	$S_{Ad\ Winter}$	F_{FSS}	$\lambda_{Single\ FSS}$
Dense Mature	0.706	0.854	0.711	0.804	2.15	1.14
	{0.628, 0.768}	{0.768, 0.908}	{0.636, 0.771}	{0.697, 0.874}	{2.03, 2.23}	{0.621, 1.573}
Dense young	0.628	0.810	0.633	0.748	2.10	0.807
	{0.544, 0.698}	{0.708, 0.876}	{0.552, 0.701}	{0.625, 0.832}	{1.94, 2.19}	{0.391, 1.205}
Open Young	0.508	0.734	0.515	0.652	1.99	0.413
	{0.407, 0.598}	{0.598, 0.828}	{0.416, 0.603}	{0.495, 0.768}	{1.77, 2.13}	{0.144, 0.765}
Open Mature	0.508	0.734	0.515	0.652	1.99	0.413
	{0.407, 0.598}	{0.598, 0.828}	{0.416, 0.603}	{0.495, 0.768}	{1.77, 2.13}	{0.144, 0.765}

Table 8. Results from landscape level projection, using four FSS types: Dense mature, Dense young, Open young, and Open mature, each with 25% of the total area. Starting population size was 500, distributed in each FSS according to the mean proportions observed in 1999. Values for λ at years 5, 10, and 15 of the model are $\lambda_{\text{Multiple FSS}}$ for the 4 FSS types, and $\lambda_{\text{Landscape}}$ for the entire population of snowshoe hares. All λ values asymptote to 0.967 by year 25. The proportions of the population in each FSS type are those of the initial population, then those observed at years 5, 10, and 15; these asymptote to a landscape where most hares (73%) are in the Dense mature FSS type.

	λ Year 5	λ Year 10	λ Year 15	Proportion of individuals in each FSS			
				Initial	Year 5	Year 10	Year 15
Dense mature	0.981	0.969	0.967	0.340	0.621	0.712	0.731
Dense young	0.797	0.908	0.954	0.528	0.235	0.152	0.135
Open young	0.905	0.951	0.964	0.044	0.072	0.068	0.067
Open mature	0.905	0.951	0.964	0.088	0.072	0.068	0.067
Landscape	0.920	0.957	0.965	1.000	1.000	1.000	1.000

Figure Legends

Figure 1. Map of the three study sites in western Montana (dark circles). Each site had one trapping grid in four forest stand structure (FSS) types: Dense mature, Dense young, Open young, and Open mature.

Figure 2. Snowshoe hare density per ha, estimated from mark-recapture trapping in different FSS types at each site from 1999 – 2003. Black squares are estimates from the first trapping period of each summer, and white squares are estimates of density from the winter. Error bars are + / - 1 S.E. Upper limits of the standard error bars are not shown for one point in Inez Dense mature (2.69) and one point in Spring creek Dense mature (2.07).

Figure 3. Distribution of maximum annual displacements for all radio collared hares with more than 3 locations (n = 144). The mean maximum displacement was 618 m (S.E. = 87 m). Displacement for one hare that traveled 9,370 m is not shown.

Figure 4. Histogram showing the frequency of FSS type use by snowshoe hares. Most snowshoe hares were located in multiple FSS types. Each bar represents the relative frequency of radio collared hares located in a FSS type within the range of percentages listed along the x-axis. For example, 12% of observed hares had between 1-20% of their locations in the Dense mature FSS type, and 22% of observed hares had between 81-100% of their locations in the Dense mature type. Frequencies for any given FSS type do not sum to 1 because hares that did not use that type are not included (for example, 32% of observed hares were not located in the Dense mature type).

Figure 5. Projected individual growth rates, $\lambda_{Individual}$ (z-axis) for snowshoe hares inhabiting up to three FSS types (Dense mature, Dense young, and Open) with varying proportions. Highest $\lambda_{Individual}$ values above 1 are predicted for hares with high occupancy

in Dense mature FSS type (x-axis). The y-axis is the proportion of the remaining

occupancy that is in the Open FSS type; lowest $\lambda_{Individual}$ values are for hares inhabiting

only Open FSS types. The dark circle is the point representing $\lambda_{Individual}$ for the observed

average proportional occupancy of different FSS types, based on all radio-collared

snowshoe hares. In this example, $\lambda_{Individual}$ = 0.79 and occupancy of Dense mature = 0.37;

because occupancy of the Open and Dense young types are 0.33 and 0.30, respectively,

the value of the y-axis is (0.33 / 0.63) = 0.52.
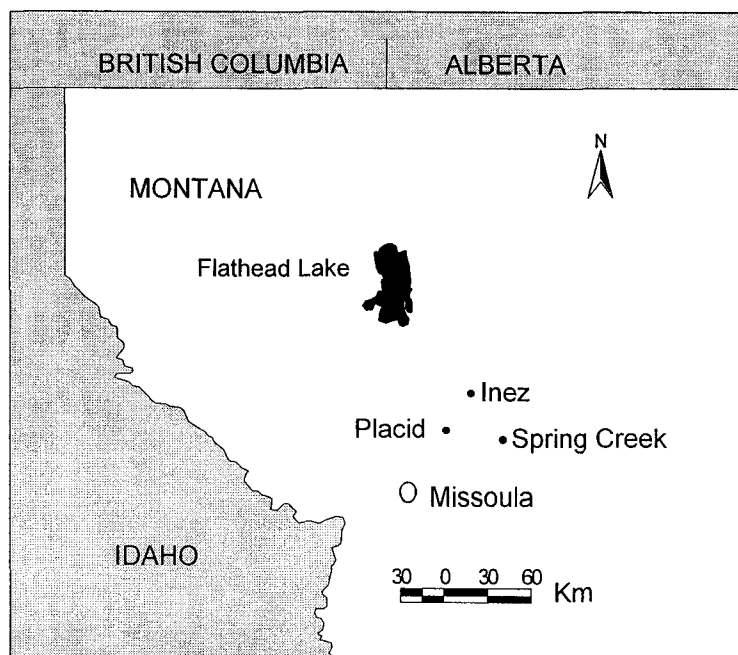
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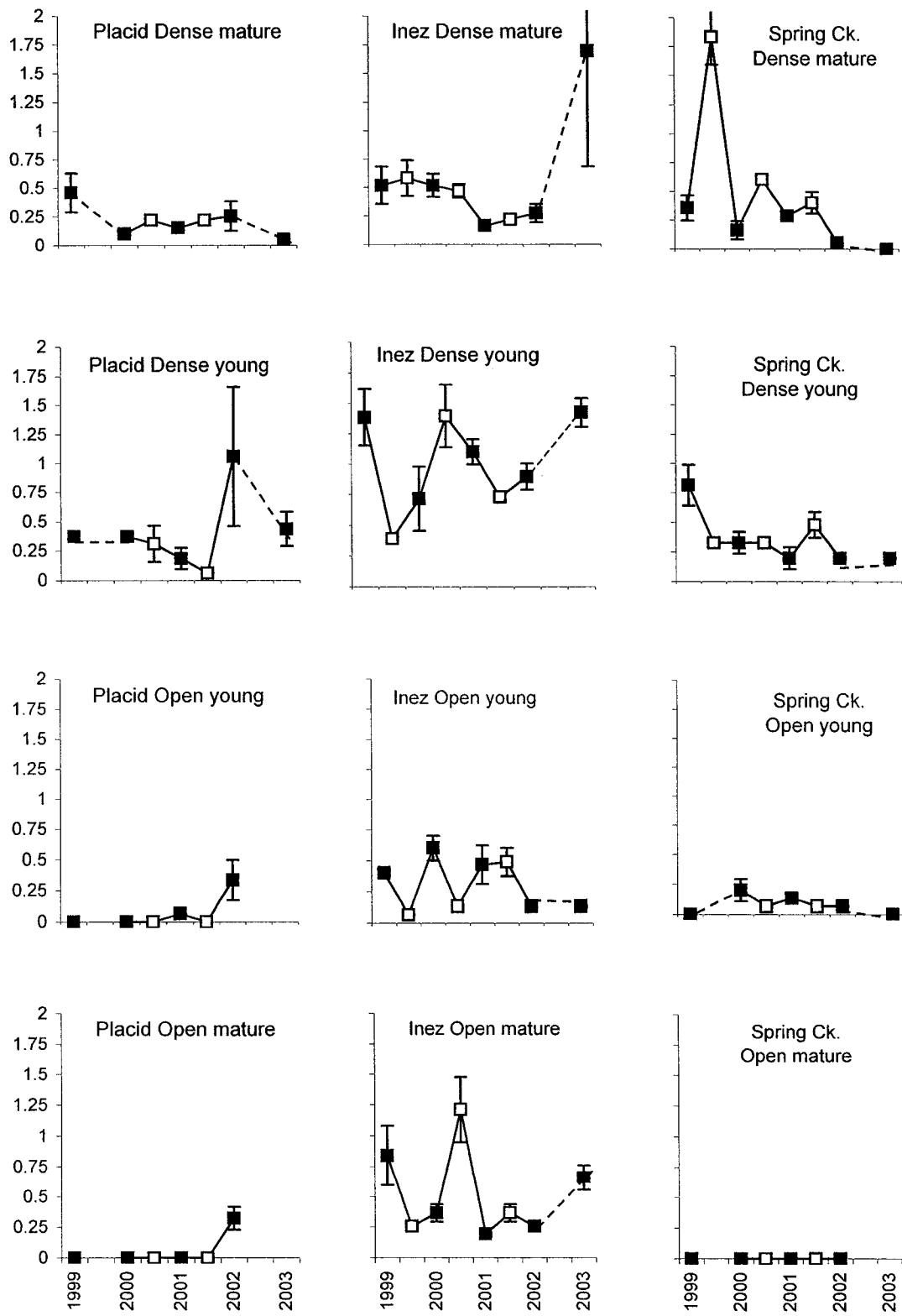
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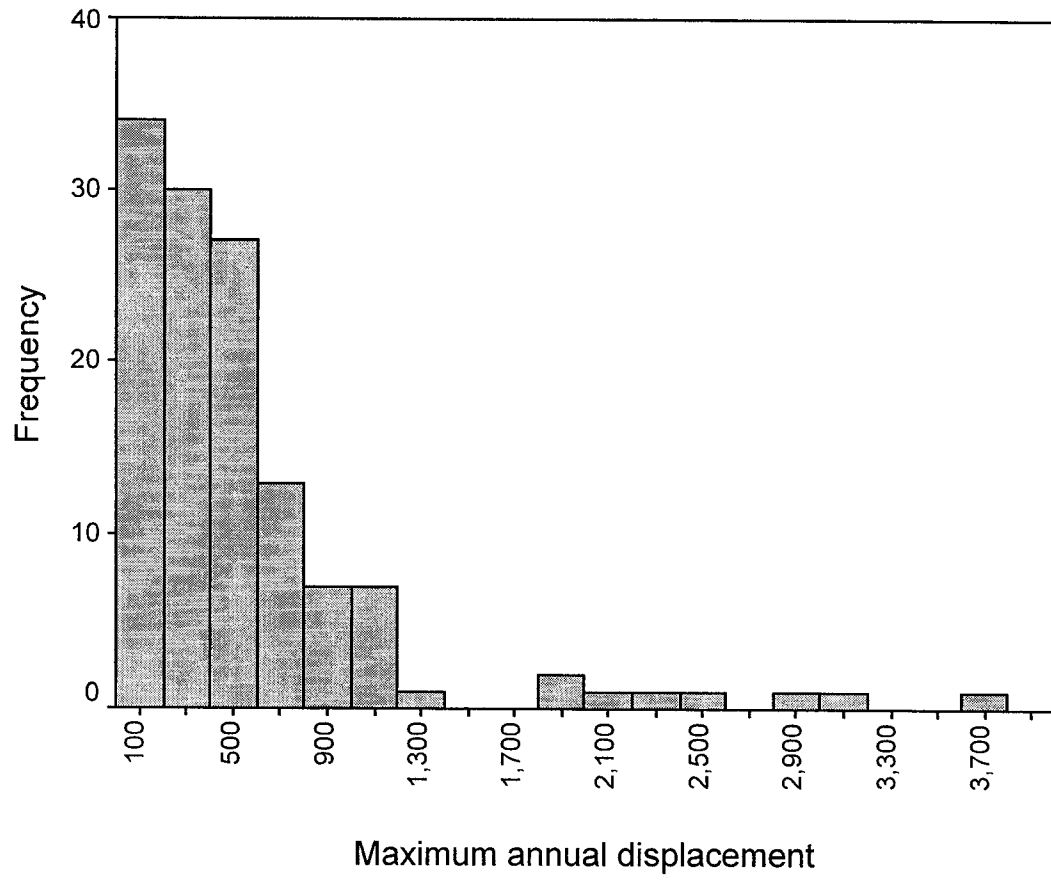
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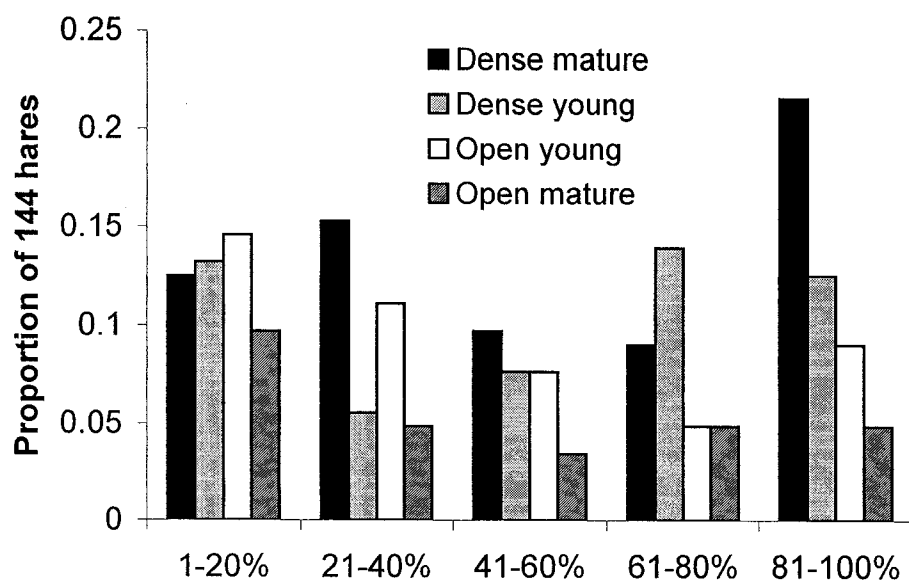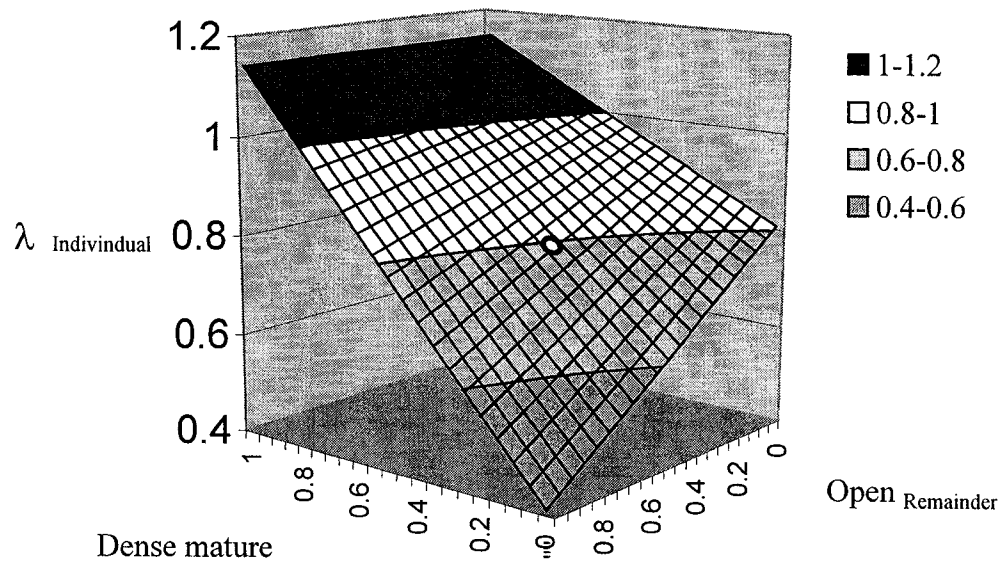
Figure 4.

Figure 5.

Chapter 4. Snowshoe hares and management of young forests

Abstract

Management of young forests is not often considered in conservation plans, but young forests provide habitat for some species of conservation concern. Snowshoe hares (*Lepus americanus*), critical prey of forest carnivores including the U.S. federally threatened Canada lynx (*Lynx canadensis*), are abundant in young montane and subalpine forests with densely-spaced saplings and shrub cover. We tested for effects of pre-commercial thinning (PCT), a silvicultural technique that reduces the number of saplings and shrubs on young forest stands, on snowshoe hare densities for two years after experimental treatment at three areas. Densities declined in stands treated with standard prescriptions of pre-commercial thinning (100% of stand area treated), compared to control stands. Compared to control stands, snowshoe hare densities declined in stands treated with pre-commercial thinning with reserves (PCT-R), where 20% of the total area was retained in uncut ¼ ha patches; these declines occurred in two out of three study areas in the second winter and second summer after treatment. Sapling density played a role in snowshoe hare density among PCT-R treated stands; two summers and two winters after treatment, PCT-R stands with higher overall sapling density in retained patches had higher snowshoe hare densities than PCT-R stands with lower sapling densities. Snowshoe hares used the retained patches more than thinned areas within the PCT-R treatment stands. These observations support conclusions that patches with high sapling density can play a role in maintaining high snowshoe hare density. We suggest that managing forests for high snowshoe hare abundance will require the creation of new young forest stands to offset their functional loss through succession and pre-commercial thinning, the

use of silvicultural techniques that retain high sapling and snowshoe hare density in existing young forest stands, and the conservation of structurally valuable mid- and late-successional forests.

Introduction

Young, regenerating forests provide valuable, if transient, habitat for many species (Hejl et al. 1995, Askins 2001, Hunter et al. 2001, Litvaitis et al. 2001). In industrial forest landscapes of the western United States, intensive forest harvest in the 20th century created large areas of early- and mid-successional stands (Agee 2000, McKelvey et al. 2000). The intensive management of young forests that has subsequently occurred on many private and public lands can decrease the time needed for development of merchantable timber (Daniel and Helms 1979) and old-growth characteristics (DeBell et al. 1997, Tappeiner et al 1997), but may reduce their value for early-successional associated species.

The Canada lynx (*Lynx canadensis*) was recently listed as "Threatened" in the U.S. (U.S. Fish and Wildlife Service 1999). Although the causes of lynx decline are not completely understood, managing forested landscapes in ways that increase snowshoe hare abundance may foster Canada lynx recovery south of the Canada – United States border (Ruggiero et al. 2000). Snowshoe hares, *Lepus americanus*, are the principal prey of the Canada lynx. In Montana, high summer and winter snowshoe hare densities are associated with young, dense forest stands (e.g., > 5000 saplings / ha; Mills et al., In Review). The same pattern is observed throughout their wide range in North America; highest densities occur where abundant young conifer saplings and tall shrubs apparently provide forage and cover from predators (Adams 1959, Dolbeer and Clark 1975, Wolff

1980, Wolfe et al. 1982, Pietz and Tester 1983, Fuller and Heisey 1986, Koehler and

Brittell 1990, Koehler 1991, Hodges 2000a, Shaw 2002). Late-seral stands with

abundant understory can also harbor high snowshoe hare densities, especially in winter

(Griffin and Mills, in preparation), and may be important for snowshoe hares in the more

southern Rocky Mountains of Colorado (Beauvais 2000). Stands with high understory

density may drive snowshoe hare population dynamics by acting as net sources of

emigrant snowshoe hares that supplement hare populations in nearby, lower-quality

habitats (Wolff 1980, Wolff 1981). Despite the high value of stands with high understory

vegetation density for hares – and therefore threatened lynx – high sapling densities can

lead to a decrease in future timber yields and loss of tree vigor (Martin and Barber 1995),

such young stands are often converted to more open young forest habitats via pre-

commercial thinning (hereafter, "PCT"). Commercial and / or ecological goals of PCT

include increased growth rates for trees that are retained (Daniel and Helms 1979,

Johnstone 1984) and increased frequency of favored tree species (Carey and Johnson

1995). The technique is used in restoration forestry to accelerate the development of late-

successional structures: it reduces the time that stands spend in the 'stem exclusion'

phase (Carey 1995, DeBell et al. 1997, Tappeiner et al. 1997). Despite these potential

benefits, the sudden decrease in stand density could dramatically affect snowshoe hares

and other species that benefit from dense understory cover.

If the decreased density associated with pre-commercial thinning causes dramatic

short-term declines of snowshoe hare abundance in the stands where snowshoe hare

density is highest, the prey base of Canada lynx could be seriously impacted. In 1999,

the U.S. Forest Service instituted a temporary moratorium on pre-commercial thinning on

its lands in potential lynx habitat as a precaution against further loss of high-quality

Canada lynx foraging habitat on public lands. Alternatively, the increased availability of

herbaceous forage near the ground may favor snowshoe hare survival and increase

density after thinning (Adams 1959, Black 1965, Sullivan and Sullivan 1988).

We tested the prediction that PCT has a negative short-term effect on snowshoe

hare abundance in summer and / or winter. Specifically, we tested the prediction that

treatment with PCT will decrease snowshoe hare densities in thinned stands relative to

paired, untreated control stands. We also tested a corollary prediction: that stands treated

with a novel PCT treatment that left isolated patch reserves of unthinned forest (hereafter

"PCT-R" treatment) would support lower hare densities than untreated control stands, but

higher than stands treated with standard PCT.

We also investigated the vegetation structures within stands that would be

valuable to maintain in future variations on PCT treatments by examining microhabitat

selection of snowshoe hares in pre-commercially thinned with reserve (PCT-R) treated

stands, which contained both thinned and unthinned young forest patches.

Methods

Study areas

All study areas were in the Seeley-Swan region of western Montana (Figure 1)

where forested landscapes have a wide distribution of snowshoe hares across time and

space (Mills et al. in review), snowy winters and a mesic climate. The region is also a

center of ongoing Canada lynx ecological studies (Squires and Laurion 2000).

We limited our studies to montane / subalpine coniferous forests at 1,450 – 1,700

m elevation. At these elevations, dominant conifers are lodgepole pine (*Pinus contorta*),

Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Of these, larch is the most commercially valuable timber species, although Douglas-fir is also highly valued for lumber. Lodgepole pine and Douglas-fir provide relatively high-quality forage for hares; spruce and fir are less valuable nutritionally and larch is deciduous, so larch needles are not available in the winter (Wirsing and Murray 2002). A wide variety of montane and subalpine shrubs and forbs also provide some cover and forage during the summer and fall.

The study consists of three areas: Spring Creek, Cold Creek, and Beaver-Finley (Figure 1). Each area had two treatments (standard PCT and PCT-R treatment) and a control within 0.1 – 1.4 km of each other (nine experimental stands total). All study stands were 15-35 year old, even-aged, regenerating stands scheduled for PCT, and were similar in elevation, sapling age, sapling density, and tree species composition. Experimental treatments were assigned randomly to stands, except at Cold Creek, where the control stand was selected by the land owner and only the standard and PCT-R treatments were randomly assigned.

Stand-level pre-commercial thinning experiment

Because PCT is usually a stand-level treatment, stands were the experimental unit and we evaluated changes in hare density at this scale (stands were $\geq$ 20 ha). Stands of this size are a minimum scale for analyses of hare density because it is roughly twice the size of average snowshoe hare home ranges, which overlap (Hodges 2000a). Studies on the effects of pre-commercial thinning with response variables measured over smaller

spatial scales (e.g., Sullivan et al. 2002) may not reflect population-level changes in snowshoe hare density.

Within each stand we marked five parallel trap lines 50 m apart, each with 10 traps spaced at 50 m intervals; these formed the 9 ha trapping grids with 50 traps each. A $\geq$ 50 m buffer between trapping grids and stand edges added confidence that indices and mark-recapture estimates reflected hare density within the stand. Before and after treatments, we sampled sapling density, overhead canopy cover, horizontal cover density, and shrub density at 6 or more 5.6 m radius plots per stand (Table 1).

The three stand treatments (Figure 2) were:

1) Control – no trees or shrubs were cut in the stand.

2) PCT– the entire stand was thinned to 3.5-4.0 m spacing between saplings left alive (~ 800 standing live conifer saplings / ha; saplings are over 0.5 m tall, but with diameter < 7.5 cm), with preference for retaining healthy western Larch, and Douglas-fir, Shrubs over ~ 0.5 m tall were left standing only in areas near wetlands (<5% area of any treated stand). Thinning 100% of the stand area is the standard for pre-commercial thinning, and the tree spacing we used was well within the range applied routinely with PCT in the western U.S.

3) PCT-R – 80% of the stand was thinned with the PCT guidelines (above), but 20% of the total area was retained with saplings uncut. The arrangement of uncut areas was in ¼ ha (50 m x 50 m) retention patches, randomly selected from the grid of ¼ ha squares defined by the perpendicular lines of the trapping grid, extended to the edges of the stand. Within the three PCT-R treatment stands we marked the retention blocks with flagging and yarn.

Density estimation from mark-recapture trapping

We used mark-recapture trapping to estimate hare density once in July before treatments, and again 2-3 weeks after treatments. For two years after treatment, we estimated hare density with one session at the end of each summer and two sessions each winter. Additionally, we estimated density at Cold Creek the winter prior to treatment. Trapping sessions were 4-6 consecutive nights (n = 75 sessions; mean = 5.5 nights / session). At each area, all three stands were trapped simultaneously to limit any confounding influence of weather on capture probability. Traps were baited with weed-free alfalfa, apple, and pelleted horse feed, and were checked every morning. Hares were individually ear-tagged, weighed, sexed, and released. Because the number of recaptures was too small to use program CAPTURE (White et al. 1982) reliably (Menkens and Anderson 1988), we used the Lincoln-Petersen estimator adjusted for small sample size (Chapman 1951, Seber 1982) to estimate abundance.

We estimated density by dividing the Lincoln-Petersen abundance estimate by the estimated effective trapping area for each grid. This area was estimated for each stand (Table 1) from the distances individuals moved between traps during trapping sessions (Litvaitis et al. 1985, Karanth and Nichols 1998, Mills et al. in review).

To evaluate the effects of our two treatments on hare density relative to the paired control stand at an area, we calculated ln(density after treatment) – ln (density before treatment); this was a measure of how snowshoe hare density had changed in each stand after treatment. We subtracted the value of this measure in each control stand from the corresponding value in the paired treated stands. A negative difference indicated that the treated stand (PCT or PCT-R) was negatively affected relative to the control. For

densities of zero, we substituted a value one tenth that of the lowest recorded density before log transformation. At the Cold Creek area, we used density before treatment estimates that corresponded in season (summer or winter) to the season of the after treatment trapping session. At the Spring Creek and Beaver-Finley areas, we used summer pre-treatment density estimates for comparisons to both summer and winter densities after treatment. We compared the relative density changes in standard PCT stands and PCT-R stands to control stands for the first winter (two trapping sessions at each area), the second winter (two trapping sessions at each area), and both summers (two summers after trapping at each area) after treatment. We did not use data from the initial period 3-4 weeks after PCT treatment because a sample of 14 radio-collared hares at Spring creek indicated high between-stand movement rates in that period (Griffin and Mills, unpublished data). We tested for effects by examining 95% confidence intervals of the relative changes in treated stands versus control stands, and with repeated measures ANOVA. Each treatment (PCT or PCT-R) was compared to the control stands based on the 2 summer density estimates, or on the 2 density estimates made during each winter.

Snow tracks and winter pellets

We used snow track counts and fecal pellet counts to test for differences in winter abundance across thinning treatments. In contrast to the mark-recapture estimator, which has associated estimates of precision, both snow track and winter pellet counts are indices with generally positive but unknown relationship to true abundance (Nichols and Pollock 1983, Nichols 1992, Rexstad 1994). We counted snow tracks in 5 parallel, 450 m-long transects in each treatment stand, using the marked trap lines. We also counted the track crossings in each 50 m segment to determine whether there was an association between

hare activity and the aggregate retention patches on the PCT-R treatments. Snowshoe hare track crossings were counted twice per winter during trapping sessions, conditions permitting. Ideal track count conditions were 24 - 48 h after snowfall, before trapping took place. We limited comparisons to counts made within single areas on the same day. We assumed that relatively high track counts indicated a greater number of hares, greater affinity of active hares for microhabitats along the transect, or both.

Summer pellet counts (Krebs et al. 1986) were not feasible in the two years after PCT because cut saplings covered the ground too completely. To count winter pellets, we systematically placed 50 dark plastic trays (52 cm x 25 cm x 5 cm deep, with multiple drainage holes and secured by 15 cm stakes) in each stand in late fall before snow accumulation. The trays sampled pellets that accumulated in the snow above them. We counted pellets in trays shortly after snowmelt, censoring dislodged, broken, and steeply-angled ($\geq 30°$) trays.

We used snow tracks, winter pellets, and a third index, the number of individual hares caught, to test for an association between snowshoe hares and aggregate retention patches within PCT-R treatment stands. Because aggregate retention patches were ¼ ha units defined by the trapping grid (Figure 2), some traps and pellet trays were located on outside corners of retained patches, and some 50 m transect segments were along edges of retained patches. We considered these traps, trays, and segments 'next to' a retention patch. These data were compared to similar metrics collected 'away from' retention patches (i.e., immediately surrounded by thinned areas). For each index we determined the number of hares caught per trap, pellets per tray, or snow tracks per segment next to retained patches and away from retained patches. Finally, we divided the 'away from'

index values by the 'next to' values. We assumed that this ratio should equal one if hares exhibited no behavioral preference, and less than one if hares exhibited a preference for retained patches.

Results

Densities and indices at experimental areas

Snowshoe hare densities varied before any treatment with PCT (Table 1), and over time after treatment (Figure 3). Five of six treated stands (PCT or PCT-R) had at least one winter trapping session when estimated density was very low (< 0.1 hares/ha). The PCT-R treatment consistently maintained higher snowshoe hare densities than the standard PCT treatment in two of three areas. In comparing the observed changes in densities within areas, control stand densities decreased less from summer to winter, and were less variable than both standard and PCT-R treated stands (Figure 4). Relative to both control and PCT-R stands, standard PCT had a negative effect on snowshoe hare densities, especially in the winter (Figure 4; Table 2). PCT-R stands had negligible differences compared to control stands in summer and variable density responses in the first winter after thinning compared to control stands, but this difference increased during the second winter after treatment (Figure 4; Table 2).

Winter snow track and fecal pellet indices at each area were concordant with winter mark-recapture density estimates: we recorded higher counts in control than treated stands for 10 of 12 measures (Table 3). The two exceptions were from in the first winter after treatment, when high snow track or pellet counts were recorded in PCT-R stands, and correspondingly high early winter densities were estimated in the same

stands. In all cases the standard PCT treatments had a substantially greater decrease in index values relative to controls than did the PCT-R treatments

Retained patches within PCT-R treatments

Higher snowshoe hare densities were associated with higher sapling densities in all stands both before and after treatment (Figure 3). The PCT-R stand that retained the greatest snowshoe hare density (at Cold Creek) also had an average sapling density more than twice as large as in any other stand treated with PCT (Table 1). In PCT-R stands, high sapling densities after PCT were the result of high sapling densities within the 20% of the total area that was retained in patches. Sapling density was reduced to the same uniformly low density (400-900 / ha) in the other 80% of the stand.

Trapping, snow track, and pellet indices indicated that snowshoe hares in PCT-R treatment stands exhibited behavioral preference for microhabitats in and near aggregate retention patches. Compared to per-trap, per-50 m transect segment, and per-tray measures for areas away from retained patches, more individuals were trapped, and more snow tracks and pellets were counted within or next to retained patches (Table 4).

Discussion

Pre-commercial thinning reduced snowshoe hare densities on experimental stands; hare densities in experimentally manipulated young forest stands support the prediction that unthinned young control stands maintain higher snowshoe hare populations than pre-commercially thinned stands. We observed greater reductions in snowshoe hare density in stands treated with both levels of PCT treatment than in unthinned control stands, except in one PCT-R replicate. Declines were most pronounced in winter, although PCT-R stands on average did not show declines relative to control

stands in the first winter. We suggest that negative effects of PCT on the prey base of lynx and other predators may not occur for at least one year after PCT. Winter is the season when Canada lynx may be at greatest danger of starvation (Poole 1994), so a decreased availability of snowshoe hares could reduce lynx survival in the second and later winters after PCT.

We did find, though, that aggregate retention patches of dense young forest can play a role in maintaining more hares within a thinned stand than would be expected after complete stand area thinning. Densities in PCT-R treatment stands that retained 20% of stand area not thinned decreased less than stands treated with standard PCT, according to most density estimates and all index measures. The PCT-R stand that retained the greatest number of hares in the winter also had the highest overall sapling density after PCT, as a result of high sapling densities in the retained patches.

High sapling densities are the very condition that motivate PCT as a silvicultural treatment in young forest, but our results corroborate the view that extremely dense understory cover provides snowshoe hares some measure of safety from predation (Wolff 1980, Sievert and Keith 1985, Litvaitis et al 1985). Live snowshoe hare affinity for the aggregate retention patches in PCT-R treated stands points to the importance of high sapling density, at least at the scale of the ¼ ha retained patches. At a fourth study area in the region, the only microhabitats where we did not find remains of dead, radio-collared snowshoe hares were those with extremely dense understory cover, i.e., sapling density $\geq$ 5,500 / ha (Griffin et al. in review).

At the scale of single stands, we suggest that PCT prescriptions should retain some very dense patches of saplings to maintain high snowshoe hare abundance. Most

trapping estimates at experimental areas indicated that retaining dense patches in PCT-R treatments kept snowshoe hare densities higher than did standard PCT treatments. We caution that PCT-R stands had more severe declines in snowshoe hare density relative to control stands in the second winter of our study, and snowshoe hare density may respond differently to the PCT-R and standard PCT treatments as stands mature. Our study was too short to address whether PCT or PCT-R actually extend the time span that stands provide good quality snowshoe hare habitat once surviving shrubs and seedlings grow tall enough to provide cover and forage (e.g. Doerr and Sandburg 1986). This is an important consideration in planning for long-term availability of favorable snowshoe hare habitats. Perhaps retention of some dense patches in a densely stocked young stand could ameliorate conditions for snowshoe hares in the short-term (relative to complete thinning), while pre-commercial thinning on other portions of the stand could lead to future food and cover availability, as thinned areas can have a prolonged period before they enter the stem exclusion successional phase (Carey 1995, DeBell et al. 1997, Tappeiner et al. 1997).

We do not know whether the relative concentration of snowshoe hares near retention patches make them easy targets for predators, but it seems clear that snowshoe hares have no place to hide in stands that are thinned with standard PCT practices. Snowshoe hares may be highly visible during spring and fall molting periods, especially in open habitats (Litvaitis 1991). While an increased hunting success in open habitats may be good for individual predators in the short term, it would not be good for predator populations if snowshoe hares, lacking refuge, were held at low abundance. There appears to be no scarcity of open habitats in managed forests of the Rocky Mountains,

and the relatively high starvation rate of lynx in Montana (J. Squires, U. S. Forest Service Rocky Mountain Research Station, personal communication) leads us to suggest that snowshoe hare abundance is rather more limiting than the availability of hunting habitat. Retention of some densely vegetated patches could potentially prolong the time periods when snowshoe hares inhabit a given stand after PCT. The size of aggregate retention patches (¼ ha in this study) could play a role in their effectiveness, with larger patches providing safe cover over more contiguous snowshoe hare home ranges.

We encourage future research to assess PCT prescriptions with more proportional area left in aggregate retention patches, and over longer time scales. Compared to standard PCT prescriptions, the PCT-R prescription retained more of the natural variation in young stand structure that is lost, at least temporarily, through standard PCT. There are many prescriptions that could accelerate growth of some large trees while still retaining much snowshoe hare cover and forage. One approach could be a 'single tree release' PCT treatment, leaving ~ 4 m radius of cleared area around 18-20 'release trees' per ha, freeing them from immediate competition for light and nutrients; this would make small clearings over only 10% of the area of young forest. Another approach could be to create open patches of PCT within a matrix of unthinned young forest. An example of this that would also leave only 10% of the total area thinned is a 10 ha stand with four ¼ ha thinned patches, each holding 200 released saplings; in this case the average density of released saplings would be 80 / ha.

The management goals for particular stands and landscapes will determine whether the higher costs coming from PCT treatments that retain some proportion of unthinned patches are outweighed by the larger population of snowshoe hares that would

result from standard PCT practices. Labor costs of the PCT-R treatment may be slightly higher until thinning crews can implement the prescription without the need for extensive marking. A second cost incurred in the future is a loss of potential future tree growth and yield in the retained patches; this could be reduced if retained patches are thinned once they have grown and no longer provide dense understory cover and forage for hares. Future agency restrictions on forest management could represent potential hidden costs of standard PCT treatments. If widespread PCT causes regional snowshoe hare densities to become or remain low in landscapes where carnivore conservation is a priority then the resulting cost of agency oversight could be more than the cost of PCT-R treatments. Instead, young forest habitat management that maintains understory cover could be an effective tool to increase the number of snowshoe hares regionally.

At the scale of the larger forest ecosystem, snowshoe hare populations require a constant availability of young or mature forest with dense understory cover. Dense young stands are useful to hares only until young tree growth shades out low branches and tall shrubs. In most regions, new young stands with ample stem and shrub density will need to be created through natural or anthropogenic disturbance. Late-seral forests with areas of dense understory can provide valuable snowshoe hare habitat (Beauvais 2000, Buskirk et al. 2000, Griffin and Mills, unpublished data); harvesting these will not generally lead to a net gain in productive habitat for snowshoe hares. Rather, mid-age forest stands could be targeted for disturbances that lead to dense understory cover. Partial harvest in mid-age stands can also lead to late-seral structures that are used by both snowshoe hare and lynx (Koehler and Brittell 1990). Our results indicate that intensive forest management, long recognized for its negative impacts on late-seral

obligate species, will also need to accommodate species associated with young forest structures, such as snowshoe hares.

Acknowledgements

Table 1. Summer pre-thinning snowshoe hare density (hares / ha), vegetation attributes and effective grid size at each of the nine stands in the study. Six plots per stand led to estimates of sapling density and percent composition of western larch (*Larix occidentalis*), before and after treatment with pre-commercial thinning; larch is the most commercially valuable tree, and generally increased in frequency with thinning. The effective area trapped for each grid is based on the mean maximum distance moved (MMDM) by hares that were recaptured within single 6-day trapping sessions. Standard errors for all measures are shown in parentheses.

Area Treatment	Density / ha (Before)	Saplings/ha (Before)	Saplings/ha (After)	Recaps, n	MMDM, m	Effective area, ha
Spring Creek						
Control	0.668 (0.095)	9135 (2232)		18	147 (22.7)	20.2 (2.00)
PCT	0.503 (0.047)	6665 (1572)	897 (145)	5*	80.3 (14.5)	14.7 (1.13)
PCT-R	0.314 (0.016)	2554 (1427)	880 (387)	9	105 (20.0)	16.7 (1.63)

Cold Creek †

Control	0.532 (0.064)	2757 (558)		45	102 (13.9)	16.4 (1.13)
PCT	0	2977 (455)	524 (88)	1*	80.3 (14.5)	14.7 (1.13)
PCT-R	0.188 (0.014)	5295 (1072)	1860 (563)	17	86.7 (15.8)	15.2 (1.24)
Beaver-Finley						
Control	0.357 (0.018)	3011 (463)		17	94.7 (15.7)	15.8 (1.26)
PCT	0.767 (0.104)	2723 (673)	406 (59)	11	81.3 (18.0)	14.8 (1.40)
PCT-R	0.465 (0.037)	3163 (804)	643 (140)	16	80.3 (14.5)	16.8 (1.26)

* Too few hares were captured to calculate MMDM for these stands. Instead, we pooled hares (n=17) caught on standard treatments at all 3 areas to find MMDM for these two stands.

† Density estimates at Cold Creek in the winter before treatment were: control = 0.486 (0.056); standard = 0.126 (0.003); PCT-R = 0.377 (0.023).

Table 2. Proportional change of snowshoe hare density in standard PCT stands and PCT-R treated stands, defined as ln(density after treatment) – ln (density before treatment), as compared to the simultaneous change in untreated control stands. Values are the means from three replicate areas, with associated 95 % confidence intervals. F-values (with d.f. for the effect of stand type and error terms in parentheses) and P-values are based on repeated measures ANOVA models, where the 2 summer trapping periods or 2 trapping periods per winter were repeated measures of the response to treatment. Values below zero indicate that the treated stands declined proportionally more than control stands. Despite the sample size of only three areas, the upper limit of the confidence interval indicates greater declines in both winters on standard pre-commercially thinned stands than on control stands at the same area. There also was a decline on PCT-R stands, compared to control stands, in the second winter.

	Mean Difference	95% C.I.	F	P
PCT vs. control, summers	-0.26	{-1.89, 1.39}	0.30 (1, 5)	0.61
PCT vs. control, first winter	-1.28	{-2.68, 0.11}	5.54 (1, 15)	0.065
PCT vs. control, second winter	-2.20	{-3.98, -0.43}	9.02 (1,15)	0.030
PCT-R vs. control, summers	-0.77	{-2.79, 1.19}	1.48 (1, 5)	0.28
PCT-R vs. control, first winter	0.22	{-0.87, 1.32}	0.20 (1, 15)	0.67
PCT-R vs. control, second winter	-0.69	{-2.10, 0.72}	11.72 (1, 15)	0.018

Table 3. Standard PCT stands and PCT-R stands had lower winter hare index counts than controls stands in most cases. The ratio of treatment stand values divided by control stand values for snow track and winter pellet counts at each area is averaged for the two winters after PCT; ratios less than one indicate lower counts on treated stands. Standard errors for up to four snow track counts and two pellet counts per stand are shown in parentheses.

	snow tracks	winter pellets
Spring Creek		
Standard / Control	0.45 (0.39)	0*
PCT-R / Control	2.9 (1.6)	0.28*
Cold Creek		
Standard / Control	0.33 (0.12)	0.016 (0.023)
PCT-R / Control	0.43 (0.18)	0.81 (0.14)
Beaver Finley		
Standard / Control	0.13 (0.06)	0.073 (0.073)
PCT-R / Control	0.53 (0.36)	1.3 (0.047)

* Winter pellets were counted only once at Spring Creek

Table 4. For four snowshoe hare indices within the PCT-R treatments only, each column

shows the ratio of indices counted away from aggregate retention patches divided by

indices counted next to aggregate retention patches. The indices were: individuals caught

per trap-night in summer and winter, average snow track counts per 50 m transect

segment, and average number of winter pellets per tray. Ratios below one indicate

preference for retained habitats; all winter measures indicate lower preference for thinned

than retained microhabitats. Standard errors are in parentheses.

Area	Individuals trapped (summer)	Individuals trapped (winter)	Snow tracks	Winter pellets
Spring Creek	0	0.34 (0.13)	0.42 (0.12)	0.18*
Cold Creek	0.34 (0.14)	0.34 (0.15)	0.53 (0.49)	0.42 (0.42)
Beaver Finley	1.58 (1.58)	0.70 (0.70)	0.77 (0.25)	0.029 (0.029)

* Winter pellets were counted only once at Spring Creek

Figure Legends

Figure 1. Study areas in western Montana, with Flathead lake shown for reference. Spring Creek, Cold creek, and Beaver-Finley were areas with experimental pre-commercial thinning.

Figure 2. Schematic diagram of one experimental replicate, with three young forest stands: control (white), standard PCT (gray), and PCT-R (checkered). Each stand holds a nine ha trapping grid with 50 trap stations. Within the PCT-R treatment, 20% of the total area is unthinned young forest, with retained ¼ ha patches arranged randomly (small white squares).

Figure 3. Snowshoe hare densities plotted against sapling densities in nine experimental stands for the summer before PCT (A), the second summer after PCT (B), and the second winter after PCT (C). Control stands are shown as dark symbols, standard PCT stands are empty symbols, and PCT-R stands are filled with light gray. The three areas are represented by squares (Spring Creek), circles (Cold Creek), and triangles (Beaver-Finley).

Figure 4. Relative change in snowshoe hare densities at the Spring creek (A), Cold Creek (B) and Beaver-Finley (C) areas. Control stands are shown as dark symbols, standard PCT stands are empty symbols, and PCT-R stands are filled with light gray. Y-axis values are ln(post-treatment density) minus ln(pre-treatment density) for individual forest stands. Times along the x-axis are post-treatment trapping occasions: one per summer for two years after treatment; two in the first winter (1A and 1B); and two in the second winter (2A and 2B).
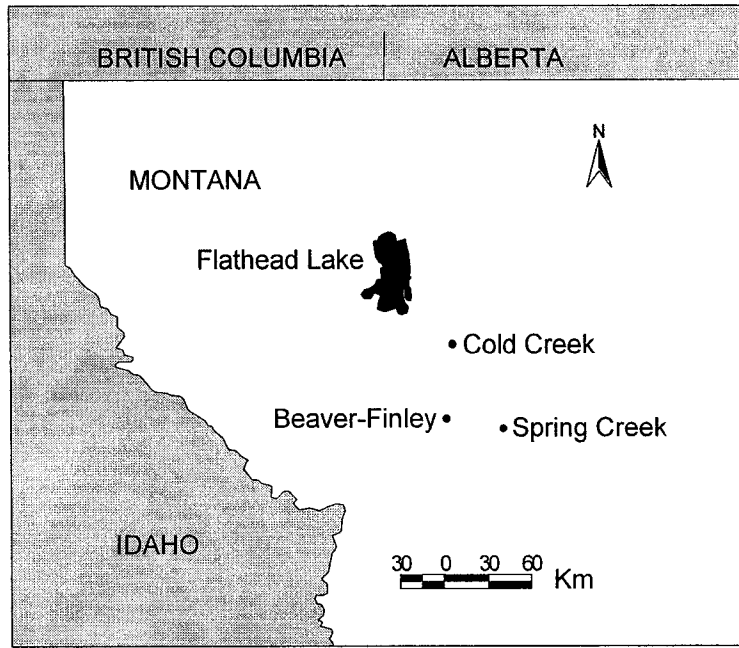
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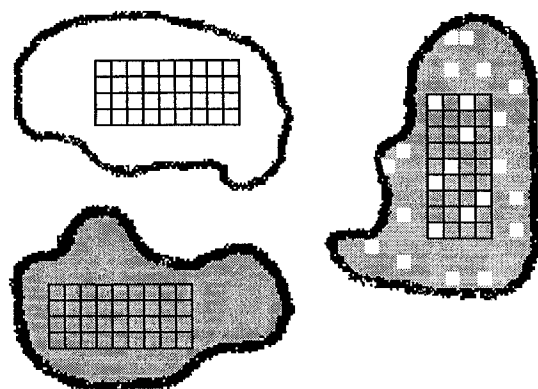
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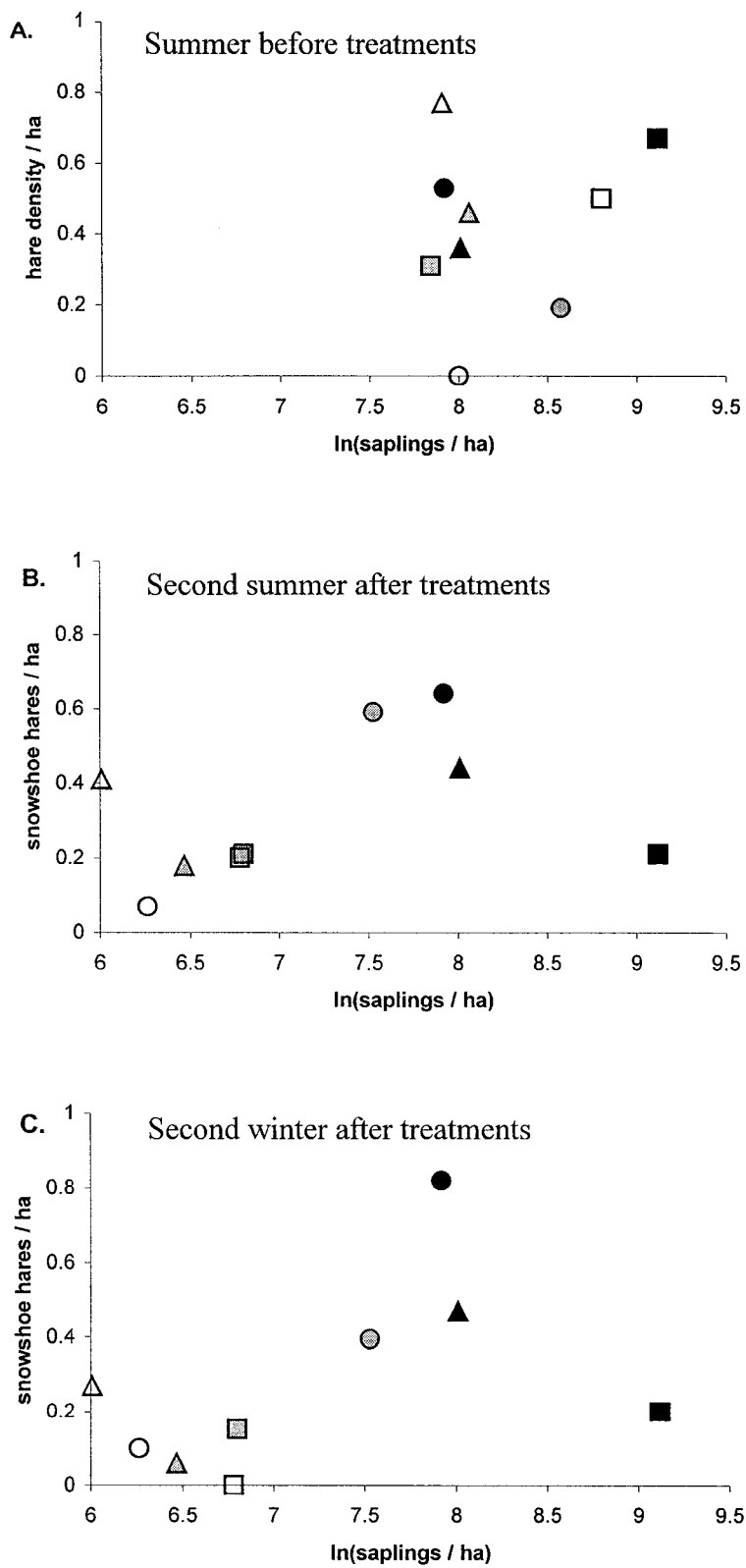
Figure 3.
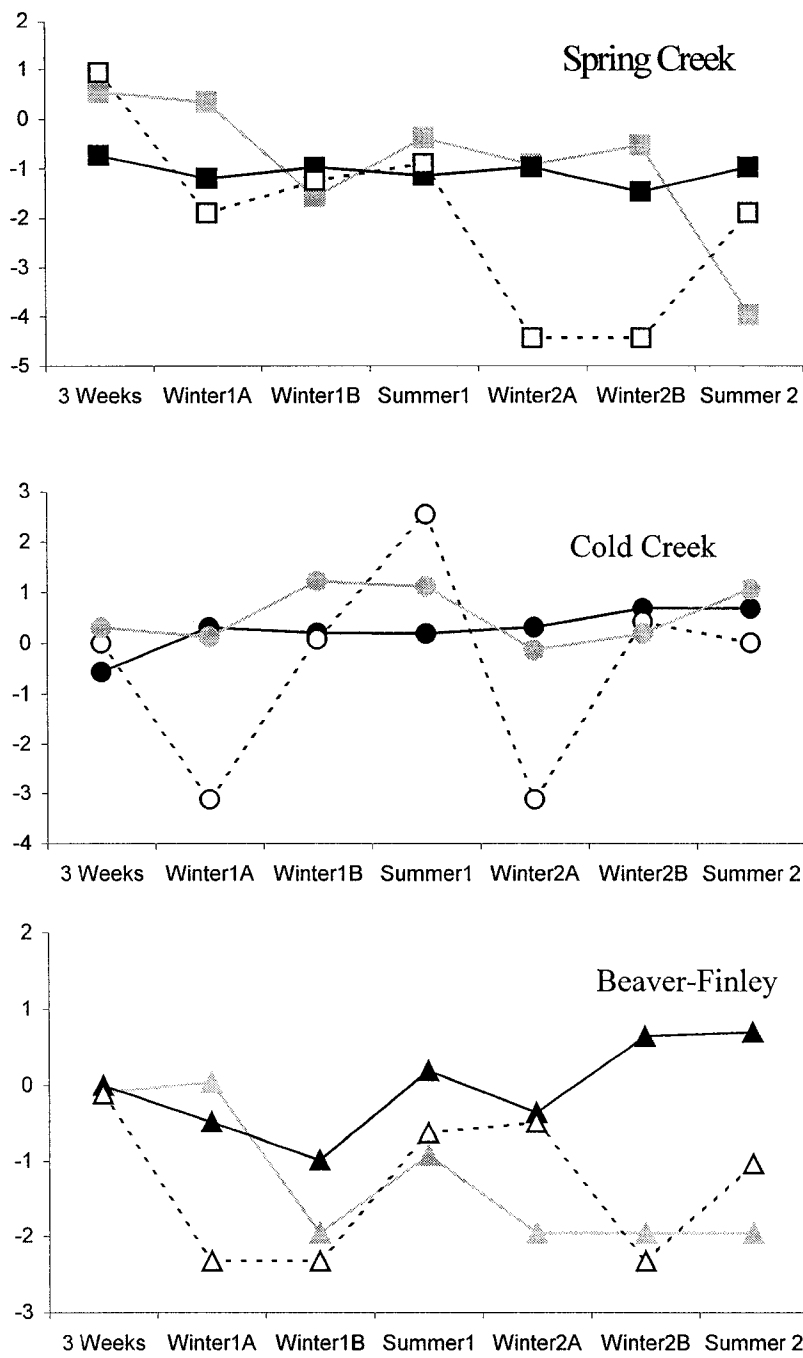
Figure 4.

Chapter 5. Snowshoe hares in a dynamic managed landscape

Introduction

Since the listing of the Canada lynx, *Lynx canadensis*, as threatened in the coterminous United States (U.S. Fish and Wildlife Service 2000), the effect of landscape-scale forest management on populations of snowshoe hares, *Lepus americanus*, has been a concern. Snowshoe hares are the central prey species of lynx (Aubry et al. 2000). Because snowshoe hare densities vary widely across different types of forested vegetation structure (Adams 1959, Dolbeer and Clark 1975, Wolff 1980, Wolfe et al. 1982), changes in forest vegetation structure through natural disturbance, succession, and silviculture can have dramatic impacts on populations. Snowshoe hare populations cycle with a regular 9-11 year period in the northern portion of the species range (Keith 1990) but evidence of a cycle to the south is mixed (Hodges 2000). Vegetative succession complicates population models (Johnson 2000). In Western Montana, we have found highest snowshoe hare densities in regenerating forest stands with high sapling density, and in uncut, late seral stage forest stands also with abundant saplings. This high quality snowshoe hare habitat in Montana can be thought of as having a bimodal distribution relative to forest stand age, with only young and much older stands providing the "closed" understoreys with abundant cover and browse (Buskirk et al. 2000). The layer of abundant shrubs and saplings that regenerates following clearcuts or large fires later disappears as the lower limbs die on growing trees, but may reappear when large trees die, creating canopy gaps (Oliver and Larson 1996). The potentially long period when the stand understorey becomes and remains comparatively "open" is a time of lower habitat quality. Anthropogenic canopy gaps in partially harvested stands can also allow stimulate

growth of a dense understorey layer under an established canopy (DeBell et al. 1997,

Tappeiner et al. 1997). Forest managers trying to maintain the prey base for lynx need to

balance the maintenance of snowshoe hare and other prey habitats with other

management goals (McKelvey et al. 2000). We used RAMAS GIS to explore the effects

of timing and placement of one type of silvicultural treatment on a population of

snowshoe hares distributed across many patches of varying quality, and highly connected

by movement.

In pre-commercial thinning of dense conifer regenerating stands in the western

U.S., live stem density is decreased from 3000-6000 / ha to 650-1300 / ha to increase tree

growth and yield, reduce future fuel load, and shift species composition (Seidel 1986,

Johnstone 1989, Martin and Barber 1995). Through pre-commercial thinning, the sudden

conversion of a "closed" understorey to an "open" understorey means the loss of cover

and forage for hares. In preliminary results from a three-year experiment, we have seen

two-fold to four-fold snowshoe hare density decreases during the two years after thinning

(Griffin and Mills, in preparation). Because dense, young forest stands were known to

hold high hare densities (Adams 1959, Wolfe et al. 1982, Hodges 2000), the U.S. Forest

Service halted pre-commercial thinning on lands defined as lynx habitat in 1999,

although the practice continues on private and state-managed lands. Because pre-

commercial thinning is a costly silvicultural investment, it may often be applied

synchronously across large contiguous areas.

Current studies are addressing whether pre-commercial thinning could accelerate

shrub and new seedling growth under the remaining trees, and what time scale is

necessary for the regrowth of understorey plants before a thinned stand is good habitat for

snowshoe hares. Similarly, uncut mature stands may lose understorey cover as a result of partial harvest operations. It is not clear how long a partially harvested mature stand must develop sufficient understorey cover to consider it equivalent in hare habitat quality to uncut mature stands where shrubs and saplings are dense.

The montane forests of the study region are dominated by subalpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occcidentalis*), lodgepole pine (*Pinus contorta*) and Engelman spruce (*Picea engelmannii*), and correspond generally to the "*Abies lasiocarpa / Menziesia ferruginea* warm phase" habitat type of Arno et al. (1985). Existing literature and successional models give a range of time necessary for development of a dense understorey in our study region (Zamora 1982, Arno et al 1985, Moeur 1985).

We parameterized our demographic model with vital rate estimates (survival, birth, and movement) from ongoing studies in the Seeley-Swan region of western Montana, where we are evaluating snowshoe hare population dynamics in four forest vegetation structural types: 1) uncut mature forest (henceforth referred to as "uncut mature"), partially harvested mature forest ("cut mature"), regenerating clearcut ("dense sapling"), and pre-commercially thinned or sparsely-regenerating clearcut ("open sapling"). These structural types were determined in the field, based on sapling density, basal area, horizontal cover, and overhead canopy cover (Table 1). Both the cut mature and open sapling structural types generally had little understorey cover. The preliminary data referred to in this chapter represent more than 4 years of intense work in 20 forest stands at 5 study sites (Griffin and Mills, in prep.).

Caution is appropriate in applying our data to larger spatial scales, for several reasons. First, by choosing four discrete vegetation structural types to study we excluded many structure types of the forest matrix. For example, what we call the uncut mature structural type has dense understorey making good cover and forage for hares; in reality many mature stands have canopies of large trees without a dense layer of shrubs or saplings. While our demographic research estimates vital rates in specific forest stands, hares can inhabit multiple structural types. Therefore hares in our model occupy a "patchy metapopulation" (Harrison 1994) with a high degree of movement between contiguous patches, each of potentially different quality.

Our second concern for modeling our data in a RAMAS GIS framework was that the conditions and timing of succession that cause stands to change from one type to another can vary dramatically depending on environmental factors, stand history, and site preparation (Arno et al. 1985).

Despite our considerable efforts in the field, the sample size and study duration are still not sufficient for us to evaluate carrying capacity and the type of density dependence. We also could not evaluate how dispersal varied according to patch type arrangement (Wiens et al. 1993). Finally, our preliminary data from a period of apparent decline give us no basis to evaluate whether vital rate estimates are close to average rates of the long term, especially for a species that may be cyclic.

Methods

Population Matrices

Our vital rate estimates are from the first 3 years of a 4-year study. Snowshoe hares born in the summer wean after 4-5 weeks (Keith 1990). Juveniles that survive to

spring are reproductive adults. Adult females at our study area could have bred in each of three synchronous pulses per summer, with nursing taking place overall during ~15 weeks. Fertility, defined here as total number of young expected per summer per reproductive female, was estimated from observed values and ultrasonographic examinations (Bienen et al., in review). We detected no difference in fertility between vegetation structure types although there were differences in litter size of newborns between the first, second, and third birth pulses.

Using known fates of 149 radio-collared hares, we estimated survival rates based on the candidate model with lowest AICc values computed in program MARK (White and Burnham 1999). The 11 models for adult and juvenile survival ranged in complexity from simple models with one parameter to models with multiple parameters for season-specific and habitat-specific survival (Griffin and Mills, in prep.). The selected model structure had the lowest AICc value by 4.57 AICc units, indicating that it is more than 10 times as likely as all other models (*after* Burnham and Anderson 1999). Based on the selected model, survival rates were equal in all vegetation structure types in the summer and winter, but differed in fall and spring, when survival was lower in structure types with "open" canopies (the cut mature and open sapling structure types). Survival rates of adult and weaned juvenile hares were indistinguishable. There was no difference between male and female survival rates, so we our matrix model reflects females only.

To reflect the seasonal differences in survival and movement, our matrix model has four time steps per year (Table 2). 40-year simulations require 160 time steps. We account for juveniles starting in the first fall after birth, so the population vector includes three juvenile stages (fall, winter, and spring) and four adult stages (summer, fall, winter,

spring). Because survival models for adult and juvenile hares were for 4-week time periods, mean seasonal survival rates were estimated by raising the 4-week rate to a power corresponding to the number of weeks in each season divided by 4 (Table 2). The fecundity term accounts for estimated survival of summer adults up to each birth pulse, fertility (number of female offspring per female per birth pulse), survival of newborns to weaning, and survival of weaned juveniles to the fall. To include all three 5-week nursing periods, the summer here is 15 weeks, and spring is 11 weeks. Over one year (4 time steps), population sizes decrease because of mortality, then increase after each summer due to reproduction.

Movement rates were specified as a dispersal function in RAMAS Metapop, based on radio-collared hare movements. Observed maximum distances that hares moved every season were log-normally distributed with a mean of approximately 275 m per season (Griffin and Mills, in prep.). More individuals left natal home ranges during the fall, so we assigned highest relative dispersal weights to fall stages.

In stochastic population models variances of vital rates should reflect the temporal and spatial variation but should exclude sampling variance, which results from uncertainty in parameter estimates owing to incomplete sampling of the population (Burnham et al. 1987, Thompson et al. 1998, Gould and Nichols 1998, Ludwig 1999, White 2000). For survival rates, we could not partition out temporal variation from total variation because the most parsimonious survival model did not include parameters for year-to-year temporal variation. Instead, standard errors for survival rate estimates were taken from the survival model and the corresponding standard deviations for seasonal survival rates used in RAMAS were found using the delta method (Agresti 1990).

Similarly, because our fecundity data were limited in temporal scale we could not partition temporal variance from total variance. We used the spatial variance in fecundity across all sites and vegetation structure types (0.75) as a proxy for temporal variance in fecundity. The implicit assumption that differences across sites are comparable to temporal variation at a single site is suspect, because differences in parameter values at different sites can result from variation in abiotic and biotic factors (Tyre et al. 2000).

In the absence of dispersal, the population projection matrix corresponding to structure types with open understories ("open matrix" for cut mature and open sapling structure types) has a yearly rate of increase of $\lambda = 0.49$. The population projection matrix for structure types with more densely vegetated understories ("closed matrix" for uncut mature and dense sapling structure types) has a yearly rate of increase of $\lambda = 1.03$.

The data from 1998-2001 were from a period of overall decline (Mills et al. In Prep). Average density estimates in summer 2001 were roughly 35% of summer 1998 values. Vital rate estimates for this period were probably influenced by whatever factor caused the declines. Because we do not know with certainly the cause of the declines, or how vital rates and movement would differ during population increases, we conducted simulations with the observed rates instead of increasing them arbitrarily to achieve stationary populations.

Model Landscapes and Succession

We limited model landscapes to four vegetation structure types (Table 1). We developed a single landscape including a simple model of succession, and evaluated the population dynamics of snowshoe hares in three additional scenarios which varied only in the timing and placement of pre-commercial thinning. We used the Spatial Data module

to create a single metapopulation map with 484 patches of 16 ha each, arranged in a square. Although snowshoe hare habitat is contiguous in reality, we included narrow 40 m boundaries so that RAMAS METAPOP could distinguish patches.

Each patch was randomly assigned an initial forest vegetation structure type. The target proportions of patches in each structure type desired were approximately 60% uncut mature, 15% dense sapling, 10% cut mature, and 5% open sapling. Our model landscape is unlike managed landscapes in western Montana because few, if any, have 60% uncut mature forest. In the Seeley Lake region the area of uncut mature forest is not more than 25%. When we initially allocated less uncut mature type, however, overall hare populations fell to zero before the end of the 40-year simulations. This decline was unacceptable for meeting the objectives of this study because we wanted to explore effects of the timing and extent of pre-commercial thinning. In including so much uncut mature type in the model, we ensured that some good quality hare habitat would remain as a source of snowshoe hares after thinning in each scenario.

Each patch was associated with snowshoe hare vital rates depending on the vegetation structure type found on the patch in each year. Uncut mature and dense sapling structure types had the higher survival rates of the "closed matrix." Cut mature and open sapling structure types had the lower survival rates of the "open matrix." The matrices for each patch at each time step were recorded in a "temporal change file" reflecting the starting vegetation structure type of each patch, and any changes in structure type that resulted from simulated succession or pre-commercial thinning.

We devised a simple model for forest succession allowing for transitions over time between the different vegetation structure types, and recorded the successional

trajectories of each patch. The successional simulation rules were used to represent

probabilistic changes between types. Transitions between types were based on mean rates

with a stochastic component analogous to demographic stochasticity, whereby transition

occurred if a random number drawn from a uniform 0-1 distribution was less than the

mean transition probability.

Any patch assigned initially as uncut mature type stayed in that condition; this

simplifying assumption ignores possible logging, catastrophic fire or insect damage that

could convert mature stands to younger structure types.

Reflecting potential tree crowding and crown lift, dense sapling type patches

could change to a vegetation structure type with an open understorey with an annual

probability of 0.015. After such a transition we left these patches with an "open" matrix

of vital rates for the remainder of the 40-year simulation. The 1.5% probability reflects

the assumption of a long residence time in the dense sapling type with the expectation of

half the patches changing to the open-understoreyed type by 45 years, given a binomial

distribution. Current management guidelines for preserving dense cover on U.S. Forest

Service lands in potential lynx habitats recommend not thinning in regenerating stands

until 45 years or older.

To signify regrowth of understorey plants to the point that open sapling type

patches support a high density of shrub and sapling cover, each patch of the open sapling

type changed to a vegetation structure type with dense understorey with annual

probability 0.033, based on the expectation that half the patches of open sapling type

should change to a structure type with a denser understorey after 20 years, given a

binomial distribution. Arno et al. (1985) indicate that high sapling coverage occurs 12-33

years after stand initiation, so the 20-year horizon is reasonable for dense growth of shrubs and small saplings.

To represent the growth of shrubs and saplings in patches starting as the cut mature type, such patches could change to and stay in a vegetation structure type with a dense understorey with annual probability of 0.02, based on an expectation that half the patches of cut mature type should develop adequate cover within 35 years, given a binomial distribution. The cut mature type had a lower probability of developing a dense understorey than the open sapling structure type because large standing trees can reduce light available for understorey growth. Tree crown area, which intercepts light, can be approximated as a linear function increasing with tree diameter and height (Moeur 1981). Shrub cover value is predicted to decline with increased basal area of a stand (Moeur 1985).

Four scenarios of landscape change

We refer to the single configuration of initial vegetation structure types and the time series of changes for that configuration as the "succession" scenario (#1). We used this configuration and time series, with changes only to those stands that were pre-commercially thinned in the three other scenarios: "upper half thin (#2)," "year 10 random thin (#3)," and "random thin (#4)." If a dense sapling type patch was thinned in a scenario, hares in that patch then had the lower survival rates associated with structure types with low understorey cover. In all three scenarios with thinning (#2, #3, #4), thinned patches could potentially convert back to the "closed" matrix with the higher survival rate as a result of succession, but only after three or more years. All scenarios were simulated 100 times.

In scenario #2, "upper half thin," we simulated spatial autocorrelation that could arise from patterns of land ownership. The randomly-assigned configuration of vegetation structure types that initialized all four scenarios included 54 dense sapling type patches in the 242 patches of the model landscape's upper half, and 68 such patches in the lower half. In the upper half thin scenario all 54 dense sapling patches were thinned at year 10. All 68 dense sapling patches in the lower half of the landscape were not thinned, and kept the same temporal change files as in the "succession" scenario.

In scenario #3, "year 10 random thin," 54 dense sapling patches were again thinned at year 10, but the placement of those patches was chosen at random from all 122 dense sapling patches.

In scenario #4, "random thin," an equal amount of thinning occurs on the landscape as in other scenarios, but it is spread out across the 40-year time period and the 122 dense sapling patches. For this, we calculated the annual risk of thinning to patches in the other scenarios by dividing the 54 thinned patches by the 122 total patches and by the 40-year duration of the simulations, giving 1.106% mean annual probability of thinning per patch. For every dense sapling patch in every year, we evaluated a random number against this quotient (0.01106) to determine whether or not it would be thinned. Fifty-five patches were thinned in this process over the 40-year simulation, while unthinned patches maintained the same temporal change files as in the "succession" scenario.

Other model parameters

We used the ceiling model for density dependence because of its simplicity and lack of evidence for a better alternative. We could not evaluate carrying capacity from

snowshoe hare time series at our sites, so we assigned it at K=42 for all 16 ha patches based on the highest density we observed (2.63 hares/ha). This is within the upper range observed in experimental plots in the Yukon (Hodges et al. 2001).

For all scenarios, we initialized all patches at a density of 0.6 hares / ha (10 individuals per patch), approximately the mean density observed in 1998. The initial distribution to stages was according to stable age distribution, with hares only in the fall juvenile and fall adult stage classes.

Model Predictions

Of the four scenarios, the "random thin" scenario maintained the highest average total snowshoe hare population size across the 40 years simulated (Figure 1). The "succession" scenario without thinning had the next highest average number of hares. The predictions of these two scenarios overlap substantially for all years simulated.

Both scenarios in which thinning occurred at year 10 maintained a lower total number of snowshoe hares than the other scenarios. On average the abundance was marginally higher in the "upper half thin" scenario than the "year 10 random thin" scenario; their standard deviation bars overlap substantially at all times.

Discussion

It is not surprising that overall abundance of hares was higher in the "succession" scenario than the "upper half thin" and "year 10 random thin" scenarios. Both of the latter scenarios include synchronous conversions of 54 out of 122 high-quality dense sapling structure type patches to low-quality open sapling type patches, with at least a 3-year lag before they could convert back to a vegetation structure type with dense understorey and higher hare survival rates.

More interesting is the possibility that, using our model assumptions, landscapes with a low level of pre-commercial thinning (the "random thinning" scenario) may support as many hares in the long term as landscapes without any thinning (the "succession" scenario). One critical assumption driving this result is that young thinned stands can eventually provide understorey cover necessary for snowshoe hares. A scenario without thinning may have supported hare higher densities, however, if stand-replacing processes such as catastrophic wildfire, insect damage, or clear-cutting had been included in the model; these would have led to regeneration of young, dense stands. Some outstanding research questions for models such as ours relate to successional rates: time for shrub and sapling growth to provide ample cover for hares; subsequent time until trees in the canopy reduce understorey light levels such that shrub and sapling cover becomes insufficient for hare survival; time to breakup of closed canopy so that understorey cover is again favorable. Also, we raise the vexing question of whether uncut mature stands can really be considered stable. For each of these successional rate questions, mean times will depend on many factors including elevation, moisture, species composition, and disturbance history. If, for example, the probability of changing from the open sapling type to a forest type with a dense understorey were lower than the value we used, then negative effects of thinning could be more severe and long-lasting.

The simulation results also hinge on the initial proportions of structure types and the other rules for our simple model of thinning treatment allocation and succession. To maintain non-zero model populations over the 40 year simulated interval, we had to assign roughly 60% of patches as high-quality uncut mature structure type. Even though patches of the dense sapling structure type were converted to open habitats by thinning in

the "random thin" scenario, these thinned patches were later available for dense understorey growth. In contrast, during the 40-year simulation the 122 patches in the "succession" scenario starting in the dense sapling vegetation structure type could only change into a type with crowded trees and an open understorey. After the creation of the starting arrangement of structure types in the landscape, the transition rates between structure types govern the overall availability of high-quality and low-quality patches. Furthermore, we simulated only one landscape arrangement in the succession scenario, which was then modified slightly under each of the thinning scenarios.

Our landscape contained only four of the many forest vegetation structure types in the region. Some other structural types may have higher vital rates than structure types with open understoreys. By assuming that pre-commercially thinned structure types had the same carrying capacity as all other structure types, we may have inflated the abundance that thinned patches could maintain.

Effects of our assumptions could be examined by linking randomized realistic models of succession to RAMAS GIS, and by estimating demographic rates in more vegetation structure types. Successional rates, especially, are expected to play a large role in the long-term dynamics of populations living in successional landscapes (Johnson 2000). Before any model such as ours is used to make management recommendations, sensitivity analysis (*sensu* Mills and Lindberg 2002) should be used to examine the effects of different landscape configurations and demographic and successional rates on projected hare population dynamics, perhaps with a program for generating large numbers of dynamic landscapes under different rules.

Populations declined over the 40-year duration of all 4 scenarios, and remained at low but relatively steady levels in the latter decades of the simulations. This happened even though the proportion of uncut mature structure type started at a frequency not found in our study region. The overall decline reflects strong declines expected in the two vegetation structure types associated with the "open" stage matrix of vital rates, and the comparatively modest growth rates of the other two vegetation structure types associated with the "closed" matrix.

The field data leading to demographic rate estimates used here were from a period when the real snowshoe hare population declined in the study region. At this time it is not clear whether the apparent snowshoe hare declines in our study area occurred because of drought or other environmental factors, because of some underlying cyclicity, or because of habitat-specific demography linked to forest age and type composition in the real landscape. Evidence is mixed as to whether snowshoe hares cycle in the southern range (Hodges 2000, Malloy 2000). If $\lambda > 1$ in all structure types during periods of increase, overall populations could periodically reach high levels despite pre-commercial thinning. Even during periods of overall population increase we would not expect vegetation structure types with open understoreys to have higher snowshoe hare survival than vegetation structure types with dense understoreys.

Despite the caution necessary in interpreting our results, the landscape modeling framework in RAMAS GIS allows us to make tentative suggestions about the influence of pre-commercial thinning on snowshoe hare populations, pending more refined information about vital rates and dispersal distances in many vegetation structure types, and rates of successional change between structure types of varying quality for hares. For

this model landscape where uncut mature forest was prevalent and stable, results suggest that snowshoe hare populations stay higher when pre-commercial thinning is not applied all at once in a landscape. In the context of less stable landscapes with a lower prevalence of favorable patches, successional transition rates should largely determine the dynamics of snowshoe hares.

Acknowledgements

Table 1. A key to the vegetation structure attributes we used to delineate the four nominal structure types used in this study. These categories leave out a large number of vegetation structure types found in the study region. Saplings are defined here as trees over 0.5 m tall, but less than 10 cm diameter at breast height.

Habitat type name	Structural attributes
Dense Sapling	Dense stands of regenerating conifers with > 5600 saplings / ha
Open Sapling	Open stands of regenerating conifers with < 3360 saplings / ha
Uncut Mature	Uncut forest stands with > 40% overhead canopy cover and basal area > 13.8 m^2 / ha (60 ft^2 / acre)
Cut Mature	Partially harvested forest with < 30% overhead canopy cover and basal area > 13. 8 m^2 / ha (60 ft^2 / acre).

	Juv(F)	Juv(W)	Juv(Sp)	Ad(Su)	Ad(F)	Ad(W)	Ad(Sp)
Juv (fall)	0	0	0	F^a	0	0	0
Juv (winter)	S_{JFa}	0	0	0	0	0	0
Juv (spring)	0	S_{JW}	0	0	0	0	0
Adult (sum)	0	0	S_{JSp}^b	0	0	0	S_{ASp}^b
Adult (fall)	0	0	0	S_{ASu}^b	0	0	0
Adult (wint)	0	0	0	0	S_{AFa}	0	0
Adult (spring)	0	0	0	0	0	S_{AW}	0

Table 2. Our stage-based projection model for snowshoe hares makes explicit the seasonal differences in survival rates. Survival rates are subscripted with J for juveniles and A for adults, then with Fa, W, Sp, and Su for fall, winter, spring, and summer. The fecundity term, F, accounts for survival of mothers up to each enumerated birth pulse, fertility per mother in each birth pulse (f_i), survival of baby leverets up to weaning in each birth pulse (S_{LevBPi}), and survival of weaned juveniles to the fall. Fertility is for female offspring only, i.e. half the total number of offspring. Adult survival rates in the fecundity term are raised to a power to indicate the number of weeks survived at that rate, out of the 15 in the summer. Juvenile survival after weaning until the fall is the same as adult summer survival (S_{ASu}).

[a] Fecundity term here is: $(f_1 {}^* S_{LevBP1} {}^* S_{ASu}^{(10/15)}) + (S_{AS}^{(5/15)} {}^* f_2 {}^* S_{LevBP2} {}^* S_{ASu}^{(5/15)}) + (S_{ASu}^{(10/15)} {}^* f_3 {}^* S_{LevBP3})$

[b] Spring survival rates reflect an 11-week period; summer survival rates reflect a 15-week period.
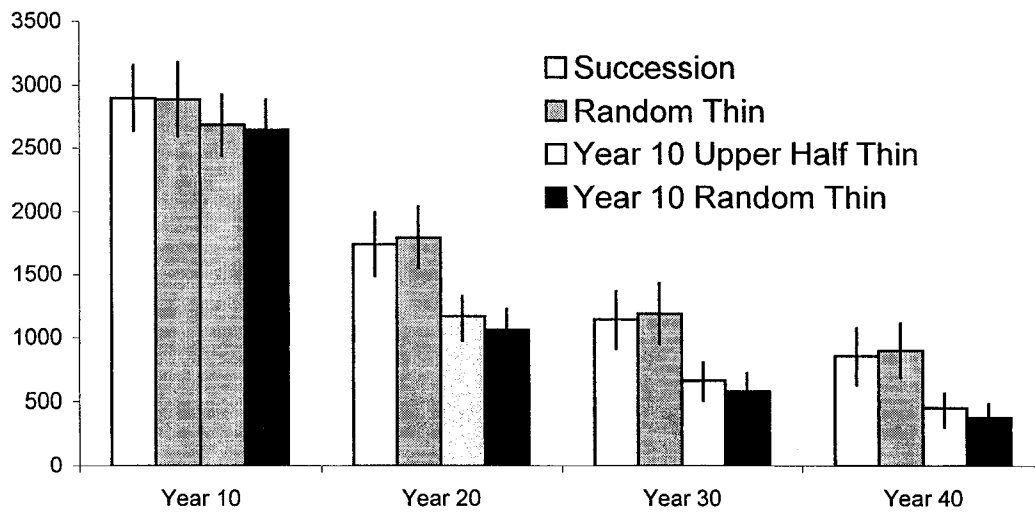
Figure 1. Overall abundance in four simulation scenarios for snowshoe hare populations at years 10, 20, 30 and 40. Scenarios in which thinning is applied in year 10 have lower trajectories than those with no thinning ("succession") or where thinning is spread out over time and space ("random thin"). Error bars are standard deviations from 100 simulations.

Appendix A. Mortality by moonlight: predation risk and the snowshoe hare

Abstract

1. Optimal behavior theory suggests that prey animals will reduce activity during intermittent periods when elevated predation risk outweighs the fitness benefits of activity. Specifically, the predation risk allocation hypothesis predicts both: that prey activity should decrease dramatically at times of high predation risk if there is high temporal variation in predation risk; and that if there is little temporal variation in predation risk, prey will have relatively uniform activity levels.

2. To test these predictions we examined the seasonably variable response of snowshoe hares to moonlight and predation risk.

3. Unlike studies finding uniform avoidance of moonlight in small mammals, we find that moonlight avoidance is seasonal and corresponds to the seasonal variation in moonlight intensity.

4. When the moon was more than half full and the ground was snow-covered, predation rates were higher and snowshoe hare movement distances were lower than near new moons. When the ground was snow-free, full moons changed predation rate only slightly, and snowshoe hare movement did not change according to moon phase. These results support the predation risk allocation hypothesis.

Key-words: moon phase; movement; predation risk; prey behavior; snowshoe hare (Lepus americanus).

Introduction

Prey animals commonly reduce activity levels in response to stimuli signaling high predation risk; this generally decreases encounter rates with predators (Lima 1998a).

Optimal prey animal behavior increases fitness by minimizing exposure to predation, while satisfying energetic needs for survival and reproduction (Rosenzweig 1974; Ghalambor & Martin 2001). Strong temporal variation in predation risk alone should dramatically reduce prey activity levels during very dangerous periods, and increase activity during relatively safer periods (Lima & Bednekoff 1999; Sih, Ziemba & Harding 2000). Conversely, if predation rates are relatively uniform across time, then prey should exhibit little variation in anti-predator response (Lima & Bednekoff 1999). These two predictions have been tested experimentally with invertebrates foraging in laboratory enclosures where predator scent was manipulated (Sih & McCarthy 2002), but not with wild vertebrates where reproduction and year-round survival determine fitness. With studies from multiple seasons we tested whether snowshoe hares follow both predictions of the predation risk allocation hypothesis (Lima & Bednekoff 1999) in response to measured changes in predation associated with moon phase.

Many researchers have used moonlight variation over the 29.5 day lunar cycle as a proxy for risk from predators (*reviewed in* Lima & Dill 1990; Lima 1998a; Lima 1998b). If predation rates depend on moonlight, then the moon's phase provides regular temporal variation in predation risk. Several studies have manipulated predation risk in semi-captive desert rodents under varying light conditions (Kotler et al. 1991; Longland & Price 1991; Bouskila 1995), but few have actually demonstrated that light from the full moon increases predation in the wild (Lima 1998a). In one exception, kangaroo rats were found to have decreased activity and increased predation during the full moon (Daly et al. 1992), but results were limited to the winter, when the difference in illumination from full and new moons is greatest.

Seasonal variation in the moon's path through the night sky changes the magnitude of variation in moonlight intensity between full and new moons. Behavioral responses to moonlight should be particularly strong in winter in the northern hemisphere because that is when the earth is closest to the sun (perihelion occurs near January 3) and lunar declination above the horizontal is maximal. For example, on a clear January night in Montana the full moon usually rises to $\sim 60°$ or more above the horizontal and has an illumination intensity $\geq \sim 0.2$ lux; in contrast, the moon is at a shallower angle of only $\sim 20°$ above the horizontal in July, illuminating at $\leq \sim 0.08$ lux (Janiczek & DeYoung 1987). The seasonal contrast in the moon's intensity becomes even more pronounced further to the north. Furthermore, in summer, foliage and the moon's low incident angle can shade the ground from moonlight, whereas in some biomes lack of deciduous foliage and the high reflective albedo of snow can further increase ambient moonlight at ground level in winter.

Snowshoe hares are prey for many forest carnivores including the Canada lynx (U.S. Fish & Wildlife Service 2000), *Lynx canadensis*, and most snowshoe hare mortality is due to predation (Boutin et al. 1986; Wirsing, Steury & Murray 2002). Snowshoe hares forage almost exclusively in twilight and night (Keith 1964; Mech, Heezen & Siniff 1966; Foresman & Pearson 1999) and may avoid open areas during moonlit nights in the winter (Gilbert & Boutin 1991). Females one year old and older reproduce in up to three or four synchronous birth pulses per summer (Keith 1990). Other reproductive behaviors are also synchronous because female receptivity to fertilization is high around the time of parturition. Annual survival rates for adults are low ($\leq 32\%$ (Hodges et al. 2001); $\leq 18\%$ (Wirsing, Steury & Murray 2002)) and under most conditions overall population growth

rate is more sensitive to juvenile survival than adult survival (Haydon et al. 1999). As a result, residual reproductive value is low, so current reproduction should contribute more to fitness than survival and reproduction the following summer (Rosenzweig 1974).

We used a natural experiment (Diamond 1986) to evaluate the effect of moonlight on snowshoe hare survival and movement in snowy and snow-free conditions. Moon phases and seasons were the natural perturbations and individual snowshoe hares were the experimental units whose response, in terms of survival and movement, could be evaluated. This system was ideal for testing the predation risk allocation hypothesis in the wild. At the latitude of the study site, the variation in moonlight intensity from full to new moon depends on the season, with highest expected variation in moonlight levels in winter, and lowest expected variation in summer. The predation risk allocation hypothesis in this context predicts that variation in snowshoe hare activity should be low when variation in lunar illumination and mortality is low, and high when variation in lunar illumination and mortality is high.

Materials and Methods

Study sites

Snowshoe hares in the survival analysis were on Richmond Ridge and Spring Creek, two areas encompassing more than 5 km^2 and separated by ~25 km in Montana's Seeley Lake region (47.3°N, 113.5°W). There are ongoing studies of Canada lynx in the region (Squires & Laurion 2000); other locally common snowshoe hare predators include coyote (*Canis latrans*), bobcat (*Lynx rufus*), great horned owl (*Bubo virginianus*), and Red-tailed hawk (*Buteo jamaicensis*). Fire and forest management here has resulted in a forest vegetation structure mosaic, with variation in canopy cover and forest understory,

so that sampled snowshoe hares inhabit multiple structural types found at both sites. Our research was conducted under University of Montana Animal Care and Use Committee protocol # 004-99(00,01).

All snowshoe hares in analyses of movement were on Richmond Ridge. Demographic studies that we have conducted since 1998 provided data concerning the timing of reproductive activity in the summers of 2000 and 2001 (Griffin et al. in press). At Richmond Ridge during this study we observed evidence of parturition on 25 June – 1 July 2000, 30 July – 8 August 2000, 31 May – 3 June 2001, 5 – 15 July 2001 and 11 – 19 August 2001. Conditions in the June 2001 full moon were snowy, due to an unseasonable storm that deposited over 50 cm of snow.

Predation risk

We monitored survival in adult and large juvenile ($\geq$ 500 g) radio-collared snowshoe hares over 32 lunar cycles (each of 29.5 days) from August 1999 – April 2002. Radio-collars were equipped with mortality switches that activated after ~ 6 hours of motionlessness. There was no systematic difference in the number of radio-collared snowshoe hares alive during the new moon periods as compared to full moon periods. In plotting the distribution of hares' estimated time of death in relation to the date of full moons we considered 4 relative moonlight categories: within 3.5 days of full, 3.5-7 days from full, 7-10.5 days from full, and 10.5-14.7 days from full (Figure 1). This categorization of moon phase ignores whether the moon is waxing or waning, but each category is associated with a total potential nighttime illumination relative to the nearest full moon; that illumination is a function of the time the moon is above the horizon and the proportion of its surface that reflects light to Earth.

Risk was defined as the observed proportion of mortality in different lunar phases. We monitored individual survival in 177 snowshoe hares every seven days or less, barring logistical problems. Of 115 observed mortalities, only three were censored from analyses because predation did not cause death. We plotted the distribution of snowshoe hare death in relation to moon phase in two broad seasonal periods, defined by the widespread absence or presence of snow on the ground, as determined by our observations and data from U.S. Forest Service Seeley Lake ranger station (~15 km from sites). Each snowshoe hare's date of death was estimated halfway between the dates last known alive and first heard dead (the "uncertainty interval"). Here we present data for the 51 snowshoe hares with uncertainty intervals ≤ 7 days; this associates each mortality confidently with either full or new moons. Results were qualitatively the same using all uncertainty intervals.

Movement

To examine movement patterns we located 7-12 snowshoe hares once per day and once per night during five-day observation periods centered on full or new moons (10 locations per animal per five-day period). To contrast the seasonal effects of moonlight we limited our observations on movements in two ways: to the new and full moon phases, and to summer and winter (Table 1). Movement distances were the nine linear distances between consecutive day-to-night and night-to-day locations. Day locations were between one hour after sunrise and one hour before sunset. Night locations were between one hour after sunset and ½ hour before sunrise. Any missed location for a snowshoe hare reduced the number of sequential distances by two. The order of animals located varied between nights. There was no biologically significant difference in the

distribution of location times for hares found under the full or new moons in summer (full

moon = 1:33 a.m., S.D.= 9 min.; new moon = 1:19 a.m., S.D. = 7 min.) or winter (full

moon = 11:27 p.m., S.D.= 31 min.; new moon = 11:36 p.m., S.D. = 32 min.).

To control for effects of habitat, sex, and individual variation in movement, we

followed the same individual snowshoe hares over multiple moon phases so that moon

phases were, in effect, treatments applied to all individuals simultaneously. The sample

was chosen from the pool of radio collared snowshoe hares available at the study site,

with attempts to balance the number of males and females, and the number of sampled

animals in different types of vegetation structure. Because of logistical constraints, we

did not include snowshoe hares in the sample that were more than 2 km from a central

access point. If individuals were killed we located additional snowshoe hares in

subsequent moon phases.

Universal Transverse Mercator (UTM) coordinates for all locations were recorded

with handheld GPS recorders (<10 m inaccurate). For 100 locations in July–August 2000

and all subsequent locations (total n=833), we determined snowshoe hare locations by

sight, or heard transmitter signals without an antenna, indicating proximity of <15 m (N.

Olson & P. C. Griffin, unpublished). If radio signals indicated a hare was moving away

from us as we approached, we did not record a location for that hare. Because of the high

accuracy, relative to the distances snowshoe hares typically move, we preferred this

walk-in method of locating hares. However, 132 triangulated locations made only in

July–August 2000 were estimated using program TelLoc7 (G. McDaniel, U.S. Forest

Service, Missoula, MT, unpublished), with uncertainty estimated using the location error

method (Zimmerman & Powell 1995). Triangulating observers were, on average, within

70 m of the snowshoe hare (S.E.=4.8 m), with mean location uncertainty 46 m (S.E.=2.3 m).

We used model selection (Burnham & Anderson 1998) to identify parameters that best explain observed snowshoe hare movement. Movement distances were the dependent variable in mixed model ANOVAs. Mixed models are conservative in estimating treatment effects because individual snowshoe hares (n = 34) are treated as a random effect, rather than using each location as independent. The five *a priori* candidate models potentially included two categorical variables, snow (snowy or snow-free) and moon phase (full or new), and an interaction between snow and moon phase. We used Akaike weights from corrected Akaike Information Criterion (AICc) values to identify the most parsimonious model.

Each night of full moon observation periods we recorded relative light level as bright or dark, based on visibility of shadows (Gilbert & Boutin 1991). Nights with intermittent shadows were considered dark. Dark full moon nights were always brighter than new moon nights because of the diffuse moonlight that penetrated clouds. We again used Akaike weights, this time to compare the fit of two mixed model ANOVAs to displacement data from full moon nights only; one model had an effect of clouds (differentiating bright and dark nights) and the simpler model did not.

Results

Mortality was nonrandom with respect to the moon in snowy conditions; 80% of observed mortality when the ground was snow-covered occurred in the two relative moonlight categories when the winter moon was half or more full (Table 2).

Correspondingly, snowshoe hares moved shorter distances during all winter full moon observation periods than during winter new moon periods (Fig. 2).

There was no difference in mortality rates between the full and new moon periods during snow-free periods (Table 2). In contrast to the winter, the full moon was not associated with lowered snowshoe hare movement in the summer except during the unusually snowy observation period in June 2001. Instead, the summer observation periods with the lowest mean distances moved (July – August 2000 new moon, June 2001 full moon and July 2001 new moon) were associated with birth pulses. Snowshoe hares of both sexes appeared to decrease movement during 5-day periods near parturition, as compared to nearby periods without parturition.

Under the most parsimonious *a priori* model for movement overall, when the ground was snow-covered snowshoe hare movement distances under full moons were 75 m shorter than during new moons (Fig. 3). This model included parameters for snow, moon, and a snow*moon interaction; the Akaike weight was 0.9999, indicating a far better fit than any other model considered. The moon was not associated with an appreciable difference in movement when the ground was snow-free.

Light level itself was the likely cue for reduced movement in winter. Considering movement only on full moon nights during snowy conditions, snowshoe hares moved slightly more when clouds darkened the moon. Our criterion to distinguish bright from dark nights was seeing a distinct shadow (Gilbert & Boutin 1991), so some cloudy nights with rather bright, but diffuse, light were classified as dark. Despite this, under the slightly more parsimonious model for movement near full moons, snowshoe hares moved 21.3 m (S.E. = 11.7 m) more on cloudy (dark) winter nights than on clear (bright) winter

nights. The Akaike weight was 0.71 for the model including an effect of clouds, and 0.29 for a simpler model without the clouds' effect.

Discussion

Our observations from a wild population over 2 ½ years support two central predictions of the predation risk allocation hypothesis (Lima & Bednekoff 1999), which has heretofore been tested only in the laboratory (Sih & McCarthy 2002). First, prey activity in winter decreased during 5-day observation periods of brightest illumination (and high danger) and increased during the contrastingly darkest 5-day, safest periods. When the ground was snowy, predation increased 4-fold under full moon phases (Table 2), and snowshoe hares displayed reduced movement during these periods (Fig. 3). Longer movement distances indicate that a snowshoe hare was traveling through a larger area, and potentially encountering more predators. By decreasing their movements during times of elevated predation risk, snowshoe hares were likely decreasing their encounter rates with predators. The increased proportion of death in the days near winter full moons was higher than expected by chance. We conclude that the moon phase played a role in the susceptibility of snowshoe hares to predation, whether that predation occurred at night or in the day.

In winter, the cyclic regularity of risk and safety may facilitate the observed behavioral response: snowshoe hares moved lesser distances when the risk of predation was high. During brief periods of reduced winter activity, low food intake or consumption of lower-quality food could reduce fitness. However, because survival until the summer breeding season is essential for individuals to have any fitness at all, behaviors that lead to higher winter survival should be favored by natural selection. The

reduced movement in full moon periods could be compensated by foraging relatively more during predictably dark periods when the moon is not high above the horizon. With every day further from the full moon there is approximately 50 minutes more darkness during which foraging should be relatively safe, so a few nights of reduced caloric intake could be followed by nights with progressively longer safe feeding periods. Interestingly, we found the highest frequency of mortality in winter during when the moon was 3.5-7 days from full (Table 2), a period for which we have no data on snowshoe hare movement, but during which we speculate hares may forage intensely to compensate for reduced activity during the height of the full moon.

Second, snowshoe hare movements did not respond to moon phase when its influence on predation was low. During snow-free periods the full moon was not associated with increased predation (Table 2) and we found no consistent reduction in movement in the five days closest to the full moon (Fig. 3). If anything, reproductive activities influenced snowshoe hare movements more than moonlight in summer, when every adult's reproductive value was at its peak. Female snowshoe hares reduce movement around parturition (Hodges 1999), and male movement is closely tied to females during the breeding season (Bider 1961). The increased activity two weeks before or after parturition may coincide with times when males assess females' spatial distribution, and when prenatal and lactating females forage intensively.

Archibald (1977) suggested that the 9-11 year snowshoe hare cycles, which are more regular and pronounced in higher latitude boreal forests (Murray 2000), may be synchronized in part by lunar phenomena that recur on a 9.3-year interval. This is half the length of the moon's 18.6-year nodal cycle that governs the moon's declination above the

horizon, the timing of moonrise and moonset and the length of time it is visible in the night sky. The brightest full moons closest to any fixed calendar date occur every 9.3 years when the moon reaches a maximum in its declination above the horizontal, its corresponding incident illumination, and its total time above that horizon. The lowest and least bright full moons near the same calendar date also occur predictably every 9.3 years, but 4-5 years after the brightest. Archibald's model (1977) did not posit a mechanism causing the correlation between the nodal cycle and snowshoe hare population dynamics, but our observations on the seasonality of predation risk and moonlight may be relevant. Snowshoe hare population growth rate is most sensitive to juvenile survival rate, followed by adult survival rate. If juvenile and adult snowshoe hares suffer higher predation rates during years with higher and brighter full moons, then population growth rates for such years should be low relative to other years, potentially leading to population declines. We lack data to test this hypothesis, but suggest that future studies focus on variation in survival rates in winter, during which we found strong effects of moonlight on snowshoe hare predation risk.

Our results support the predation risk allocation hypothesis and suggest that the mediating effect of the lunar illumination on many predator-prey interactions could vary seasonally. Prey that reliably assess the safety and danger of the moon phases in different seasons should have relatively higher fitness, and be favored by natural selection.

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TABLE 1. Moon phase and dates of intensive snowshoe hare movement observation periods, with sample size of snowshoe hares (n), the snow condition on the ground at the time.

Moon phase and dates	n	Snow condition
Full, 13-19 July 2000	12	snow-free
New, 28 July – 3 August 2000	12	snow-free
Full, 6-11 February 2001	7	snowy
New, 21-25 February 2001	7	snowy
Full, 7-11 March 2001	9	snowy
New, 19-23 May 2001	9	snow-free
Full, 4-8 June 2001	9	snowy
New, 18-22 July 2001	9	snow-free
Full, 2-6 August 2001	10	snow-free
New, 11-15 January 2002	10	snowy
Full, 25-30 January 2002	7	snowy

Table 2. The distribution of estimated snowshoe hare mortalities in relation to the 4 moonlight categories from full moon (0-3.5 days from full) to new moon (10.5 – 14.7 days from full). The two columns represent the snowshoe hare mortalities recorded during snowy periods and periods without complete snow cover. There was pronouncedly higher mortality near the full moon when the ground was snowy but not when it was snow-free; the distribution of mortality dates with respect to the four relative moonlight categories was nonrandom in the winter (χ^2; P=0.0285), but may have resulted from chance in the summer (χ^2; P=0.239).

Days from full moon	Snowy	Snow-free
0 – 3.5	7	7
3.5 – 7	9	12
7 – 10.5	3	4
10.5 – 14.7	1	8
Total	20	31

Figure Legends

Figure 1. Four categories of relative moonlight illumination used to examine patterns of snowshoe hare mortality, as defined by length of time from a full moon. The four moonlight categories are overlaid on the 29.5 day lunar cycle. The moon is ~ 85% to 50% as bright as the nearest full moon in the 3.5-7 d period, ~ 50% to 15% as bright in the 7-10.5 d period, and ~ 15% to 0% as bright in the 10.5-14.7 d period

Figure 2. In snowy conditions, snowshoe hares moved less during the full moon (light bars) than the new moon (dark bars). Values are chronologically ordered means + 1 S.E., based on all snowshoe hares in each five-day observation period, and up to nine movements per snowshoe hare. There was snow during the first full moon in summer 2001, but all other summer observation periods were snow-free.

Figure 3. Expected movement distances under the most parsimonious model for snowshoe hares under new moons (dark circles) and full moons (open circles) ± 1 S.E. Full moons reduced movement when conditions were snowy (right pair), but not when conditions were snow-free (left pair).
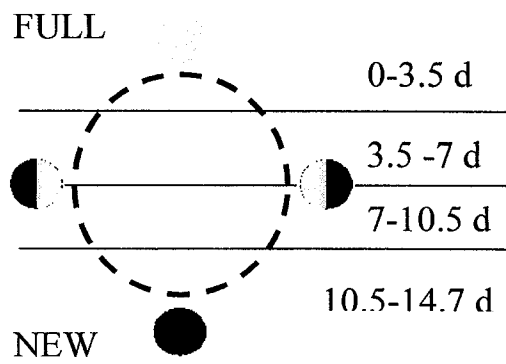
FULL
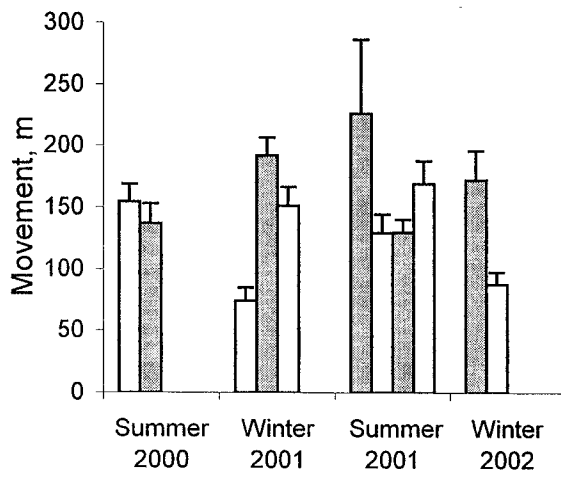
0-3.5 d

3.5 -7 d

7-10.5 d

10.5-14.7 d

NEW

Figure 1.

Figure 2.
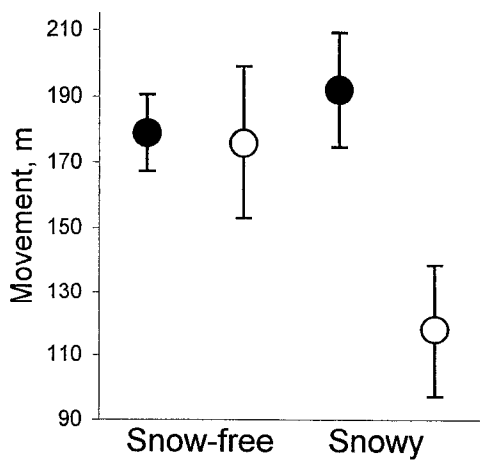

Figure 3.

Appendix C. Forest microhabitats associated with dead snowshoe hares

Abstract

The vegetation structure microhabitat at 49 locations where dead radio-collared snowshoe hares were found were compared to 98 locations sampled systematically throughout a study site in the Seeley Lake region of western Montana. No dead radio-collared hares were located in patches with high sapling density (e.g., > 13,000 / ha) , although they were found in all other vegetation structures represented on the site. Conversely, dead radio-collared snowshoe hare remains were found more often in microhabitats with very little understory cover (e.g., < 800 saplings / ha) than samples of available microhabitats at the site would have predicted. These observations support conclusions that patches with high sapling density can play a role in snowshoe hare survival.

Introduction

Snowshoe hares, *Lepus americanus*, are the principal prey of the Canada lynx, *Lynx canadensis*, which was recently listed as threatened in the coterminous 48 states south of Canada (USFWS 1999). As a result there is increased attention on managing forested landscapes within the range of Canada lynx to maintain landscape and vegetative features that increase snowshoe hare abundance, thereby potentially increasing the abundance of Canada lynx (Ruggiero et al. 2000).

Throughout their wide range in North America; highest snowshoe hare densities occur with abundant young conifer saplings and tall shrubs (Adams 1959, Dolbeer and Clark 1975, Wolff 1980, Wolfe et al. 1982, Pietz and Tester 1983, Fuller and Heisey 1986, Koehler and Brittell 1990, Koehler 1991, Hodges 2000a, Shaw 2002). The observed high densities could result from some combination of preferential movement into; higher survival in; or higher reproduction in such habitats.

Wolff (1980, 1981) hypothesized that stands with high understory density act as net sources of emigrant snowshoe hares that supplement hare populations in nearby, lower-quality habitats. The predicted outflow of hares can only result if the microhabitats with dense shrub and sapling cover have higher survival and / or reproductive rates than surrounding habitats.

We investigated the vegetation structures within stands that would be valuable to maintain high snowshoe hare abundance in the overall landscape. We tested test whether

there was an association between vegetation structure at the microhabitat scale and snowshoe hare mortality locations.

Methods

The study site was in the Seeley-Swan region of western Montana, where forested landscapes have relatively high densities of snowshoe hares, snowy winters and a mesic climate. The region is also a center of ongoing Canada lynx ecological studies (Squires and Laurion 2000). At the elevations of the site (1,450 – 1,600 m), dominant conifers are lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). A wide variety of montane and subalpine shrubs and forbs also provide some cover and forage during the summer and fall.

From August 1999 to April 2002 we radio-collared snowshoe hares and followed their movements and fates (Griffin and Mills, in press). We used handheld GPS recorders accurate to ≤10 m to mark locations where radio collars of dead snowshoe hares were found. To assess the vegetation structure characteristics of surrounding microhabitats we returned to all 49 of these "mortality locations" that were found before July 2001 and that had precise coordinate positions; these were distributed throughout the site. We measured vegetation structure at plots centered on the point where the radio collar was found. Around each plot center where the dead snowshoe hare was found we recorded sapling density, shrub cover, coarse woody debris, horizontal cover and overhead canopy cover in 3 subplots per plot. The 2 m radius subplots were centered at the end of 3 lines (5 m long) emanating from the plot center, with 120° angles between each line. We used a relaskop (Speigel Ltd., Germany) to determine the extent of variable-radius plots, in which we measured basal area and diameter of large trees (>10 cm diameter at 1.4 m height). For comparison to other available microhabitats, we made the same measurements at 98 plots throughout the Richmond Ridge study site. These were sampled from a population of 348 snowshoe hare trap locations, which were placed systematically throughout the study site. The vegetation plot locations were centered 10 m away from the trap location in a direction perpendicular to any trap line, to ensure that the vegetation measured was not influenced by human foot traffic.

To test the null prediction that the 49 hare mortality locations were typical of vegetation structures found throughout the site, we used principle components analysis (Johnson 1998) to classify the vegetation structure at the 98 systematic plots. This identified a combination of variables that separates vegetation structures at the Richmond Ridge study site into orthogonal axes. We then used the resulting equations to project the 49 mortality locations in the same coordinate space, and looked for differences in the two distributions.

Results

Four out of seven total vegetation structure variables were selected in a PCA model that described 81% of variation between the 98 vegetation plots that were not associated with dead hares. These variables were sapling density (mean = 1318 /ha; S.D. = 1604 /ha), large tree basal area (mean = 12.8 m^2/ha; S.D. = 14.9 m^2/ha), overhead canopy cover (mean = 24 % ; S.D. = 21%) and horizontal cover (mean = 33 %; S.D. = 21 %). Principal component axis 1 (PC1; 43% of variation explained) was heavily influenced by large trees and canopy cover; the value on this axis is high when a plot includes many large trees and has dense overhead cover. Principal component axis 2 (PC2; 38% of variation explained) was heavily influenced by saplings and horizontal cover; the value on this axis is high when a plot has high understory cover. Principal axes 3 and 4 were less informative, comprising 11% and 8% of variation explained, respectively.

Vegetation structures at snowshoe hare mortality sites were mostly similar to those sampled in plots throughout the site, as indicated by the largely overlapping distribution of vegetation structure for the two sets of vegetation plots projected into two dimensions (Figure 1). We found, however, a region of available vegetation structure space where no dead hare locations were found; six of the 98 systematic plots, but none of the 49 mortality locations, had PC2 axis values $\geq$ 2.3. Sapling densities at PC2 of 2.3 would be > 5,500 / ha at mean values for basal area, canopy cover, and horizontal cover. Two measured plots with PC2 values of ~ 2.5 held sapling densities over 13,000 / ha. Three mortality sites, but no systematic plots, were found at values of PC2 $\leq$ -1.6; these were microhabitats with very low sapling density (0, 530, and 795 / ha) and little horizontal cover.

Discussion

The only microhabitats where we did not find remains of dead, radio-collared snowshoe hares were those with extremely dense understory cover (i.e. sapling density ≥ 5,500 / ha). The lack of mortality locations in such microhabitats support the prediction that snowshoe hares are safer where understory cover is particularly dense. We recognize that some locations where we found radio collars may have reflected the locations where predators took dead hares to consume, although we did not identify any locations as such. Even if this was the case for some radio collar locations, the lack of locations in extremely dense microhabitats suggests that predators there have limited predation success.

Our results help to explain the well-documented prevalence of snowshoe hares in habitats with very high understory density. The lower proportion of dead individuals in habitats with dense understories suggests that such microhabitats provide safe refuge for hares from their many predators.

Figure Legend

Figure 1. Scatterplot of vegetation structure attributes at snowshoe hare mortality sites
(crosses) and systematically located sites (circles). Coefficients in the PC1 and PC2
principle component axes are multiplied by standardized overhead canopy (CAN), basal
area (BA), sapling density (SAP), and horizontal cover (HOR) values. PC1 =
0.898*(CAN) + 0.843*(BA) + 0.163*(SAP) + 0.427*(HOR). PC2 = -0.184*(CAN) –
0.360*(BA) + 0.866*(SAP) + 0.767*(HOR).
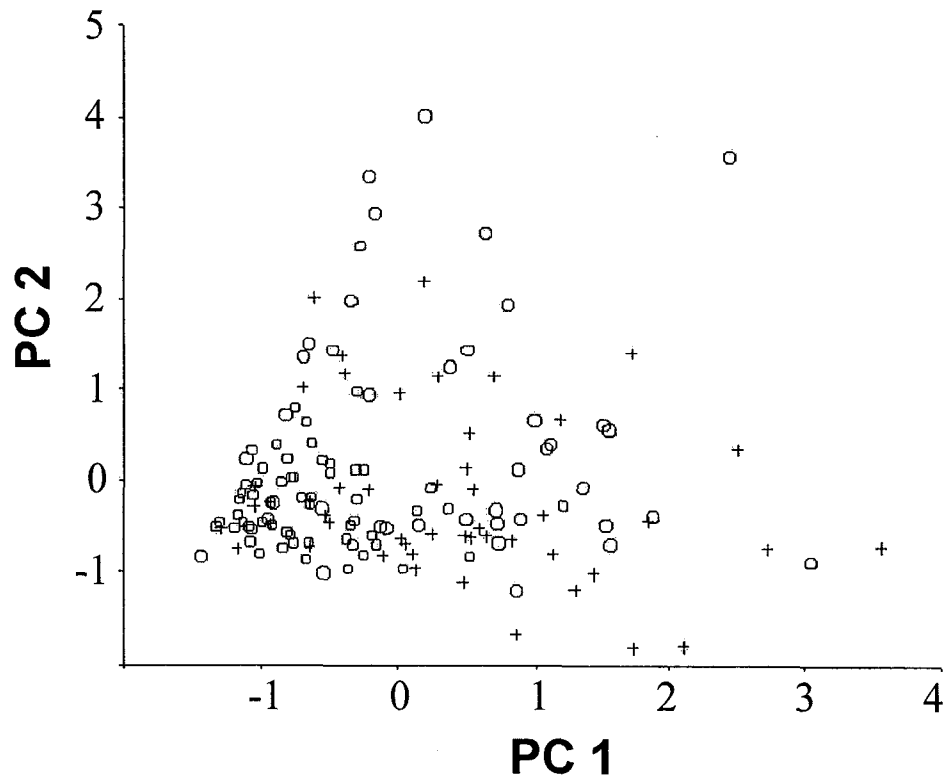
Figure 1.

Literature Cited

Adams, L. 1959. An analysis of a population of snowshoe hares in northwestern

Montana. Ecological Monographs 29:141-170.

Agee, J. K. 2000. Disturbance ecology of north American boreal forests and associated

northern mixed/subalpine forests. Pages 39-82 *in* L.F. Ruggiero, K.B. Aubry, S.W.

Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey and J. R. Squires, *editors*. The

scientific basis for lynx conservation. University Press of Colorado, Boulder.

Agresti, A. 1990. Categorical data analysis. Wiley, New York.

Akaike, H. 1973. Information theory as an extension of the maximum likelihood

principle. Pages 267-281 *in* B.N. Petrov and F. Csaki, editors. Second international

symposium on information theory. Akademiai Kiado, Budapest, Hungary.

Akçakaya, H. R. 2002. RAMAS GIS: linking spatial data with population viability

analysis, version 4.0. Applied Biomathematics, Setauket, New York.

Archibald, H.L. 1977. Is the 10-year wildlife cycle induced by a lunar cycle? Wildlife

Society Bulletin 5: 126-129.

Arno, S. P., Simmerman, D. G., and Keane, R. E. 1985. Forest succession on four habitat

types in western Montana. General Technical Report INT-177. U.S. Department of

Agriculture, Forest Service, Intermountain Forest and Range Experiment Station,

Ogden, Utah.

Askins, R. A. 2001. Sustaining biological diversity in early successional communities:

the challenge of managing unpopular habitats. Wildlife Society Bulletin 29:407-412.

Aubry, K. B., Koehler, G. M., and Squires, J. R. 2000. Ecology of Canada lynx in

southern boreal forests. Pages 373–396 in L.F. Ruggiero, K.B. Aubry, S.W. Buskirk,

G.M. Koehler, C.J. Krebs, K.S. McKelvey and J. R. Squires, *editors*. The scientific

basis for lynx conservation. University Press of Colorado, Boulder.

Beauvais, G. P. 2000. Mammalian responses to forest fragmentation in the central and

southern Rocky Mountains. Pages 177-199 *in* Forest Fragmentation in the Southern

Rocky Mountains, R. L. Knight, F. W. Smith, S. W. Buskirk, W. H. Romme, and W.

L. Baker, *editors*. University Press of Colorado, Boulder.

Beregi, A., V. Molnar, S. Zorn, Cs. Felkai, and K. Voros. 2000. Abdominal

ultrasonography in pet guinea pigs. Acta Veterinaria Hungarica 43: 261-269.

Bider, R.J. 1961. An ecological study of the hare *Lepus americanus*. Canadian Journal of

Zoology 39: 81-103.

Bjørnstad, O. N., H. P. Andreassen, and R. A. Ims. 1998. Effects of habitat patchiness

and connectivity on the ecology of the root vole *Microtus oeconomus*. Journal of

Animal Ecology 67: 127–140.

Black, H.C. 1965. An analysis of a population of snowshoe hares, *Lepus americanus*

washintonii Bairdi, in Western Oregon. Doctoral Dissertation, Oregon State

University.

Bookhout, T. A. 1964. Prenatal development of snowshoe hares. Journal of Wildlife

Management 28: 338-345.

Boulanger, J.G. and G.C. White. 1990. A comparison of home-range estimators using

Monte Carlo simulation. Journal of Wildlife Management 54:310-316.

Bouskila, A. 1995. Interactions between predation risk and competition: a field study of

kangaroo rats and snakes. Ecology 76: 165-178.

Boutin, S.A., Krebs, C.J., Sinclair, A.R.E. and Smith, J.N.M. 1986. Proximate causes of loss in a snowshoe hare population. Canadian Journal of Zoology 64: 606-610.

Buehler, D.A. and L.B. Keith. 1982. Snowshoe hare distribution and habitat use in Wisconsin. Canadian Field-Naturalist 96:19–29.

Burgman, M.A., S. Ferson and H.R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London.

Burnham, K. and D. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., and Pollock, K. H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. Monograph 5. American Fisheries Society, Bethesda, Maryland.

Buskirk, S. W., L. F. Ruggiero, K. B. Aubry, D. E. Pearson, J. R. Squires, and K. S. McKelvey. 2000. Comparative ecology of lynx in North America. Pages 397–418 *in* L. F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey and J. R. Squires, *editors*. The scientific basis for lynx conservation. University Press of Colorado, Boulder.

Carey, A. 1995. Sciurids in Pacific northwest managed and old-growth forests. Ecological Applications 5:648-661.

Cary, J. R., and Keith, L. B. 1979. Reproductive change in the 10-year cycle of snowshoe hares. Canadian Journal of Zoology 57:375-390.

Caswell, H. 1989. Matrix population models. Sinauer Publishers, Massachusetts.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with

application to zoological censuses. University of California Publications on Statistics

1: 131–160.

Cox, D.R. and D. Oakes. 1984. Analysis of survival data. Chapman and Hall, New York.

Cubberly, D. A., T. G. Lee, C. L. Laughlin, B. Weintraub, M. R. Caudle, and V. D.

Nielson. 1982. Importance of ultrasound determination of pregnancy in the rabbit.

American Journal of Veterinary Research 43:1802-1803.

Daly, M., Behrends, P.R., Wilson, M.I. and Jacobs, L.F. 1992. Behavioural modification

of predation risk: moonlight avoidance and crepuscular compensation in nocturnal

desert rodent, *Dipodomys merriami*. Animal Behaviour 44: 1-9.

Daniel, T. W., J. A. Helms, and F. S. Baker. 1979. Principles of silviculture, 2nd edition.

McGraw-Hill, New York.

Davies, K. F., C. Gascon, and C. R. Margules. 2001 Habitat fragmentation;

consequences, management, and future research priorities. *In* Soulé, M. E., and G. H.

Orians, *eds.*, Conservation Biology; research priorities for the next decade, pp.81–98.

Island Press, Washington, D.C.

DeBell, D.S., R.O. Curtis, C.A. Harrington, and J.C. Tappeiner. 1997. Shaping stand

development through silvicultural practices. Pages 141-149 *in* Kohm, K.A. and J.F.

Franklin, *editors*. Creating a forestry for the 21st century; the science of ecosystem

management. Island Press, Washington, D.C.

Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural

experiments. Pages 3 – 22 in Community Ecology, J. Diamond and T.J. Case,

editors. Harper and Row, New York.

Diffendorfer, J.E. 1998. Testing models of source-sink dynamics and balanced dispersal. Oikos 81:417–433.

Doerr, J. G., and N. H. Sandburg. 1986. Effects of precommercial thinning on understory vegetation and deer habitat utilization on Big level island in southeast Alaska. Forest Science 32: 1092-1095.

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.

Elton, C. 1924. Periodic fluctuations in the numbers of animals; their causes and effects. British Journal of Experimental Biology 2: 119–163.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. Journal of Animal Ecology 11: 215–244.

Foresman, K.R. and Pearson, D.E. 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.

Fuller, T. K., and D. M. Heisey. 1986. Density-related changes in winter distribution of snowshoe hares in northcentral Minnesota. Journal of Wildlife Management 50:261-264.

Ghalambor, C.K., and Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. Science 292: 494-497.

Gilbert, B.S. and Boutin, S. 1991. Effect of moonlight on winter activity of snowshoe hares. Arctic and Alpine Research 23: 61-65.

Gillis, E., and C. J. Krebs. 2000. Survival of dispersing versus philopatric juvenile snowshoe hares: do dispersers die? Oikos 90: 343–346.

Gilpin, M.E. and I. Hanski, eds. 1991. Metapopulation dynamics: empirical and theoretical investigations. Biological Journal of the Linnean Society 42: 1–336.

Gould, W. R., and Nichols, J. D. 1998. Estimation of temporal variability of survival in animal populations. Ecology 79: 2531–2539.

Griffin, P. C., and L. S. Mills. 2004. Snowshoe hares in a dynamic managed landscape. *In* Species Conservation and Management: Case Studies, H.R. Akcakaya, M.A. Burgman, O. Kindvall, C. Wood, P. Sjögren-Gulve, J. Hatfield, and M.A. McCarthy, *eds*. Oxford University Press.

Griffin, P. C., and L. S. Mills. Snowshoe hare demography in heterogeneous southern landscapes. In preparation for submission to Ecology (This dissertation, Chapter 3).

Griffin, P. C., L. Bienen, C. Gillin, and L. S. Mills. 2004. Estimating pregnancy rates and litter size in snowshoe hares using ultrasound. Wildlife Society Bulletin. In Press.

Griffin, P.C., and L. S. Mills. Young forest management and snowshoe hares. In review, Conservation Biology (This dissertation, Chapter 4).

Griffin, P.C., C. Waroquiers, S. Cox, and L.S. Mills. Effects of moonlight on snowshoe hare movement. In review, Journal of Animal Ecology (This dissertation, Appx. A).

Gyllenburg, M., I. Hanski, and A. Hastings. 1997. Structured metapopulation models. *In* Hanski, I., and M. E. Gilpin, *eds.*, Metapopulation biology, pp. 93–122. Academic Press, San Diego, CA.

Hanski, I. 1997. Metapopulation dynamics: from concepts and observations to predictive models. *In* Hanski, I., and M. E. Gilpin, *eds.*, Metapopulation biology, pp. 69–92. Academic Press, San Diego, CA.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *In* Hanski, I., and M. E. Gilpin, *eds.*, Metapopulation biology, pp. 5–26. Academic Press, San Diego, CA.

Harkness, J. E., and J. E. Wagner. 1995. The Biology and Medicine of Rabbits and Rodents. Lippincott, Williams and Wilkins Press. Baltimore, Maryland, USA.

Harrison, S. 1994. Metapopulations and conservation. *In* P.J. Edwards, R.M. May, and N. R Webb, *eds.* Large-scale ecology and conservation ecology, pp. 111-128. Blackwell Science, Oxford.

Haydon, D. T., E. A. Gillis, C. I. Stefan and C. J. Krebs. 1999. Biases in the estimation of the demographic parameters of a snowshoe hare population. Journal of Animal Ecology 68:501–512.

Hejl, S. J., R. L. Hutto, C. R. Preston, and D. M. Finch. 1995. The effects of silvicultural treatments on forest birds in the Rocky Mountains. Pages 220-244 *in* Martin, T. E. and D. M. Finch., *editors*. Ecology and management of neotropical migratory birds. Oxford University Press, New York.

Hillyer E. V., and K. E. Quesenberry. 1997. Ferrets, Rabbits, and Rodents. Clinical Medicine and Surgery. W.B. Saunders Company, Philadelphia, Pennsylvania, USA.

Hodges, K. 2000a. The ecology of snowshoe hares in northern boreal forests. Pages 117-161 *in* Ruggiero, L.F., K.B. Aubry, S.W. Buskirk, G. M Koehler, C.J. Krebs, K.S. McKelvey, and J.R. Squires, *editors*. The scientific basis for lynx conservation. University Press of Colorado, Boulder.

Hodges, K. 2000*b*. Ecology of snowshoe hares in southern boreal and montane forests. *In* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S.

McKelvey and J. R. Squires, editors. The scientific basis for lynx conservation, *pp.* 163–207. University Press of Colorado, Boulder, Colorado, USA.

Hodges, K. E. 1998. Snowshoe hare demography and behaviour during a cyclic population low phase. Ph. D. Dissertation, University of British Columbia , Vancouver, B.C.

Hodges, K. E. 1999. Proximate factors affecting snowshoe hare movements during a cyclic population low phase. Ecoscience 6:487–496.

Hodges, K.E., Krebs, C.J. Hik, D.S., Stefan, C.J., Gillis, E.A. & Doyle, C.E. 2001. Snowshoe hare demography. Pages 141-178 in Ecosystem dynamics of the boreal forest: the Kluane project, C. J. Krebs, S. Boutin and R. Boonstra, *editors*. Oxford University Press, New York.

Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28: 181–208.

Howell, A. B. 1923. Periodic fluctuations in the numbers of small mammals. Journal of Mammalogy 4:149-155.

Hunter, W. C., D. A. Buehler, R. A. Canterbury, J. L. Confer, and P. B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin 29: 440-455.

Inaba, T., J. Mori, and R. Tori. 1986. Use of echography in rabbits for pregnancy diagnosis. Japanese Journal of Veterinary Science 48: 1003-1006.

Janiczek, P.M., and DeYoung, J.A. 1987. Computer programs for sun and moon illuminance with contingent tables and diagrams. U. S. Naval Observatory Circ. 171.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22:227-237.

Johnson, D. E. 1998. Applied multivariate methods for data analysis. Brooks / Cole Publishing, Pacific Grove, California.

Johnson, M. P. 2000. The influence of patch demographics on metapopulations, with particular reference to successional landscapes. Oikos 88: 67–74.

Johnstone, W. D. 1984. Thinning lodgepole pine. Page 253-262 *in* D. M. Baumgartner, R. G. Krebill, J. T. Arnott, G. F. Weetman, *editors*. Lodepole pine; the species and its management, symposium proceedings.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. Ecology 79:2852-2862.

Keith, L. B. 1963. Wildlife's ten-year cycle. University of Wisconsin Press, Madison.

Keith, L. B. 1983. Role of food in hare population cycles. Oikos 40: 385–395.

Keith, L. B. 1990. Dynamics of snowshoe hare populations. *In* H.H. Genoways, editor. Current Mammalogy. Volume 2, pp. 119-195. Plenum, New York, New York, USA.

Keith, L. B., and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildlife Monographs 58:1–70.

Keith, L. B., E. C. Meslow, and O. J. Rongstad. 1968. Techniques for snowshoe hare population studies. Journal of Wildlife Management 32:801-812.

Keith, L.B. 1964. Daily activity pattern of snowshoe hares. Journal of Mammalogy 45: 626–627.

Keith, L.B., S.E.M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Canadian Journal of Zoology 71:1385–1939.

Koehler, G. M. 1991. 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.

Koehler, G. M. and J. D. Brittell. 1990. Managing spruce-fir habitat for lynx and snowshoe hares. Journal of Forestry 88:10-15.

Kotler, B.P., Brown, J.S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72: 2249-2260.

Krebs, C. J., B. S. Gilbert, S. Boutin, and R. Boonstra. 1987. Estimation of snowshoe hare population density from turd transects. Canadian Journal of Zoology 65:565-567.

Krebs, C. J., S. Boutin, and R. Boonstra. 2001. Ecosystem dynamics of the boreal forest; the Kluane project. Oxford University Press, New York.

Krebs, C. J., S. Bouting, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1992. Impact of food and predation on the snowshoe hare cycle. Science 269: 1112–1115.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15: 237–240.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

Lima, S.L. 1998a. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27: 215-290.

Lima, S.L. 1998b. Nonlethal effects in the ecology of predator-prey interactions. Bioscience 48: 25-34.

Lima, S.L., and P. A. Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153: 649-659.

Litvaitis, J. A. 1991. Habitat use by snowshoe hares, *Lepus americanus*, in relation to pelage color. The Canadian Field-Naturalist 105: 275-277.

Litvaitis, J. A. 2001. Importance of early successional habitats to mammals in eastern forests. Wildlife Society Bulletin 29: 466-473.

Litvaitis, J. A., J. A. Sherburne and J.A. Bissonette. 1985a. Influence of understory characteristics on snowshoe hare habitat use and density. Journal of Wildlife Management 49:866–873.

Litvaitis, J.A., J.A. Sherburne and J.A. Bissonette. 1985. A comparison of methods used to examine snowshoe hare habitat use. Journal of Wildlife Management 49:693–695.

Longland, W.S. and Price, M.V. 1991. Direct observations of owls and Heteromyid rodents: can predation risk explain microhabitat use? Ecology 72: 2261-2273.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80: 298–310.

Malloy, J. C. 2000. Snowshoe hare, *Lepus americanus,* fecal pellet fluctuations in western Montana. *Canadian Field Naturalist* 114: 409–412.

Martin, F. C., and H. W. Barber, Jr. 1995. Precommercial thinning response in 7-year-old and 5-year-old western larch: past growth and future prognosis. U.S. Forest Service General Technical Report GTR-INT-319. Ogden, Utah.

Mattoon, J. S., and T. G. Nyland. 1995. Ultrasonography of the genital system. Pages 141-164 *in* T. G. Nyland and J. S. Mattoon, editors. Veterinary diagnostic ultrasound. W. B. Saunders Company, Philadelphia, Pennsylvania.

McGraw, J. B., and H. Caswell. 1996. Estimation of individual fitness from life-history data. American Naturalist 147:47–64.

McKelvey, K. S., K. B. Aubry, J. K. Agee, S. W. Buskirk, L. F. Ruggiero, and G. M. Koehler. Lynx conservation in an ecosystem management context. Pages 419-441 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey and J. R. Squires, editors. The scientific basis for lynx conservation. University Press of Colorado, Boulder, Colorado, USA.

McPeek, M.A. and R.D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. American Naturalist 140: 1010–1027.

Mech, L.D., Heezen, K.L. and Siniff, D.B. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Animal Behaviour 14: 410-413.

Menkens, G. E. Jr., and S. H. Anderson. 1988. Estimation of small-mammal population size. Ecology 69:1952-1959.

Meslow, E. C., and L. B. Keith. 1971. Demographic parameters of a snowshoe hare population. Journal of Wildlife Management 32: 812–834.

Mills, L. S. and M. Lindberg. 2001. Sensitivity analysis to evaluate the consequences of conservation actions. *In* S. R. Beisinger and D. R. McCullough, *eds.*, Population viability analysis. University of Chicago Press.

Mills, L. S., P.C. Griffin, K. Hodges, T. Ulizio, and K. McKelvey. Pellet count indices compared to mark-recapture estimates for evaluating snowshoe hare density. In review.

Moeur, M. 1981. *Crown width and foliage weight of Northern Rocky Mountain conifers.* Research Paper INT-283. U.S. Department of Agriculture. Forest Service. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Moeur, M. 1985. COVER: a user's guide to the CANOPY and SHRUBS extension of the stand prognosis model. General Technical Report INT-190. U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah.

Mohr, C. O., and W. A. Stumpf. 1966. Comparison of areas for calculating areas of animal activity. Journal of Wildlife Management 53:340-342.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. Australian Journal of Zoology 1: 163–173.

Murray, D.L. 2000. A geographic analysis of snowshoe hare population demography. Canadian Journal of Zoology 78:1207–1217.

Nichols, J. D. 1992. Capture-recapture models. Bioscience 42:94-102.

Nichols, J. D., and K. H. Pollock. 1983. Estimation methodology in contemporary small mammal capture-recapture studies. Journal of Mammalogy 64, 253-260.

Noon, B. R., and K. S. McKelvey. 1996. A common framework for conservation planning: linking individual and metapopulation models. In Metapopulations and Wildlife Conservation Management, pp. 139–162. Island Press, Covelo, California.

O'Donoghue, M. 1994. Early survival of juvenile snowshoe hares. Ecology 75:1582-1592.

O'Donoghue, M. and C. J. Krebs. 1992. Effects of supplemental food on snowshoe hare reproduction and juvenile growth at a cyclic population peak. Journal of Animal Ecology 61:631-641.

Oliver, C.D., and B.C. Larson. 1990. Forest stand dynamics. McGraw-Hill, New York.

Pietz, P., and J. R. Tester. 1983. Habitat selection by hares in north central Minnesota. Journal of Wildlife Management 47: 686-696.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. Journal of Wildlife Management 46: 757–760.

Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. Journal of Wildlife Management 58:608-618.

Pouderoux, L., P. C. Griffin and L. S. Mills. Forest microhabitats associated with dead snowshoe hares. In preparation (This dissertation, Appendix B).

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Pulliam, H.R. and B.J. Danielson. 1991. Sources, sinks, and habitat selection: landscape perspective on population dynamics. American Naturalist 137 (supplement): S50–S66.

Rexstad, E. 1994. Detecting differences in wildlife populations across time and space. Pages 219-228, 59th North American Natural Resources and Wildlife Conference.

Rongstad, O. J., and J. R. Tester. 1971. Behavior and maternal relations of young snowshoe hares. Journal of Wildlife Management 35: 338-346.

Rosenzweig, M.L. 1974. On the optimal aboveground activity of bannertail kangaroo rats. Journal of Mammalogy 55: 193-199.

Ruggiero, L. F., K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires. 2000. The scientific basis for lynx conservation : qualified insights. Pages 443-454 *in* L. F. Ruggiero, K.B. Aubry, S.W. Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey and J. R. Squires, *editors*. The scientific basis for lynx conservation. University Press of Colorado, Boulder.

Schwartz, C. C., M. A. Haroldson, and G. C. White. In review. Survival for cub and yearling grizzly bears in the greater Yellowstone ecosystem, 1983 – 2002.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters, 2nd ed. Oxford University Press, New York.

Seidel, K. W. 1986. Growth and yield of western larch in response to several density levels and two thinning methods: 15-year results. Research Note PNW-RN-455. U.S. Forest Service, Portland, Oregon.

Severaid, J. H. 1942. The snowshoe hare, its life history and artificial propagation. Maine Department of Inland Fish and Game Bulletin, Maine, USA.

Shaw, J. D. 2002. Silvicultural systems for maintenance of structure in a forest landscape. Ph.D. dissertation, Utah State University, Logan, UT.

Short, D. J. 1967. Handling, sexing, and palpating laboratory animals. Pages 3-15 *in*, M. L. Conalty, editor. Husbandry of laboratory animals. Academic Press, New York, New York, USA.

Sievert, P. R., and L. B. Keith. 1985. Survival of snowshoe hares at a geographic range boundary. Journal of Wildlife Management 49:854-866.

Sih, A., and McCarthy, T.M. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. Animal Behaviour 63: 437-443.

Sih, A., Ziemba, R. and Harding, K.C. 2000. New insights on how temporal variation in

predation risk shapes prey behavior. Trends in Ecology and Evolution 15: 3-4.

Squires, J.R. and Laurion, T. 2000. Lynx home range and movements in Montana and

Wyoming: preliminary results. Pages 337-350 in L.F. Ruggiero, K.B. Aubry, S.W.

Buskirk, G.M. Koehler, C.J. Krebs, K.S. McKelvey and J. R. Squires, *editors*. The

scientific basis for lynx conservation. University Press of Colorado, Boulder.

Stefan, C. I. and C. J. Krebs. 2001. Reproductive change in a cyclic population of

snowshoe hares. Canadian Journal of Zoology 79: 2101-2108.

Sterling, K., P. C. Griffin, and L. S. Mills. Movement and survival of newborn snowshoe

hares in Montana. In preparation.

Sullivan, T.P. and D.S. Sullivan. 1988. Influence of Stand thinning on snowshoe hare

population dynamics and feeding damage in lodgepole pine forest. Journal of

Applied Ecology 25: 791-805.

Sullivan, T.P., D.S. Sullivan, P.M.F. Lindgren, and J.O. Boateng. 2002. Influence of

conventional and chemical thinning on stand structure and diversity of plant and

mammal communities in young lodgepole forest. Forest Ecology and Management

170:173-187.

Tainturier, D. 1988. Diagnostic de gestation chez la lapine par echotomographie.

Recueil de Médicine Vétérinaire 164:141-144.

Tappeiner, J.C., D. Lavender, J. Walstad, R.O. Curtis, and D.S. DeBell. 1997.

Silvicultural systems and regeneration methods: current practices and new

alternatives. Pages 151-164 *in* Kohm, K.A. and J.F. Franklin, *editors*. Creating a

forestry for the 21st century; the science of ecosystem management. Island Press, Washington, D.C.

Thomas, C.D., and W.E. Kunin. 1999. The spatial structure of animal populations. Journal of Animal Ecology 68:647–657.

Thompson, W. L., White, G. C., and Gowan, C. 1998. Monitoring vertebrate populations. Academic Press, San Diego.

Thrall, P. H., J. J. Burdon, and B. R. Murray. 2000. The metapopulation paradigm: a fragmented view of conservation biology. *In* Genetics, demography and viability of fragmented populations, A. G. Young and G. M. Clarke, *eds.*, pp. 75–95. Cambridge University Press, Cambridge, England.

Thurmonn, J. C., W. J. Tranquilli, G. J. Benson, W. V. Lumb, and E. W. Jones, editors. 1996. Lumb and Jones' Veterinary Anesthesia. Third edition. Williams and Wilkins, Baltimore, Maryland, USA.

Tilman, D., and C. L. Lehman. 1997. Habitat destriction and species extinctions. *In* Tilman, D. and P. Kareiva, *eds.*, Spatial ecology, pp. 233–249. Princeton University Press, Princeton, New Jersey.

Tyre, A. J., Tenhumberg, B., McCarthy, M. A., and Possingham, H. P. 2000. Swapping space for time and unfair tests of ecological models. *Austral Ecology* 25: 327–331.

U. S. Fish & Wildlife Service. 2000. Determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule; final rule. U.S. Federal Register 65:16051–16086.

Watkinson A.R. and W.J. Sutherland. 1995. Sources, sinks, and pseudo-sinks. Journal of Animal Ecology 64: 126–130.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in L. Boitani and T. K. Fuller (eds.), Research techniques in animal ecology. Columbia University Press, New York.

White, G. C., and Burnham, K. P. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46(Suppl.): 120–138.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico.

White, G.C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288–331 in L. Boitani and T. K. Fuller, editors. Research techniques in animal ecology. Columbia University, New York, USA.

White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimations from populations of marked animals. Bird Study 46 supplement, 120–138.

Wiens, J. A., Stenseth, N. C., Van Horne, B., and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. Oikos 66: 369–380.

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. and D. L. Murray. 2002. Patterns in consumption of woody plants by snowshoe hares in the northwestern United States. Ecoscience 9:440-449.

Wirsing, A.J., Steury, T.D., and Murray, D.L. 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.

Wisdom, M. J., L. S. Mills, and D. F. Doak. 2000. Life-stage simulation analysis estimating vital rate effects on population growth for conservation. Ecology 81: 628-641.

Wolfe, M.L., N.V. Debyle, C.S. Winchell and T.R. McCabe. 1982. Snowshoe hare cover relationships in northern Utah. Journal of Wildlife Management 46:662–670.

Wolff, J. O. 1980. The role of habitat patchiness in the population dynamics of snowshoe hares. Ecological Monographs 50:111–130.

Wolff, J. O. 1981. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. Pages 441-449 *in* K. Myers, and C. D. MacInnes, *editors*, Proceedings of the World Lagomorph Conference. University of Guelph, Ontario.

Wooton, J.T., and D.A. Bell. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. Ecological Applications 2: 307–321.

Zamora, B. A. 1982. Understorey development in forest succession: an example from the inland northwest. Pages 63–69 in Forest succession and stand development research in the northwest, J. E. Means *editor*. Oregon State University, Corvallis.

Zimmerman, J.W., and Powell, R.A. 1995. Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Canadian Journal of Zoology 73:1123–1133.