SURVIVAL AND ACTIVITY PATTERNS OF SNOWSHOE HARES (LEPUS AMERICANUS) IN INTERIOR ALASKA

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A

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ABSTRACT

Snowshoe hare (*Lepus americanus*) survival depends on the interaction of habitat characteristics with numerous biological and environmental variables. In boreal regions where considerable habitat heterogeneity exists, hares balance food availability with predation risk by moving among habitats seasonally, but it is largely unknown how often they move at shorter time scales. I investigated the seasonal effects of habitat, weather, and individual hare characteristics on survival and movement in two common but fundamentally different boreal habitats. Survival was highest in summer, for hares with higher body condition, and in black spruce rather than early successional forest. Hares moved among core use areas in different habitats twice per day on average, using more open areas at night when they were presumably feeding on preferred browse. Movement rates were lowest in mid-afternoon when hares appeared to be resting under dense cover. Behavior of individuals varied greatly with some hares repeatedly moving up to 1 km between defined patches in less than 5 hours and others remaining roughly within a 1 ha area. These findings illustrate the complexity of snowshoe hare ecology in an area where habitat variation promotes daily movement of hares among radically different habitats over a few hundred meters.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

Page

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DEDICATION

For my parents who have shown limitless love, support, and encouragement, and for my brother who worked with me against our parents’ will to create a domestic zoo; he kept me laughing all the way through.

GENERAL INTRODUCTION

Snowshoe hares (*Lepus americanus*) are an important herbivore and prey species in the boreal forests of North America (Krebs et al. 2001) where cyclical changes in their abundance strongly impact the structure of the vertebrate community (Boutin et al. 1995). Populations of lynx (*Lynx canadensis*), coyotes (*Canis latrans*), great horned owls (*Bubo virginianus*), and goshawks (*Accipiter gentilis*) track snowshoe hare abundance (Keith et al. 1977, Rohner 1996, O'Donoghue et al. 1997), but with a time lag such that predators are still abundant when hares become scarce. Predation pressure may then be transferred to other prey species such as red squirrels (*Tamiasciurus hudsonicus*) (O'Donoghue et al. 1998), as well as grouse and ptarmigan whose populations decline along with hares (Boutin et al. 1995). Herbivory by hares has been implicated as a factor in broad-scale processes that include the acceleration carbon and nitrogen turnover in ecosystems (Butler and Kielland 2008), the succession of river floodplains in interior Alaska (Bryant 1987), and the growth and concentration of secondary compounds in birch (*Betula spp.*) (Bryant et al. 1983). Hares may therefore impact other herbivores such as moose (*Alces alces*) that also forage on birch in winter (Dodds 1960).

Snowshoe hares experience a broad range of environmental conditions each year with extreme changes in weather, photoperiod, food availability, and predation pressure. The habitats occupied by snowshoe hares mediate the interactive effects of these and numerous other environmental and biological variables on hare survival by providing cover from predators and acting as thermal refugia. Snowshoe hares inhabit a variety of vegetation communities within the boreal forest but prefer those with dense vegetative cover, while food availability and species composition appear to be secondary in habitat selection (Carreker 1985, Litvaitis et al. 1985). Habitat selection by hares is affected by seasonal changes in snow cover and presence of deciduous leaves, and hares move among habitats seasonally to maximize use of preferred browse species when cover is sufficient (Wolff 1980). Hares also disperse into less suitable habitats at times of high density during the peak in the population cycle (Wolff 1981) with differences in cover having consequences for survival (Keith et al. 1993) and sources of mortality (Murray et al. 1994, Rohner and Krebs 1996). Thus, there are likely to be habitat-dependent changes in survival rates and sources of mortality among seasons and years for cyclic populations of snowshoe hares.

The frequent use of forest edges by hares (Ferron and Ouellet 1992) suggests that, while typically choosing to use areas of dense cover, they benefit from being in close proximity to open areas where they are likely to find a greater availability of preferred browse. The use of complementary habitats in a landscape (Dunning et al. 1992) occurs in other herbivores such as white-tailed deer (*Odocoileus virginianus*), which have home ranges incorporating productive open sites for foraging and closed forests for seeking refuge from predators and weather (Walter et al. 2009, Massé and Côté 2012). Little attention has been given to daily movements of hares, but it is an important scale of activity for those residing in a mosaic of suitable habitats where differences in food availability and cover exist. Additionally, the daily activity patterns and movement of hares between habitats are likely to differ among seasons as dramatic changes in photoperiod and vegetative cover take place.

My study took place during the late-increase, peak, and initial decline phases of a cyclic population in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to January 2013. I focused my research in two characteristic snowshoe hare habitats where high densities of hares are found: mature black spruce forest and early successional forest dominated by willow (*Salix sp*.), alder (*Alnus tenuifolia*), and balsam poplar (*Populus balsamifera*). The primary goals of my thesis were to 1) investigate the seasonal and annual effects of habitat, weather, and individual hare characteristics on survival; 2) identify the sources of mortality and primary predators of hares in Alaskan boreal forest; 3) assess the relationship between predation and structural cover provided by different habitats; and 4) examine habitat use and daily movement rates of hares among habitats. The first 3 goals are addressed in Chapter 1 where I describe the use of radio-telemetry to track and identify hare mortalities and to estimate survival rates of hares using known-fate models. The effect of cover on sources and rates of predation was examined by measuring lateral and canopy cover at predation sites and comparing them with the study grids in which the hares were released. I predicted that survival would be higher in summer than other seasons, and higher in black spruce than early successional forest in all seasons except summer when deciduous leaves are abundant. I also predicted that predation would be lowest in early successional forest during summer but constant in black spruce forest across seasons, and that predation would occur in sites with low amounts of cover relative to average availability. In Chapter 2, I address the movement of snowshoe hares using radio transmitters to monitor their emigration from the trapping grids. The use of GPS data loggers on snowshoe hares in summer and winter enabled the quantification of fine-scale movement among, and time spent in, different habitats on a daily basis, while also investigating differences in diel activity patterns in different seasons. I predicted that hares would move among habitats more frequently in winter when food was scarce and disparities in cover were greater, and consequently that hares would have larger home ranges in winter. My study greatly expands on our limited knowledge of snowshoe hare ecology in interior Alaska where community dynamics are likely to differ from other research locations, such as those in the boreal forest of Canada. The movement of hares among habitats of different ages will have implications for the management of forest stands for populations of hares and their primary predator, the lynx.

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CHAPTER 1

Spatial and Temporal Patterns of Survival for Snowshoe Hares (*Lepus americanus*) in Interior Alaska[1]

ABSTRACT

We investigated survival and causes of mortalities of snowshoe hares (*Lepus americanus*) during the cyclical increase, peak, and decline phase in interior Alaska. We used survival models to gauge the importance of interacting biotic and abiotic variables in hare survival. While snowshoe hares are known to be the primary prey for numerous mammalian and avian predators in the boreal forests of Canada, our study was the first to identify sources of predation for snowshoe hares in Alaska. We radio-tagged 288 hares on 2 trapping sites in early successional and black spruce (*Picea mariana*) forests and used known-fate models in program MARK to estimate survival rates from June 2008 to May 2012. We evaluated 85 *a priori* models that included variables for sex, age, and body condition of study hares, as well as study site, month, season, year, snowfall, snow depth, and air temperature. We selected the best model using Akaike's information criterion with correction for small sample size. Model results indicated that month, capture site, and body condition were the most important variables in explaining survival

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[1] Feierabend, D.F. and K. Kielland. 2013. Snowshoe hare survival: temporal effects of biotic variables on predation. Prepared for submission to Journal of Wildlife Management.

rates. Survival was highest in July when alternative prey was available to predators of hares. Survival was lowest in May when hares breed and molt, and in November when hares molt again. We identified predation as the cause of mortality in 86% of hare deaths. When the source of predation could be determined, most hares were killed by goshawks (*Accipiter gentilis*) in early successional forest (30%), whereas lynx (*Lynx canadensis*) accounted for most of the predation in black spruce forest (31%). Great horned owls (*Bubo virginianus*) and coyotes (*Canis latrans*) represented smaller proportions of hare predation while non-predatory causes were a negligible source (4%) of mortality. Hares rely on vegetative cover for concealment from predators, so we compared both canopy and horizontal cover among early successional, black spruce, and mixed forest habitat. We found cover to be greater during summer than other seasons, with horizontal cover being greater in black spruce than other sites in all seasons, and canopy cover being greater in mixed forest than other sites in all seasons. In our study area, the type of vegetation community appeared to influence sources of predation more than cover characteristics. Hares were most susceptible to goshawk predation in early successional and black spruce forest, and most susceptible to great horned owl predation in mixed forest. Lynx primarily killed hares in black spruce forest, while the majority of coyote predation took place in early successional forest. As one of the dominant herbivores and prey species in the boreal forest of North America, snowshoe hares have a direct impact on the abundance of fur-bearing predators such as lynx and coyotes, while indirectly influencing moose populations through competition for resources and effects on community composition. The results from our study impart a greater understanding of hare ecology in interior Alaska with broader applicability to wildlife management in other regions of the boreal forest.

INTRODUCTION

Snowshoe hares (*Lepus americanus*) in northern regions inhabit a wide range of vegetation communities and move among them seasonally to optimize browse quality, seek cover from predators, and engage in breeding activity (Wolff 1980). Hares are also likely to use forest edges and move frequently between habitats in search of high quality browse during daily foraging bouts (Wolff 1980, Ferron and Ouellet 1992). Survival rates for hares depend largely on the amount of vegetative cover present in the habitats they occupy (Keith et al. 1993), in part due to differences in risk of predation by various predators (Murray et al. 1994, Murray et al. 1995, Rohner and Krebs 1996). Consequently, the sources and rates of mortality on hares could be expected to change seasonally according to the cover in the habitats they use. Hares in northern regions also experience annual changes in mortality rates as their populations undergo regular cycles in abundance (Krebs et al. 1986, Trostel et al. 1987, Keith 1990). Populations of several predators change with those of hares, exhibiting functional and numerical responses to hare numbers (Boutin et al. 1995, O'Donoghue et al. 1998a, O'Donoghue et al. 1998b). Thus, sources of mortality for hares can be expected to change annually as well.

Habitat selection by snowshoe hares influences survival rates through the effect of food availability on body condition and the effect of vegetative cover in concealing hares from predators. Hares prefer habitats with dense cover, while plant species composition and food availability appear to be less important in habitat selection and survival of hares (Carreker 1985, Litvaitis et al. 1985). The disparity in cover and browse availability between young deciduous and dense coniferous forests (two habitats often used by hares) suggests a tradeoff between predation risk and food quality, most notably in the peak and decline of the population cycle (Wolff 1980). At this time, hares disperse into habitats with less cover, which are used less frequently during periods of low density (Wolff 1980;1981, Boutin et al. 1985). Structural cover of the habitat used by snowshoe hares influences mortality from predation. For example, in the southwest Yukon Territory, Canada, fewer hares were predated by great horned owls (*Bubo virginianus*) in closed forests or in areas with dense shrubs than in open forests (Rohner and Krebs 1996) while coyotes (*Canis latrans*) killed more hares in dense spruce forest than open spruce, deciduous, or shrub habitats (Murray et al. 1994). Cover availability changes seasonally with the loss of deciduous leaves in fall, accumulation of snow in winter, and leafing events in spring and summer. Thus, sources and rates of predation on hares could be expected to vary seasonally with changes in cover, and differ between coniferous and deciduous forests.

We examined temporal and spatial patterns in snowshoe hare survival and predation during the late-increase, peak, and initial decline phase of a population cycle in young deciduous and dense coniferous forest using radio-tagged hares. Our study is the first to quantify snowshoe hare survival rates and sources of mortality in an Alaskan boreal forest using radio telemetry, which is a more informed and therefore preferable method of estimating survival when compared with live-trapping (Boutin and Krebs 1986). While similar studies have been conducted in the Kluane region of the Yukon Territory, Canada (Krebs et al. 2001), the different vegetation communities represented in interior Alaska likely lead to differences in habitat use by competing herbivores and predators with subsequent influences on habitat-specific survival and predation for snowshoe hares. Our study expands on what is known regarding the consequences of habitat use in relation to snowshoe hare predation rates by investigating the effects of vegetative cover, weather parameters, individual hare characteristics, survival, and predation at different temporal scales.

Based on previous work suggesting a tradeoff between understory cover and food availability (Wolff 1980, Carreker 1985, Ferron and Ouellet 1992), we hypothesized that survival and mortality sources would exhibit pronounced spatial and temporal patterns. Deciduous forest should provide higher quality food to hares than coniferous forest throughout the year but lack sufficient cover in non-leaf seasons, whereas coniferous forest should provide hares with considerable cover in all seasons, so we predicted that 1) snowshoe hare survival would be highest in deciduous forest during the summer when leaves were available for browsing and offered cover from predators, but that survival would be higher in coniferous forest during other times of the year; 2) both mammalian and avian predation would be highest in deciduous forest during non-leaf seasons, but would be constant across seasons in coniferous forest; and 3) all predation would occur in areas with lower than average understory cover, and avian predation would occur in areas with lower than average canopy cover.

STUDY AREA

This study took place in the Bonanza Creek Experimental Forest (64° N, 148° W), located approximately 20 km southwest of Fairbanks, Alaska. This area is covered by a mosaic of floodplain, lowland, and upland vegetation types that include early successional forest, balsam poplar, white spruce, black spruce, muskeg, wetland, mixed forest, scrub, birch, aspen, and recently burned communities. Snowshoe hare population dynamics have been monitored here since 1998 (Kielland et al. 2010). We used established trapping grids in two representative snowshoe hare habitats (hereafter referred to as “DECIDUOUS” and “CONIFER”) with populations sufficiently large for estimating hare densities and survival. The DECIDUOUS grid was in an early successional community dominated by willow, thin-leaf alder (*Alnus tenuifolia*), and balsam poplar, situated adjacent to the Tanana River. Understory species included *Epilobium angustifolium*, *Cornus canadensis*, *Calamagrostis canadensis*, and *Equisetum sp.*. The CONIFER grid was in a mature black spruce community with an understory composed of *Ledum sp.*, *Rosa acicularis*, *Vaccinium vitis-idaea*, *Salix sp.*, *Chamaedaphne calyculata*, mosses, and lichens. Each trapping grid was 9 ha in size with 50 traps arranged on 10 transects (5 traps/transect) in a rectangular pattern with 50 m between traps. The two trapping grids were separated by 1.5 km and most of the intervening vegetation was poor hare habitat (e.g., open muskeg, wetland). No hares were observed moving between grids during 12 years of population monitoring. However, it was not uncommon for study hares to move up to 1 km from the trapping grids and we observed 5 hares moving more than 5 km from their respective capture sites.

METHODS

Snowshoe Hare Capture and Collaring

We captured hares in #3 Havahart live traps (model 1085, Lititz, PA) and marked them with Monel ear tags (National Band and Tag Co., Newport, KY) for use in ongoing population estimates. Traps were baited with alfalfa and carrots, and we provided snow (when available) for moisture; they were opened during mid-day and checked the following morning. Trapping did not take place at temperatures below -18° C. Capture and handling of snowshoe hares followed animal care and use guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (protocol #09-57) and the Alaska Department of Fish and Game (Permit 135211-5).

Between May 2008 and August 2012, we radio-tagged with VHF transmitters a subset of the hares captured during routine 4-night trapping sessions in June and September for population estimates, and during 1- to 3-night trapping sessions conducted as needed in all seasons to deploy radio transmitters when sample size was reduced by attrition. We initially fitted 8 and 12 hares in DECIDUOUS and CONIFER, respectively, with VHF radio transmitters in June 2008 and increased the sample to 20 individuals per grid by September. Transmitters weighed 20-26 g (models M1555, M1565, M1575, Advanced Telemetry Systems, Isanti, MN) and were equipped with a mortality switch that was activated by a lack of movement for 6 hours. We collared additional hares with VHF transmitters as mortalities occurred in an attempt to maintain approximately 25 collared individuals on each grid at any given time (20-95% of the hare population depending on the time of year). Hares were collared through June 2012, but hare abundance was too low in DECIDUOUS to deploy any transmitters after November 2011. Less than 5 hares in DECIDUOUS carried collars by mid-December 2011 and none by mid-May 2012. We fitted transmitters to hares weighing over 900 g (so that the transmitter never exceeded 3% of the hare's body weight), which only excluded younger juveniles; thus, our sample population was comprised of older juvenile and adult hares.

Up to 6 hares were fitted with collars equipped with GPS loggers (model G30L, Advanced Telemetry Systems; model Quantum 4000, Telemetry Solutions, Concord, CA) and VHF transmitters in DECIDUOUS between June and October of 2010 and May and September 2011, and in CONIFER between February and April 2012, for a concurrent study on hare movement and activity patterns. GPS collars were removed and replaced with VHF collars when GPS batteries expired, usually after 2-3 weeks. The maximum weight of GPS collars was 40 g (4% of a hare's mass) and not expected to affect survival (Sikes and Gannon 2011), so we included data from individuals fitted with GPS collars in our survival estimates.

Monitoring and Mortality Identification

We monitored radio-collared hares every 1-7 days using a directional Yagi antenna and hand-held receiver (model R1000 receiver; Communications Specialists Inc., Orange, California). When transmitter signal strength or location suggested that a hare had moved away from a trapping grid, we tracked the individual in an attempt to visually confirm its location, although this was not always possible. We right-censored (i.e. removed from the study) hares with transmitters that stopped functioning.

Mortalities were typically located within 1 week of death, and the source of death was identified as mammalian or avian predation using field sign such as tracks, hair, scat, whitewash, feathers, wing marks, regurgitated pellets, and the portion of the hare consumed. The species of predator was identified whenever possible using methods by Krebs et al. (2001). Deceased hares lacking external signs of predation were necropsied for signs of subcutaneous bruising or puncturing that would indicate predation. If none were found, we considered the cause of death to be non-predatory.

Scavenging of hare carcasses was rarely a complication in identifying the source of mortality. Hare carcasses monitored by cameras in the trapping grids were generally not scavenged until 10 or more days following death. This is similar to scavenging patterns observed in the Yukon Territory (Boutin et al. 1986). Additionally, the majority of scavenging was done by animals typically incapable of preying on older juvenile or adult hares, such as common raven (*Corvus corax*), gray jay (*Perisoreus canadensis*) or red squirrel (*Tamiasciurus hudsonicus*). Lynx (*Lynx canadensis*) and northern goshawks (*Accipiter gentilis*) were observed scavenging carcasses on 3 occasions after other species had already begun scavenging the carcass.

Structural and Vegetative Cover

To evaluate any relationship between structural cover and hare survival, we measured lateral cover density (i.e., visual obstruction) and canopy cover at 50 locations in each trapping grid in spring, when both snow and deciduous leaves were absent (May); summer (July-August); and winter, when snow depth was greatest (March-April). We assumed structural cover in the fall was the same as in spring because neither deciduous leaves nor snow were present at these times. Five sampling points were selected at random distances along each of the 10 established transect lines in the trapping grids. We also measured canopy cover and lateral cover density at each hare predation site in the season the predation event occurred if we were confident the carcass remains had not been moved by predators or scavengers.

We measured canopy cover at each sampling point and predation site using a concave spherical densiometer (Lemmon 1956). Lateral cover density was measured as the percentage of a 0.3 x 2.5 m profile board obscured by vegetation at distances of 5, 10, 15, 20, 25, and 30 m. Preliminary analysis indicated that lateral cover density was most variable among habitats at a distance of 10 m, so we used data from this distance in later analysis. At predation sites, we averaged lateral cover density measured in the 4 cardinal directions. At sampling points, we randomly selected a direction perpendicular to the transect line. Snowshoe hares require vegetative cover approximately 1 m in height for concealment from terrestrial predators, and 3 m in height for protection from avian predators (Wolff 1980). Therefore, we recorded lateral cover density from ground level (or top of the snowpack in winter) to a height of 2.5 m. Measurements were taken in five 0.5-m high sections (Nudds 1977), where each section was subdivided into 4 quadrants to improve reading accuracy, then averaged across the entire 2.5 m. We observed the board from 0-1.0 m above ground from a kneeling position, and from 1.0-2.5 m from a standing position, in order to maintain a nearly horizontal viewing plane.

In addition to measuring lateral cover density and canopy cover in the trapping grids, we did so in a stand of mixed white spruce-birch forest (MIXED) located adjacent to CONIFER after we observed frequent use of this stand by study hares collared in CONIFER. We took measurements in summer and winter only, assuming similar values for spring, fall, and winter. We used the same methodology as on the trapping grids, but sampled every 50 m in a 14 ha grid.

We used a vegetation layer encompassing the Bonanza Creek Experimental Forest (Baird 2011) in a GIS (ArcGIS Desktop: Release 10. ESRI, Redlands, CA: Environmental Systems Research Institute) to identify the vegetation communities on the trapping grids and at predation sites. We identified the entirety of the DECIDUOUS grid as early successional forest, and the CONIFER grid as black spruce forest.

Analyses

We investigated the importance of biotic and abiotic variables to snowshoe hare survival from 10 June 2008 to 31 May 2012 using known-fate models with a daily interval in program MARK (White and Burnham 1999). This allowed for staggered entry of new animals and censoring of individuals whose transmitters failed (Pollock et al. 1989, White and Garrott 1990). We examined the effects of time, capture site, age, sex, body condition, and environmental variables (Table 1.1, Appendix 1.A) on daily survival rates by forming a set of 85 *a priori* models that included additive models with up to 3 variables or simple interaction models containing only 2 variables. These models were compared using Akaike's information criterion corrected for small sample size (AIC_c) and Akaike model weights (Burnham and Anderson 2002). Goodness-of-fit testing is not available for known fate data with individual covariates (Crawford et al. 2010), so we assumed little to no overdispersion in the data and used a value of 1.0 for the overdispersion parameter c-hat. However, we compared model rankings obtained using c-hat values of 1.0, 2.0, and 3.0 to gauge the potential effects of any unexpected overdispersion.

We tested for differences in sources of predation between black spruce, early successional, and mixed forest by comparing the number of hares killed by a given predator in each habitat, first by predator class and then by predator species, using Chi-Square tests of independence.

To test for seasonal changes in vegetative cover, we compared canopy cover and lateral cover density among the CONIFER, DECIDUOUS, and MIXED grids using repeated measures analysis of variance with the Greenhouse-Geisser adjusted F-test to account for a violation of sphericity, followed by Tukey's HSD multiple comparisons. Canopy cover and lateral cover density measurements were arcsine square root transformed before analysis. We also compared canopy cover and lateral cover density between predation sites and study grids within a given season using Wilcoxon Signed Rank tests with Bonferroni corrections.

Unless otherwise indicated, we used the statistical program JMP (Version 7. SAS Institute Inc., Cary, NC, 1989-2007) for analyses, used an alpha of 0.05 in assigning statistical significance, and report standard error with means.

RESULTS

Snowshoe Hare Survival

We radio-tagged a total of 288 hares between 10 June 2008 and 31 May 2012 (Table 1.2). The support for the most parsimonious survival model, *S* (site + body condition + month), was 52.9%, given the model set, and was 4.5 times more likely to be the best model than the model with the next highest $\mathrm{AIC_c}$ weight (Table 1.3). The top model indicated that 1) hares with a higher body condition index had higher survival rates, 2) hares radio-tagged in CONIFER were more likely to survive than hares tagged in DECIDUOUS, and 3) survival rate differed among months in the year. Month and site were components of all models with $\Delta\ \mathrm{AIC_c}$ values < 4.0, and had summed model weights of 0.862 and 0.841, respectively. Body condition was a variable in 3 of 7 models with $\Delta\ \mathrm{AIC_c}$ values < 7.0 with a variable weight of 0.661. Together, these 3 variables explained most of the variation in hare survival in our study (Table 1.4). There was some support for higher survival of adult than juvenile hares. Classifying hares of unknown age as adults, as we did, should provide a conservative estimate of the importance of age in estimating survival if adults have a higher chance of surviving than juveniles. There was weak support for differences in survival among seasons, indicating a possibility of higher survival of hares in summer and fall than in winter and spring. We found very little support for a difference in survival between sexes, among study years, or in relation to measures of snow cover or air temperature.

Estimated daily survival rate (based on an average body condition index of 10.4) was highest in July for hares tagged in both trapping grids (CONIFER: 0.9995 ± 0.0003;

DECIDUOUS: 0.9993 ± 0.0005) and lowest in November (CONIFER: 0.9924 ± 0.0015; DECIDUOUS: 0.9890 ± 0.0022; Figure 1.1). These values equate to an estimated 30-day survival rate of ~0.98 in July for hares in both trapping grids, and 0.80 and 0.72 in November for CONIFER and DECIDUOUS, respectively. Survival differed most between trapping grids in November when estimated survival was lowest, but there was a high level of uncertainty in monthly estimates and considerable overlap between sites (Figures 1.1 and 1.2). Body condition had a smaller effect on estimated daily survival rate during months where survival was high, such that body condition made little difference to daily survival in July and had the greatest influence on survival in May and November.

Despite a lack of support for differences in survival among years, we note that, averaged across the two trapping grids, estimated annual survival rate increased from 0.16 ± 0.03 in 2008-09 to 0.30 ± 0.03 in 2009-10 and 0.41 ± 0.05 in 2010-11, before declining to 0.33 ± 0.06 in 2011-12. Estimated annual survival was ~15% higher for hares tagged in CONIFER than in DECIDUOUS in all years except 2009-10 when they were roughly equal.

When adjusting the overdispersion parameter c-hat to a value of 2.0 or 3.0, the model rankings still reflected the importance of a temporal component, but emphasized seasonal differences in survival rather than monthly differences. Site was still included in many of the top models, and body condition and age remained important individual covariates. We conclude that using a c-hat = 1.0 was appropriate for the data.

Sources of Predation

We observed slightly more predation of hares by mammals than avian predators (Figure 1.3). Lynx, goshawks, and great horned owls were responsible for the majority of kills for which we could identify the predator species, but coyote predation was rarely observed. There was scant evidence of predation by any other species: e.g. red fox (*Vulpes vulpes*), mink (*Mustela vison*), ermine (*M. erminea*), and marten (*Martes americana*). In 2 of 3 cases where mink or ermine were associated with hare mortalities, the carcasses were cached intact and scavenging of either trap-sick hares or surplus kills was suspected. We could not identify the predator species for 57% of hare kills, and this was most often the case when hares had been killed by mammals in weather conditions that did not allow for track identification.

There was no difference in the proportion of hare predation by mammalian and avian predator classes among black spruce, early successional, or mixed forests (χ^2 = 0.455, df = 2, *P* = 0.103; Figure 1.3). However, we did find a difference in species-specific predation by lynx and goshawks between black spruce and early successional forests (χ^2 = 8.67, df = 1, *P* = 0.003). Far more hares were killed by lynx in black spruce forest (60%) than early successional forest (7%), while roughly equal numbers of hares were killed by goshawks in black spruce and early successional forest. Great horned owls preyed on hares most in mixed forest (42%).

Predation took place nearly twice as frequently in black spruce than early successional forest, and three times more frequently than in mixed forest (Figure 1.4). It should be noted that the DECIDUOUS grid was in close proximity to white spruce and black spruce forest, while the CONIFER grid was in close proximity to mixed forest but not early successional forest. Not surprisingly, for hares killed by predators, 61% trapped in CONIFER died in black spruce forest, while 23% died in mixed forest and none in early successional forest. Predator-killed hares trapped in DECIDUOUS also died in black spruce forest (27%), while 40% died in early successional forest.

The majority of hare predation (56%) took place during winter (Figure 1.3), but after adjusting for different season lengths, predation rates (number per month) were roughly equal in spring, fall, and winter, and very low during the summer. Avian predation rates were highest in spring, largely owing to goshawk predation (54%), and lowest during summer. However, great horned owl predation rates were highest in winter, while goshawk predation rates were highest in spring and fall. Mammalian predation rates were highest in fall and winter, and very low in spring and summer, but tracks were not available for identification in the latter seasons. Hares were killed by lynx more than twice as frequently in winter (31%) than any other season, and coyotes were only observed killing hares in fall and winter. We observed ~10-25% more predation of hares by mammals than birds in all seasons except spring, when avian predation was 4 times more frequent than mammalian predation.

We also observed inter-annual variation in sources of snowshoe hare predation. There was a monotonic increase in the proportion of hares killed by avian predators in the study area across each of the 4 study years, and a corresponding decrease in the proportion of mammalian predation observed in the final 3 years. Great horned owls appear to be responsible for the increase in avian predation in 2011-12, while goshawk predation was relatively consistent from June 2009 to May 2012. Lynx predation was dramatically reduced in 2010-11 and 2011-12, while we saw more hares killed by coyotes in 2011-12 than any other year.

Structural Cover

Canopy cover in CONIFER was 9% greater during summer than winter, while canopy cover in DECIDUOUS was 60% greater during summer than any other season ($F_{1.43,140.58} = 262.77$, $P < 0.001$). Canopy cover was 13% greater in CONIFER than DECIDUOUS during spring and winter when deciduous leaves were absent, but 39% greater in DECIDUOUS than CONIFER during summer when deciduous leaves were fully expanded ($F_{1.43,140.58} = 151.00$, $P < 0.001$). MIXED had 41% more canopy cover than CONIFER during summer, and at least 21% more canopy cover than both CONIFER and DECIDUOUS during winter ($F_{2,147} = 107.14$, $P < 0.001$). There was 29% more canopy cover in MIXED during summer than winter ($F_{1,147} = 477.43$, $P < 0.001$).

Lateral cover density was 24-50% higher during summer than other seasons in CONIFER and DECIDUOUS ($F_{1.83,179.17} = 79.79$, $P < 0.001$), and 19-38% higher in CONIFER than DECIDUOUS during all seasons ($F_{1.83,179.17} = 0.79$, $P = 0.44$). Lateral cover density in MIXED was 20% higher during summer than winter ($F_{1,147} = 247.85$, $P < 0.001$), but remained 19-61% less than CONIFER and DECIDUOUS during all seasons ($F_{2,147} = 7.47$, $P < 0.001$).

We measured structural cover in 123 predation sites, 50 of which were in black spruce forest, 32 in early successional forest, 15 in mixed forest, and the remainder in white spruce, birch, scrub, wetland, or on snow-covered ice. Where differences existed, there was less lateral cover but more canopy cover in predation sites than CONIFER, but more lateral cover and canopy cover in predation sites than MIXED and DECIDUOUS (except in summer when DECIDUOUS had greater canopy cover). When comparing predation within a specific habitat type, hare kills in black spruce forest during fall took place in areas with 32% more lateral cover ($Z = 3.25$, $P = 0.001$) than CONIFER in that season. Hare kills in early successional forest during fall took place in areas with 24% more lateral cover ($Z = 3.65$, $P < 0.001$) than DECIDUOUS in that season, owing largely to goshawk predation which coincidentally took place in sites with 14% more canopy cover ($Z = 2.42$, $P = 0.048$) than DECIDUOUS. Predation in mixed forest during winter took place in areas with 11% more lateral cover ($Z = 2.89$, $P = 0.004$) and 15% more canopy cover ($Z = 2.27$, $P = 0.023$) than MIXED in that season.

DISCUSSION

Estimated daily survival rates of snowshoe hares were higher during summer than in other seasons, likely associated with greater vegetative cover across all habitats and lower predation rates (Boutin et al. 1986). Additionally, from May through August each year, there presumably were leverets and newly weaned juvenile hares in the area, which would have served as a more accessible food source for predators that might have otherwise captured older hares (O'Donoghue 1994). We speculate that this change in prey availability temporarily alleviated the rate of predation on the older age classes for which we estimated survival rates. In addition, alternative prey sources such as small mammals and migratory birds are also in greater abundance during the summer, which may have further contributed to the lower predation rates on hares.

Depressed survival rates in April and May coincide with the vernal pelage change and an increase in activity associated with breeding behavior (O'Farrell 1965, Hearn et al. 1987). Hares are more visible to predators during these times due to frequent mismatch of their pelage color with the surrounding environment, as well as lower availability of vegetative cover when deciduous leaves and snow are largely absent. Declining survival rates of hares in October and November may reflect a similar scenario where autumnal molting and sparse cover make hares more visible to predators. There is evidence that hares with white or mottled pelage use areas with denser vegetative cover than hares with brown fur during times when snow is not present (Litvaitis 1991). Thus, hares may shift habitat use toward thick conifer forest in response to increased vulnerability to predation during molting periods. In addition, juvenile hares in our study were first available for collaring in September after reaching weights of 900 g. Previous studies found lower survival rates of juveniles than adult hares (Gillis 1998). We therefore expect a drop in estimated survival rates when younger juveniles are added to a sample population comprised entirely of adult hares in September. Moreover, the ratio of juveniles to adults typically decreases significantly over winter in our study area without evidence of different emigration rates between age groups (Kielland et al. 2010), supporting the hypothesis that juveniles have lower survival rates than adult hares. Finally, from September to November, hares are in the transition from feeding on summer foliage to a winter diet comprised mostly of woody browse, while simultaneously experiencing dropping environmental temperatures and adjusting to initial snow accumulation. All of these factors are likely to reduce survival via changes in behavior and physiology to cope with environmental stressors in fall, yet snowshoe hares are well adapted to winter conditions later in the year. Hares experiencing extreme winter temperatures in western Canada exhibited lower resting and field metabolic rates, thermal conductance, and lower critical temperatures than hares in fall (Sheriff et al. 2009b, 2009c). The energetic demands of molting into denser and longer winter pelage (Sheriff et al. 2009b) while remaining vulnerable to environmental stressors in fall may temporarily lead to depressed body condition; hares suffering from malnutrition then succumb more readily to either starvation (Keith et al. 1984) or predation (Sievert and Keith 1985).

Our models (Table 1.2) indicated higher survival of hares that were captured in a black spruce forest than hares in an early successional forest, with the greatest difference occurring during times when deciduous leaves were absent. With the vast majority of hare mortalities resulting from predation, the greater structural cover available to hares in black spruce likely offered considerably more protection from predators during non-leaf seasons than the open habitat of the early successional forest. However, over half of the hares that died were found beyond the boundaries of the trapping grids, often in markedly different habitat than where the hares had been radio-tagged. Due to logistic constraints, we were unable to routinely locate all individuals that moved beyond the grid boundaries, and therefore can only attribute survival rates to the grid in which the hare was initially radio-tagged. However, when hares tagged in black spruce forest died in other habitats, those habitats typically had greater visibility than the trapping grid, while hares dying outside of the early successional forest in which they were tagged generally did so in habitats with lower visibility than the trapping grid. Therefore, the difference in estimated survival rates for hares in black spruce and early successional forests should be conservative in that we expect lower predation rates for hares in habitats with lower visibility (Wolff 1980).

We found no support for differences in survival among study years which was surprising given the more than 10-fold variation in hare density over the course of the study, as well as the large differences in annual survival rates observed in other studies (0.5% to 32%; Hodges et al. 2001). Using estimates derived from an ongoing mark-recapture study as part of the Bonanza Creek LTER program from 1998 to present, the hare population reached a cyclical peak in the autumn of 2009 with densities of 5.4 and 3.3 hares/ha in CONIFER and DECIDUOUS, respectively (Bonanza Creek Long-Term Ecological Research [BNZ LTER] 2013). By autumn of 2011, the density had dropped to ~2 hares/ha on both trap sites and by spring of 2012 was less than 1 hare/ha. Elevated survival rates of hares in our study in 2009-10 agree with other studies that found similarly high survival rates during population peaks (Krebs et al. 1986, Trostel et al. 1987, Keith 1990). However, we anticipated lower annual survival rates in the first two years of the population decline based on dramatically reduced survival observed within two years of the peak in Kluane (Hodges et al. 2001). Predator-induced stress in hares, which peaks with predator abundance, can lead to lower birth rates and fewer viable young for females in the decline phase of the population cycle (Stefan and Krebs 2001; Sheriff et al. 2009a, 2009c). Given that non-predatory sources of mortality represented a negligible proportion of hare deaths throughout our study, as has been found elsewhere (e.g., Hodges et al. 2001), we surmise that the sharp population decline was due to reduced recruitment attributable to lower fecundity, lower leveret survival, or a combination thereof.

Our survival models suggest that higher body condition in hares was associated with higher survival rates, especially during months of low survival and for hares in early successional forest. The apparent winter diet (based on fecal pellet analysis) of hares in the CONIFER grid was dominated by spruce with a minor component of birch (BNZ LTER 2013). By contrast, hares in the DECIDUOUS grid had a more diversified diet comprised of willow, balsam poplar, alder, and spruce, indicating greater availability of high-quality winter forage in this early successional habitat. However, qualitative observations indicated very low stem densities of willows in the DECIDUOUS grid which, when coupled with the relatively low amount of structural cover in winter, could have resulted in greater high-risk foraging behavior by hares. Given that 95% of hare deaths for which the cause was known were due to predation, higher body mass for a given skeletal size (indicating better health) probably conferred an advantage for escaping predation, especially in early successional forest where high-risk foraging made hares vulnerable to predators. We used average weight when calculating body condition for hares captured on multiple occasions. Hares tend to lose mass through the winter (Hodges et al. 2006, Kielland et al. 2010), so allowing weight to change monthly for individuals in the survival models would have been more informative for estimating the importance of body condition for hare survival. However, recapture rates for collared hares were inconsistent and weights were often taken months apart for individuals. Rather than use only the last weight measured, which was often recorded in a different season than when mortality occurred, we averaged available weights (Appendix 1.B), which changed approximately 12% between seasonal trapping sessions. By comparison, hares averaged 5% changes in weight between consecutive trapping nights due largely to bait consumption or bowel evacuation.

Snowshoe hares are the predominant prey species for several mammalian and avian predators with broad distributions in North America, including lynx, coyotes, northern goshawks, and great horned owls (Keith et al. 1977, O'Donoghue et al. 1997, Hodges et al. 2001). Hare mortality in our study area was dominated by these four primary hare predators, but with less coyote predation than was observed in the Yukon (O'Donoghue et al. 2001). While we could not identify the predator species in nearly half of the hare deaths by mammalian predators, we suspect that lynx and coyotes were responsible for the vast majority, and we have no reason to believe that the proportion of kills by each predator would differ from those that were positively identified. However, coyote scat and tracks were fairly common in and around both trapping sites throughout the year and we expected more hare predation by this species based on findings in central and western Canada (Brand et al. 1975, Keith et al. 1993, Mowat et al. 2000, O'Donoghue et al. 2001).

We documented seasonal differences in sources of hare predation that mirrored observations made elsewhere (O'Donoghue et al. 1997, 1998a, 1998b). We also observed changes in predation during the peak and decline phase of the hare cycle, which might be attributed to numeric and/or functional responses of predators in relation to hare densities (Keith 1990, Boutin et al. 1995, O'Donoghue et al. 1998b). Without direct estimates of predator abundance in the area, it is difficult to say whether the changes in predation were due to local movement of individual predators or to a more widespread trend in populations. Trapping pressure on lynx was intense in our study area and might explain the decrease in lynx predation by way of a reduction in local abundance of these predators. In an ongoing companion study of lynx in the Bonanza Creek study area, all deaths of collared lynx (*n* = 20) were due to trapping during the same study period (K. Kielland, University of Alaska Fairbanks, unpublished data). This might also have allowed coyotes to make greater use of areas otherwise hunted by lynx, as has been hypothesized in another study (Murray et al. 1994). Moreover, fur sealing data from the Alaska Department of Fish and Game indicate that lynx harvest declined 64% from 2009-10 to 2011-12 in the game management unit containing our study area (Alaska Department of Fish and Game [ADFG] 2012), suggestive of declining lynx populations. With the vast majority of lynx being trapped between December and February (ADFG 2012), hares may have experienced dramatically lower predation pressure in winter, leading to the unexpectedly high survival rates we observed during this season. Coyotes were considered scarce by trappers during the winter and their harvest was miniscule when compared with lynx (ADFG 2012).

Within a given habitat, there was a slight tendency for predation to take place in locations with more lateral and canopy cover than what was available on average, entirely opposite of our predictions. It seems feasible that lynx might have benefited from dense vegetation in black spruce forest when stalking and ambushing hares (Murray et al. 1995). However, we would not expect kills by goshawks and great horned owls in dense vegetation unless hares were limited to those areas. In general, great horned owls did kill hares in more open habitat: all kills took place in shrub habitat with sparse cover during fall, and primarily in a mixed forest with open understory in other seasons. Previous studies suggest that this is more suitable foraging habitat than black spruce for both great horned owls and goshawks (Rohner and Krebs 1996, Squires 2000), but all identifiable goshawk kills during summer were located in black spruce forest, and more kills were found collectively in early successional, mature white spruce, and black spruce forest than in mixed forest during the remainder of the year.

Our findings suggest that survival rates of snowshoe hares differ markedly from month to month, and more generally across seasons, depending in part on the habitat hares occupy. Sources of predation also differ considerably as a function of seasonality and habitat, but it is unclear whether vegetative cover is the primary reason for these differences. Despite the fact that black spruce forest provides refuge from predators in the boreal forest, hares are still highly susceptible to lynx predation in this habitat. Avian predation appears to be more variable in time and space, while coyote predation in our study area appears to be highly localized both spatially and temporally. The absence of significant decreases in annual survival of older juvenile and adult hares during the population decline suggests that other demographic processes, such as natality and leveret survival, exert important controls over population dynamics (Sheriff et al. 2009a). Moreover, greater body condition confers higher survival probability, but this relationship was only biologically significant during seasons of low survival (spring and fall). These observations underscore how the interaction of a diverse set of biotic variables (habitat, predators, body condition, age, etc.) controls survival in snowshoe hares both within and across seasons.

MANAGEMENT IMPLICATIONS

Snowshoe hares are hunted and trapped as small game throughout their range and serve as an important source of prey for furbearing predators such as lynx and coyotes. Lynx populations especially are inextricably linked to snowshoe hare abundance, and management of one species naturally implicates management of the other. Our study confirmed that mature black spruce forests are important habitats for hares in Alaska, and this is likely to hold true for lynx as well, given the high predation rates we observed in this vegetation type. Early successional forests appear to represent ideal seasonal hare habitats during the decline phase of the hare cycle, and a year-round habitat during the late-increase and peak phase for both hares and their mammalian predators, while avian predators regularly use mixed forests to hunt hares. A mosaic of these forest types would therefore be beneficial to the maintenance of healthy populations of hares and their predators.

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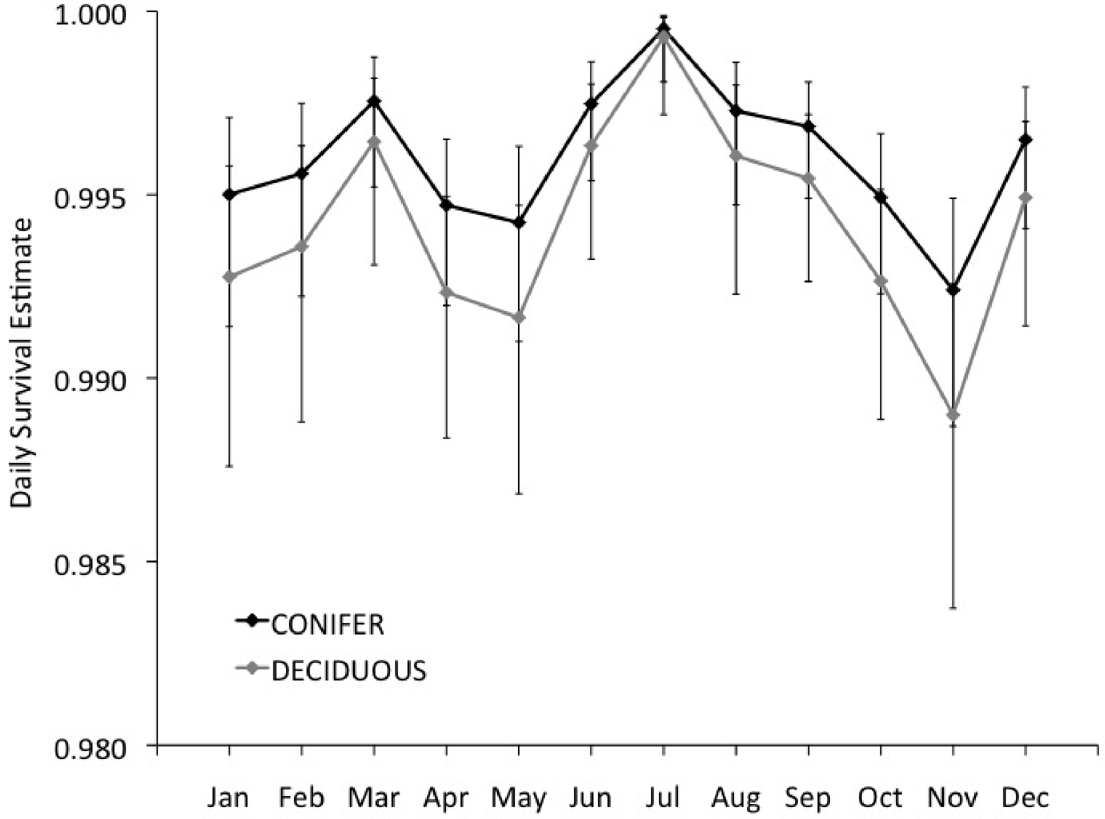

Figure 1.1 Snowshoe hare daily survival rate estimates for CONIFER and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012. Estimates are based on the model S (Body Condition + Site + Month) and reported for a mean body condition index of 10.4. Error bars represent 95% CI.

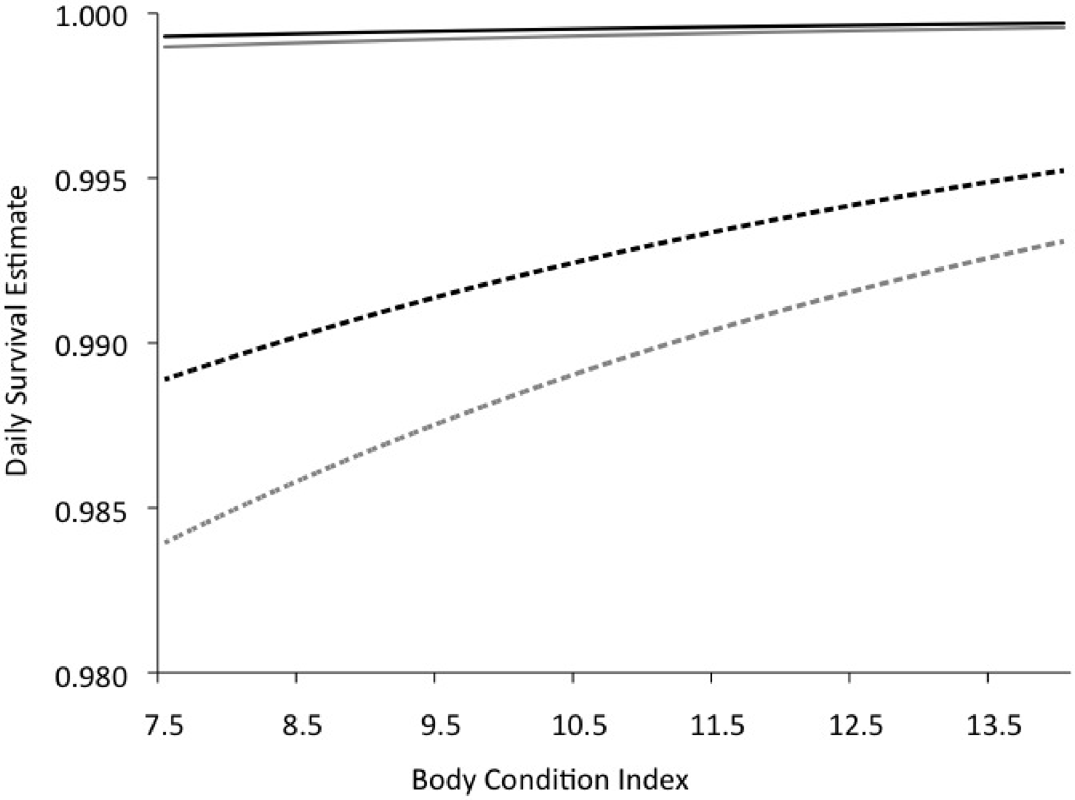

Figure 1.2 Relationship between estimated daily survival rate and body condition index for snowshoe hares in the CONIFER (black lines) and DECIDUOUS (grey lines) trapping grids in July (solid lines) and November (dashed lines) (the months of highest and lowest snowshoe hare survival) in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012. Estimates are based on the model *S* (Body Condition + Site + Month). Confidence intervals (95%, not shown) indicated some overlap between trapping grids within a season.

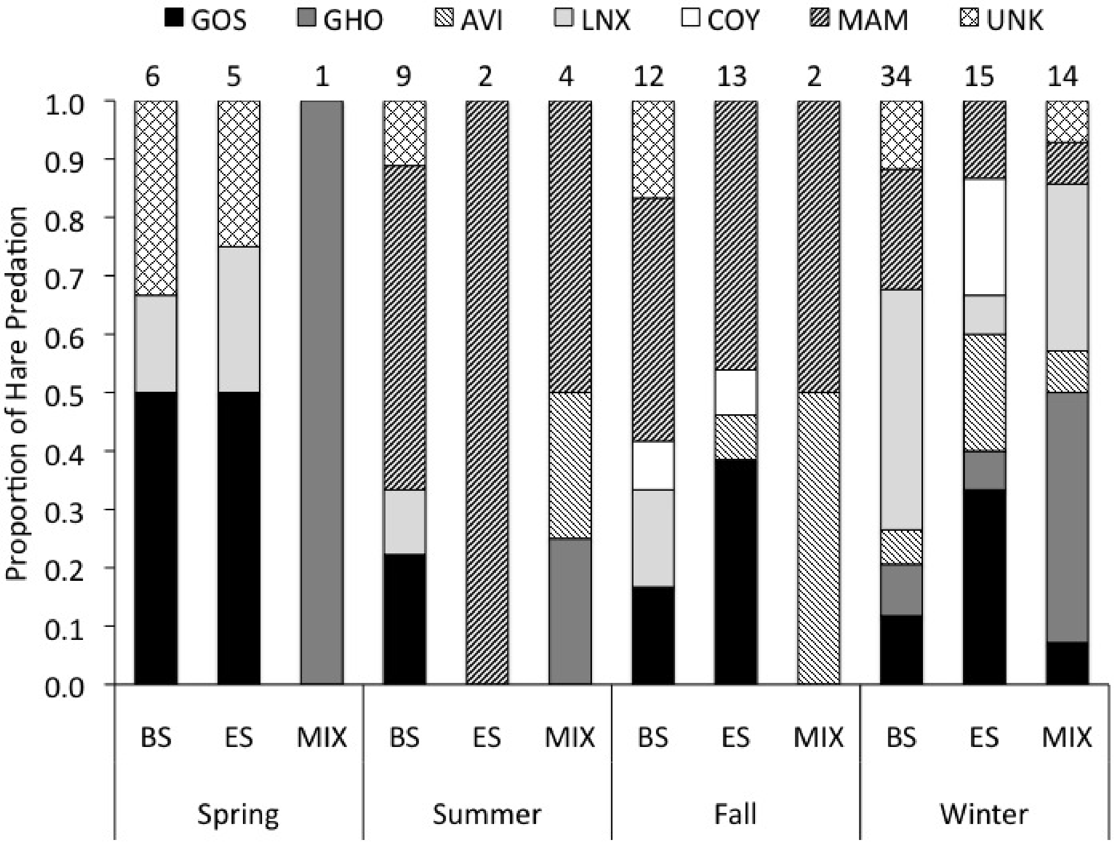

Figure 1.3 Proportion of snowshoe hare predation by predator class or species, by season and habitat type, in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012. Habitat types are black spruce forest (BS), early successional forest (ES), and mixed forest (MIX). Only the habitats most frequently used by hares in our study are shown. Predators are goshawk (GOS), great horned owl (GHO), unidentified raptor (AVI), lynx (LNX), coyote (COY), and unidentified mammal (MAM). Sample size is given above each column.

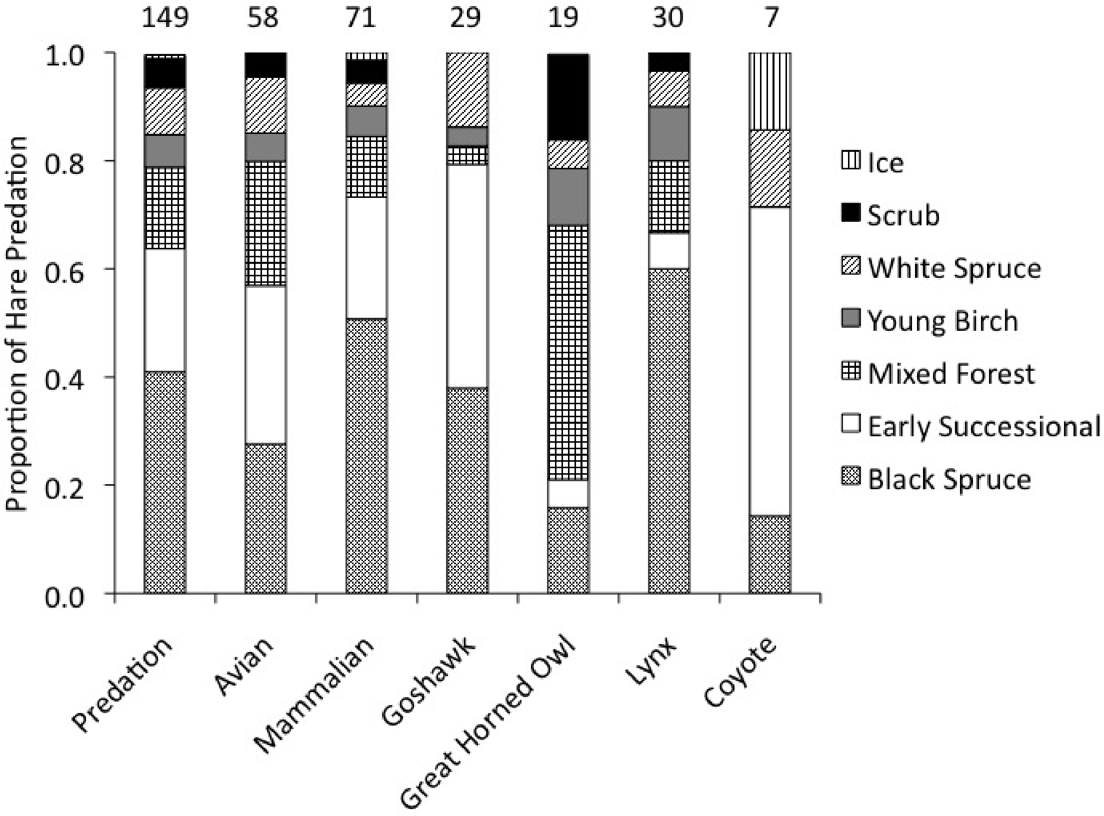

Figure 1.4 Proportion of snowshoe hare predation events by habitat type, for predator species or class, in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012. Sample size is given above each column.

Table 1.1 Variables used to construct *a priori* survival models for snowshoe hares in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

Parameter	Description
Age	Age (juvenile or adult) at time of radio-tagging. Juveniles became adults after March 1. We were unable to identify the age of hares captured after mid-September, so hares of unknown age were categorized as adults.
Sex	Sex (male, female, or unknown).
Body Condition	An index of body condition calculated as (weight / hind foot). If a hare was captured more than once, measurements for weight and hind foot were averaged over the time that hare carried a radio transmitter.
Site	Trapping grid (DECIDUOUS or CONIFER) in which hare was radio-tagged.
Month	Calendar month.
Season	Summer (~1 Jun to ~1 Sep) was defined by the presence of deciduous leaves and absence of snow. Fall (~1 Sep to ~15 Oct) was defined by the senescence of deciduous leaves and absence of snow. Winter (~15 Oct to ~1 May) was defined by the absence of deciduous leaves and presence of snow. Spring (~1 May to ~1 Jun) was defined by the absence of both deciduous leaves and snow.
Year	Annual period from 1 June to 31 May.
Air Temperature*	Average air temperature at 50 cm above ground when snow depth is <50 cm, or 150 cm above ground when snow depth is >50 cm.
Snow Presence*	Presence of at least 0.5 cm of snow on ground persisting for more than 1 day.
Snow Depth*	Average depth of snow on ground during monitoring interval, measured to 0.1 cm.
Snowfall*	Total precipitation falling as snow during monitoring interval, measured to 0.1 cm.

*Weather data were collected by Bonanza Creek LTER at a weather station located 500 m from the DECIDUOUS trapping grid and 1.5 km from the CONIFER grid, and are summarized in Appendix 1.A.

Table 1.2 Classification and fates of radio-tagged snowshoe hares in the CONIFEROUS and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

	CONIFER	DECIDUOUS
Total Collared	159	129
Male / Female / Unknown	76 / 80 / 3	37 / 88 / 4
Adult / Juvenile / Unknown	92 / 12 / 55	83 / 15 / 31
Fate		
Predation	84	66
Non-predation (i.e. Starvation)	4	4
Unknown	16	32
Right Censored	36	27
Remaining Alive	19	0

Table 1.3 Top 15 models for estimation of survival rates of snowshoe hares in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

Model	AIC_c[a]	Δ AIC_c	AIC_c Weight	Model Likelihood	K[b]
S (site + month + body condition)	1720.35	0.00	0.529	1.000	14
S (site + month + age)	1723.36	3.01	0.117	0.222	14
S (site + month)	1723.95	3.60	0.088	0.166	13
S (site + body condition + season)	1724.25	4.07	0.069	0.131	6
S (month + body condition)	1724.78	4.43	0.058	0.109	13
S (month + age)	1725.42	5.06	0.042	0.080	13
S (month)	1727.10	6.75	0.018	0.034	12
S (site + season)	1727.94	7.59	0.012	0.023	5
S (site * season)	1727.97	7.62	0.012	0.022	8
S (site + season + age)	1728.26	7.91	0.010	0.019	6
S (body condition + season)	1728.83	8.47	0.008	0.015	5
S (month * age)	1729.56	9.20	0.005	0.010	23
S (month + sex)	1730.25	9.90	0.004	0.007	14
S (season + age)	1730.59	10.24	0.003	0.006	5
S (season)	1731.06	10.70	0.003	0.005	4

[a] Akaike's Information Criterion adjusted for small sample size.

[b] Number of parameters.

Table 1.4 Summed model weights (over all models in the model set) for all variables in known-fate models for estimating survival rates of snowshoe hares in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

Variable	Weight	# Models
Month	0.862	10
Site	0.841	36
Body Condition	0.667	20
Age	0.181	23
Season	0.119	10
Sex	0.004	13
Air Temperature	0.001	22
Snow Presence	0.003	12
Snow Depth	0	12
Snowfall	0	12
Year	0	10

APPENDIX 1.A SUMMARY OF ENVIRONMENTAL CONDITIONS

Table 1.A-1 Summary of environmental conditions in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Average Temp (°C)	-22	-27	-18	-15	-2	9	13	14	10	4	-7	-19
Average Min Temp (°C)	-27	-31	-23	-22	-8	1	8	9	5	0	-11	-23
Average Snowfall (cm)	35	24	16	38	3	0	0	0	0	0	35	50
Average Snow Depth (cm)	25	32	40	48	22	0	0	0	0	0	5	17

APPENDIX 1.B MASS AND HIND FOOT LENGTHS FOR SNOWSHOE HARES

Table 1.B-1 Mass (g) and hind foot lengths (mm), reported as mean ± SE (range), for radio-tagged snowshoe hares in the CONIFER and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to May 2012.

	CONIFER			DECIDUOUS		
Age	n	Mass	Hind Foot	n	Mass	Hind Foot
Adult	92	1431 ± 17 (1100–2170)	139 ± 1 (125–152)	83	1545 ± 23 (770–2105)	139 ± 1 (125–151)
Juvenile	12	1319 ± 51 (853–1534)	137 ± 3 (113–150)	15	1187 ± 70 (820–1620)	128 ± 3 (109–147)
Unknown	55	1415 ± 24 (1120–1720)	141 ± 1 (132–159)	31	1364 ± 20 (1120–1670)	137 ± 1 (120–150)

CHAPTER 2

Movement, activity patterns, and habitat use of snowshoe hares (*Lepus americanus*) in interior Alaska[2]

ABSTRACT

Snowshoe hares (*Lepus americanus*) are generally sedentary, but are known to use different habitats in summer and winter in addition to making exploratory movements at various times of the year. Hares in the boreal forest may also move among suitable habitats on a shorter time scale in search of preferred foods and cover from predators. We investigated movement patterns of hares from two characteristic boreal habitats using VHF radio collars (n = 209) monitored weekly and GPS collars (n = 18) programmed to record locations at 30-120 min intervals. We used transmitter recoveries to estimate distance from capture to mortality site. Approximately 90% of transmitters were recovered from hares within 1 km of their initial capture locations while 5% were recovered 2.5-8.5 km from the capture locations. Transmitters were recovered farthest from capture sites in winter and farther away for adult females than adult males. We used locations of GPS-collared hares to estimate seasonal home range size, habitat use, and diel patterns of movement among and within habitats. Seasonal home ranges (90% isopleths) were marginally larger in a black spruce (*Picea mariana*) forest during winter

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[2] Feierabend, D.F. and K. Kielland. 2013. Movement of snowshoe hares (*Lepus americanus*) in interior Alaska. Prepared for submission in Journal of Mammalogy.

(2.3-5.4 ha) than in an early successional forest during summer (0.6-4.3 ha). Hares captured in a black spruce forest in late winter had multiple core use areas that regularly included white spruce (*P. glauca*)-birch (*Betula alaskana*) forest. Hares captured in an early successional forest in summer spent the majority of time in that habitat but also regularly used white spruce and black spruce forest. Movement rates, measured as the distance between animal locations recorded every 2 hours, were highest around midnight and lowest between 1200 and 1600 with at least a 4-fold difference in movement rate between peak and nadir. The majority of movement between habitat types was coincident with times of peak movement rates. Our findings indicate that hares living in a mosaic of vegetation communities often concentrate their habitat use in multiple vegetation types even when food and cover are apparently abundant in a single habitat. Hares move between these areas on a daily basis, probably to make use of better foraging opportunities in one location and return to resting sites located in dense cover in a different location.

INTRODUCTION

The snowshoe hare (*Lepus americanus*) is a foundational prey species in the boreal forests of North America (Krebs et al. 2001) and faces drastically different weather conditions, food availability, and predation pressure throughout the year. In response to changing environmental challenges, snowshoe hares shift their home ranges to habitats with denser cover when more predators are present (Boutin 1984a; Wolff 1980), apparently sacrificing access to preferred browse for safety (Keith et al. 1984; Sievert and Keith 1985). Snowshoe hares also compensate for seasonal changes in vegetative cover and predation risk by occupying denser conifer stands during winter when deciduous leaves are absent (Wolff 1980). Snowshoe hares then expand or shift their ranges to include mixed-vegetation stands in the summer when deciduous browse is available (Wolff 1980), presumably tracking the availability of high-quality food as mountain hares (*L. timidus*) do in European boreal forests (Dahl 2005; Kauhala et al. 2005).

Snowshoe hares prefer habitats with dense cover (Litvaitis et al. 1985), but the use of habitat edges (Ferron and Ouellet 1992) suggests that they benefit from being in close proximity to open areas where preferred food species are probably more abundant. Hares in a landscape with fine-scale habitat heterogeneity are likely to move among habitats on a daily basis in order to capitalize on differences in food availability and cover, and the dramatic seasonal changes in these environmental parameters should in turn affect the rates of movement and habitat use.

We investigated diel movement patterns of snowshoe hares among different habitat types in interior Alaska in summer and winter, using GPS collars to measure movement rates and habitat use on a fine spatial scale. We also estimated the home ranges and core use areas of hares in both seasons. We predicted that hares would move among habitats most frequently during winter when their diet is limited to low-quality woody browse and food stress is most prevalent; an increase in movement among habitats would then result in larger home ranges. Snowshoe hares primarily limit their movement and activity to the dark hours of the day (Keith 1964), so we predicted that the extended darkness during winter in interior Alaska would result in longer periods of diel movement than during summer. Finally, we measured rates of travel away from capture sites by locating hares collared with VHF transmitters after they had died. By understanding the frequency and timing of these fine-scale movements, we gain insight into the importance of habitat heterogeneity to hares and the indirect impact it may have on closely associated predators such as lynx (*Lynx canadensis*).

MATERIALS AND METHODS

Study Area

This study took place in the Bonanza Creek Long-Term Ecological Research site and Bonanza Creek Experimental Forest (68° N, 148° W), located approximately 20 km southwest of Fairbanks, Alaska. Snowshoe hare populations have been monitored at two sites here since 1998 (Kielland et al. 2010). These populations showed cyclic peaks in the fall of 1999 and 2009. Habitat type differs between the two sites. The first site, situated adjacent to the Tanana River, was early successional community (hereafter referred to as the DECIDUOUS site) dominated by willow (*Salix spp.*), thin-leaf alder (*Alnus tenuifolia*), and balsam poplar (*Populus balsamifera*). Understory species included *Epilobium angustifolium, Cornus canadensis, Calamagrostis canadensis*, and *Equisetum sp.*. The second site was in a mature black spruce (*Picea mariana*) community (hereafter referred to as the CONIFER site) with an understory composed of *Ledum sp.*, *Rosa acicularis*, *Vaccinium vitis-idaea*, *Salix sp*., *Chamaedaphne calyculata*, mosses, and lichens. Other habitats in the area include floodplain white spruce (*Picea glauca*), poplar, mixed white spruce-birch (*Betula neoalaskana*), aspen (*Populus tremuloides*), and regenerating stands of birch and aspen in areas that burned in the last 30 years.

Snowshoe Hare Capture and Collaring

Within each site we used an established 9-ha rectangular trapping grid with 10 transects spaced 50 m apart and 5 traps spaced 50 m apart on each transect (50 traps total). The two trapping grids were separated by 1.5 km. We captured hares in #3 Havahart live traps (model 1085, Lititz, PA) and aged, sexed, weighed and sized them, and marked them with Monel ear tags (National Band and Tag Co., Newport, KY) for ongoing population studies. We could not distinguish between juveniles and adults after mid-September, so hares first captured after this time were classified as adults. It is likely that many juveniles born on or near the trapping grids were thus classified as adults, so any differences observed between adults and juveniles should be highly conservative. Traps were baited with alfalfa, carrots, and snow (when available) for moisture. Traps were opened during mid-day and checked the following morning. Trapping sessions were conducted once every 3 months; sessions ranged in length from 1-4 consecutive nights and were discontinued if temperatures fell below -18° C. Capture and handling procedures followed animal care and use guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (protocol #09-57) and the Alaska Department of Fish and Game (Permit 135211-5).

Between June 2008 and January 2013, we equipped a subset of trapped hares with VHF radio collars. Collars weighed between 20 and 26 g (models M1555, M1565, M1575, Advanced Telemetry Systems, Isanti, MN) and were equipped with a mortality switch activated by a lack of movement over 6 consecutive hours. Collars were only put on hares weighing over 900 g so that collars did not exceed 3% of the hare's body weight; this restricted our study to adult and older juvenile hares.

We fitted VHF radio transmitters to 8 and 12 hares in the DECIDUOUS and CONIFER sites, respectively, in June 2008. Sample size increased to 24 in DECIDUOUS and 19 in CONIFER by September 2008. We collared additional hares as mortalities occurred in an attempt to maintain at least 25 collared individuals in each site at any given time (representing 20-90% of the hare population depending on the time of year), conducting additional trapping sessions as needed. Hares were collared through January 2013 in CONIFER. However, hare abundance was too low in DECIDUOUS to collar additional hares after November 2011. Fewer than 5 collared hares remained in DECIDUOUS by mid-December 2011 and none by mid-May 2012. We equipped adult hares with GPS loggers and VHF transmitters (model G30L, Advanced Telemetry Systems; model Quantum 4000, Telemetry Solutions, Concord, CA). Only females were collared in DECIDUOUS: 7 between May and September 2010 and 5 between May and August 2011. We collared 4 females and 2 males in CONIFER between February and April 2012. These collars were programmed to take fixes at half-hour (n = 3) or 1.5-hour (n = 4) intervals in 2010, 1-hour (n = 3) or 2-hour (n = 2) intervals in 2011, and 2-hour (n = 6) intervals in 2012. We used different fix intervals for the two collar models to determine battery life of the collars before settling on 2-hour intervals in 2012. GPS collars were removed and replaced with VHF collars when the GPS batteries expired, usually after 2-3 weeks. The maximum weight of GPS collars was 40 g (4% of a hare's mass) and was not expected to affect survival (Sikes and Gannon 2011).

We monitored VHF-collared hares (including those with GPS) every 1-7 days using a directional Yagi antenna and hand-held receiver (model R1000 receiver; Communications Specialists Inc., Orange, California) to detect movement of hares off the trapping grids and locate mortalities. When transmitter signal strength or location suggested that a hare had moved more than 500 m from its trapping grid, we attempted to find and visually confirm its location. Mortalities were typically recovered within 1 week of death and their locations were recorded using a handheld GPS unit.

Analysis

For VHF-collared hares, we calculated the linear distance between the location of initial collaring and the site where a collar was recovered after death. This served as an indication of how far a hare might travel from its capture site (presumably located within its home range) in different seasons. While we could not be sure if collars were moved by predators or scavengers after a hare had died, our observations suggested this was negligible in most cases. We used a 3-factor analysis of variance to compare the log-transformed linear distance from initial capture to mortality site between trapping grids, sexes, and seasons. Due to low sample sizes in non-winter seasons, we pooled data for spring (May), summer (Jun-Aug), and fall (Sep-Oct), and compared these to winter (Nov-

Apr). We did not include age as a factor in the ANOVA due to unbalanced sample sizes, but instead compared distances for juveniles and adults using a student t-test.

We estimated seasonal home range sizes for GPS-collared hares using the fixed kernel method (Worton 1989). We considered the seasonal home range to be the range of a hare used within a single season, measured here in summer (late-May to late-September) and late-winter (late-February to mid-April). GPS collars had a 46-97% success rate for scheduled fixes. Accuracy varied depending on the orientation of the GPS antenna to the sky and the number and configuration of satellites available, but was generally believed to be within 10 m of the true location based on field tests. We censored animal locations that were obviously incorrect, such as those occurring in the Tanana River during summer. We used all remaining fixes (mean: 433 ± 92, range: 78-1802) over all days fixes were obtained (mean: 30 ± 5, range: 6-54). Although the number of fixes and time over which fixes were obtained were highly variable, there was no correlation between the number of fixes and seasonal home range size ($r^2 = 0.08$, $p = 0.75$) or between the number of fix days and seasonal home range size ($r^2 = 0.10$, $p = 0.69$). Further, subsampling of animal locations has been shown to underestimate range size (Blundell et al. 2001), so we used all available fixes in range estimation. We calculated utilization distributions using the kde kernel density function in Geospatial Modeling Environment (GME). After calculating 90% isopleths using all available bandwidth algorithms (LSCV, SCV, BCV, PLUG-IN, CVH), we judged the appropriateness of each method by visually assessing the general fit of the isopleths to the data. Finding the SCV method most consistent across individuals, we applied this algorithm to all datasets and used a cell size of 1 to calculate both seasonal home ranges (90% isopleths) and core use areas (50% isopleths) (Börger et al. 2006). We compared seasonal home range sizes between trapping grids/seasons using the Kruskal-Wallis test.

To understand fine-scale habitat use, we used a vegetation layer in ArcGIS for Bonanza Creek Experimental Forest to identify the vegetation composition in the seasonal home ranges based on floristic classifications (Baird 2011). Habitat use was quantified using the number of GPS locations in each vegetation community rather than the areas within the 90% isopleths because the latter tended to overestimate range boundaries in places with small numbers of isolated points. In order to address any diel patterns of habitat use, we compared the proportion of GPS locations in each habitat type used in 2-hour periods throughout the day, beginning at midnight (2400-0200, 0200-0400, 0400-0600, etc.).

To investigate diel changes in movement rates, we calculated the linear distance moved in the same 2-hour periods as above. For individuals with 0.5-hour, 1-hour, or 2-hour fix intervals, linear distance for a 2-hour period was calculated between fix locations recorded at the beginning and end of the period. For 1.5-hour fix intervals, linear distance for a 2-hour period was calculated between fix locations at the beginning and end of the 1.5-hour interval. We multiplied these distances by a factor of 1.3 to correct for the shorter time interval; they are slightly positively biased compared to linear distances estimated from fixes taken at the beginning and end of a 2-hour period. The distances for 1.5-hour intervals were assigned to the 2-hour period with which they overlapped most. For each individual, movement was averaged over all days for each 2-

hour period; we then averaged movement over all individuals from a trapping grid/season for each period.

We quantified diel patterns of hare movement among habitats over the same 2-hour periods by calculating the number of times an individual was located in different habitats at the beginning and end of a period, then dividing by the total number of instances that individual moved among habitats in all periods. The proportion of movements among habitats that occurred in each period was then averaged across all individuals that moved among habitats (we excluded 6 hares from DECIDUOUS/summer that moved among habitats <5 times as they would have had undue influence on the few time periods in which their movements took place). As before, the movements for fixes taken at 1.5-hour intervals were assigned to the 2-hour period with which they overlapped most.

Statistical analyses were conducted using program JMP version 10 (SAS Institute Inc., Cary, NC). Means are reported with standard error unless otherwise noted.

RESULTS

General Movements

We collared a total of 300 hares with VHF transmitters (including those with GPS loggers) from 10 June 2008 to 17 January 2013 (Table 2.1). We recovered 203 transmitters from mortality events, 23% of which were within 100 m, 82% within 500 m, and 95% within 2 km of their deployment locations (Figure 2.1). One transmitter was recovered from a dead hare 8.7 km from the site of initial capture, and another live hare was last estimated at a linear distance of over 14 km from its initial capture point after crossing at least two major roads in the process. In general, we documented more movement of collared hares off the trapping sites in winter than other seasons, and 18 of 21 transmitters located over 1 km from the trapping sites were recovered in winter. Distances between collaring and recovery locations were on average >2.5 times greater in winter than non-winter seasons ($F_{3,196} = 5.9$, $P < 0.001$) but did not differ between sites or sexes (Table 2.2), although adult females averaged distances >2 times farther than adult males. Distances were similar in spring (208 ± 36 m), summer (385 ± 119 m), and fall (336 ± 97 m). Mean distances did not differ between juveniles and adults ($t_{201} = 0.12$, $P = 0.91$).

When transmitters were found in different habitats than the initial capture location, hares from DECIDUOUS often appeared to have moved north (towards the CONIFER grid) into either white or black spruce forest (Figure 2.2). However, 7 of the farthest dispersals from DECIDUOUS resulted when hares crossed the main channel of the frozen Tanana River during winter, traveling up to 7 km from the trapping grid across a patchwork of different habitats. In contrast, only a single transmitter from CONIFER was recovered across the river from the trapping grids. Most of the transmitters recovered beyond the CONIFER grid were to the north and west in upland mixed forest, or in young regenerating birch and aspen stands in recent burn sites in the uplands.

Seasonal Home Range Size

Seasonal home ranges for GPS-collared hares varied from 0.6-5.5 ha and core use areas ranged from 0.1-1.1 ha. Hares from DECIDUOUS/summer had smaller home ranges ($Z = 2.67$, $P = 0.008$) and core use areas than hares from CONIFER/winter (Table 2.3). Home ranges for males from CONIFER/winter averaged 3.1 ± 0.7 ha (range: 2.3-3.8, $n = 2$) and females averaged 4.0 ± 0.6 ha (range: 2.7-5.5, $n = 4$). Core use areas represented 24% of seasonal home ranges regardless of site/season. The radii of home ranges and core use areas were less than 650 m and 200 m, respectively, indicating that hares rarely moved more than 500 m from the cores of their ranges. Due to an inability to incorporate physical boundaries into range estimation using kernel density estimators (Getz et al. 2007), range areas for hares collared in DECIDUOUS often included open water, either from the Tanana River or from wetlands. These portions, which represented no more than 16% of any range area, were removed before calculating the range sizes reported here.

Habitat Use

The space use patterns by hares with GPS collars from DECIDUOUS/summer varied greatly among individuals (Figure 2.3). All hares primarily used early successional forest (82% of locations), but 6 also used adjacent habitat types such as black spruce forest (11% of locations). Hares with smaller ranges primarily spent their time in early successional habitat, whereas those with larger ranges moved frequently between early successional and conifer forests, spending little time in the gradient between these habitats. Three hares had home ranges comprised of 2 discontinuous areas with centers ~150-250 m apart, 4 had multiple core areas ~150-250 m apart that included both early successional and conifer habitats, and 1 had a range comprised of 3 discontinuous areas with centers ~500 m apart.

Hares from CONIFER/winter spent most of their time in black spruce forest (68% of locations), but all hares from this site/season also regularly used other habitat types including mixed forest (12% of locations) and burned areas characterized by shrubs and regenerating birch and aspen trees (19% of locations). Additionally, all but 1 hare from CONIFER/winter had multiple core areas located in different habitats. All hares avoided areas in contiguous black spruce forest in and around the CONIFER trapping grid where tree height and density were lower, which was visible in aerial images of the study area.

Hares from CONIFER/winter increased their use of mixed forest and burned areas during dark hours of the day, but spent the majority of daylight hours in black spruce forest (Figure 2.4). Hares from DECIDUOUS/summer exhibited a greater variety of diel habitat use patterns. Two individuals spent most daylight hours in a mature white spruce forest or along its edge, repeatedly using the same sites (~30 m diameter), then spent night hours in a broader area of nearby early successional forest. Other hares repeatedly used small areas in early successional forest during daylight hours, and moved among a variety of white spruce, early successional, and alder-dominated habitats during the night. We also observed hares using nearby conifer forests at various times throughout the day without evident patterns except the concentration of use along habitat edges.

Hares from both sites/seasons also repeatedly made large movements among habitats over short time periods. One hare from DECIDUOUS/summer traveled >1 km along the bank of the Tanana River on 4 separate occasions, moving rapidly between the same 3 areas in which it stayed from 1.5 h to 4 d. A hare from CONIFER/winter repeatedly traveled 250 m across a sparsely vegetated burn area, situated between the margins of black spruce forest and a regenerating young birch forest, using a pathway through discontinuous islands of spruce and thick shrubs. A different hare from CONIFER/winter traveled 1 km through contiguous black spruce forest in 4 hours, remaining in a small 0.4 ha area of birch trees for ~48 h before returning to its starting point over another 4-hour period.

Diel Movement Patterns

Regardless of site/season, GPS-collared hares showed peak movement rates between 1800 and 0800 h (Figure 2.5). Movement was lowest during mid-afternoon, presumably when hares were resting. Peak movement rates at night were 4-7 times higher than movement rates during mid-afternoon, the difference being most pronounced for hares from CONIFER/winter.

Inter-habitat Movement

GPS-collared hares from CONIFER/winter moved among habitats several times per day (mean of 2.0 ± 0.4, range: 1-3.3). The majority of time spent outside of black spruce forest was restricted to less than a single night, but it was not uncommon for hares to spend up to 2 consecutive days in these other habitats at least once during a 30-day period. We documented <5 movements among habitats for 6 of 12 hares from DECIDUOUS/summer; the other 6 moved among habitats with the same frequency as hares from CONIFER/winter (mean of 2.0 ± 0.5, range: 0.3-4.3). Over half of the movements among habitats (57%) for hares from CONIFER/winter took place between

2200 and 0600, compared to 45% for hares from DECIDUOUS/summer during the same time period (Figure 2.6). Regardless of site/season, movements between habitats generally took place at times when hares were most active, which was in the darkest hours of the day.

DISCUSSION

Snowshoe hares living in a variable landscape with many available habitat types could optimize food intake and safety by foraging in productive open areas and seeking refuge from predators in denser vegetation nearby. Such opportunities abound in much of the boreal forest where mosaics of suitable habitat exist. We found that hares captured in a black spruce forest and an early successional forest moved among habitats approximately twice per day and that this generally corresponded with movement between disparate core use areas. Black spruce forest offered dense cover to hares throughout the year but lacked an abundance or variety of preferred browse, especially during winter. Early successional forest offered an abundance of browse species preferred by hares, especially during summer when deciduous leaves were present, but lacked any significant cover in seasons when deciduous leaves were absent. Thus, hares from these trapping sites probably sought different habitats for opposite reasons: in winter, individuals moving from black spruce forest to mixed forest, regenerating birch/aspen stands, or shrubby areas were likely searching for stems of deciduous plants such as *Rosa acicularis*, *Salix* *spp.*, and *Betula spp.*, whereas hares moving from early successional forest to conifer forest during summer were likely seeking safer resting sites or possibly caring for young.

Movement among habitats should change seasonally according to the benefits offered by different structural and vegetative characteristics of the habitats. Snowshoe hares in Minnesota generally preferred lowland and edge sites where food and cover were available throughout the year, but hares were observed in upland sites more frequently in snow-free seasons when deciduous foliage was available (Pietz and Tester 1983). Similarly, snowshoe hares in eastern Canada selected habitat types with different characteristics in summer and winter, with some individuals moving over 1 km between summer ranges in dense deciduous stands and winter ranges in mature spruce stands (Beaudoin et al. 2004). In a study that took place near our own, hares consistently occupied dense black spruce forest during winter and moved into areas with more deciduous foliage during summer (Wolff 1980). Such seasonal changes in habitat use can affect home range size, as was the case for mountain hares in boreal regions of Finland and Sweden where seasonal ranges were smallest in autumn and summer, and largest in late-winter and spring (Dahl 2005; Kauhala et al. 2005) as hares changed their movements based on the availability of preferred browse. Snowshoe hares in boreal habitats experience similar changes in availability of deciduous browse in summer and woody browse in winter, and have been shown to reduce their home range size in response to increased food supply (Boutin 1984a). Using GPS-collars, we found that home ranges were smaller in summer than in winter, suggesting that a high availability of leafy browse in summer did reduce range size. We also observed lower movement rates of hares in summer than in winter, which was probably directly related to smaller average seasonal range size and more prevalent use of singular core areas in early successional forest. This makes sense if movement in winter is driven by foraging and seeking thermal refugia, and movement in summer serves to maximize total area covered, in part to find mates (Hodges 1999). In summer, GPS collars were only carried by females, which move relatively little to find mates when compared to males and would be expected to move more in winter when food and shelter are sought in different areas. However, we note that hares in our study were captured in radically different habitats in summer and winter, and the surrounding habitat availability differed greatly between capture sites. Furthermore, we cannot address the effects of sex on seasonal range size or movement; however, the 4 females captured in black spruce forest in winter did average larger ranges than those of hares in early successional forest in summer, indicating a real difference in home range size between sites/seasons for females.

One explanation for smaller summer ranges is that females with litters must revisit the same nursing site each night, which may constrict home range size. This has been suggested for snowshoe hares (Jekielek 1996), although Dahl and Willebrand (2005) report larger winter-spring than summer-autumn home ranges for mountain hares, attributable to breeding activity in spring. Surprisingly, our GPS data suggested that only 1 of 12 adult females nursed young (see below), despite the fact that sampling usually spanned periods long enough to detect nursing. If females were not nursing young, then the difference in seasonal home range size seems best explained by differences in cover and food availability.

Hares collared in early successional forest in summer spent the great majority of time in that habitat, but many hares also used conifer forests to a lesser extent. With an abundance of deciduous browse and sufficient structural cover to offer protection from predators during the summer, early successional forest is an ideal seasonal habitat for adult hares, but conifer forests may offer increased safety, especially for leverets and juveniles (Dolbeer and Clark 1975). In our study, an adult female fitted with a GPS collar in early successional forest in late May repeatedly moved to and from the same 50 m radius area in a stand of mature white spruce every night around midnight for 28 days. She occasionally shifted her activity to black spruce forest for ~24 hours, but typically returned to early successional forest for the duration of daylight hours. Following this 28-day period, she was located primarily in shrubby wetland habitat and a small copse of paper birch, or in an adjacent black spruce forest, but she rarely returned to her previous location in white spruce and never to early successional forest. O’Donoghue and Bergman (1992) reported that lactating female snowshoe hares returned to the same site at the same time every night to nurse young, regardless of where the young had been located during the day. Similarly, female mountain hares restrict their nursing sites to small 4 m^2-areas (Dahl and Willebrand 2005). The behavior we observed suggests that this particular female may have initially been caring for a litter whose natal site was at the shrubby edge of a white spruce forest. The range shift to shrubby birch and black spruce forest after 28 days may have followed the weaning of a first litter and coincided with the production of a second litter.

Our study took place during a cyclic peak and decline of the local hare population when dispersal rates and distances should be greatest (Windberg and Keith 1976). While transmitter recovery from a dead hare cannot be used to accurately measure dispersal because it precludes any opportunity for that hare to return to its home range, it does serve as an indication of mobility from the initial collaring site. The recovery of transmitters at great distances from capture sites throughout the year in our study corroborates previous findings that hares disperse in all seasons (Windberg and Keith 1976). However, we recovered transmitters considerably farther from capture sites in winter than in other seasons, similar in timing to seasonally high emigration rates during fall and winter for snowshoe hares in Montana (Griffin and Mills 2009), which suggests that they are more mobile and potentially dispersing at higher rates during this time. These movements follow peak hare and predator densities in the fall when deciduous habitats no longer offer significant cover and the diets of hares in coniferous forests are becoming constrained by the lack of deciduous browse. In effect, carrying capacity may decline over winter in some habitats, motivating hares to explore new areas. On several occasions, hares moved away from the CONIFER trapping site for several months during winter before ultimately returning. Similar exploratory movements have been observed during winter for snowshoe hares in western Canada (Boutin 1984a; Boutin et al. 1985) and for mountain hares in boreal Sweden (Dahl and Willebrand 2005).

Previous studies of snowshoe hares have found higher rates of dispersal by juveniles than adults (Boutin 1984b; Keith et al. 1993; Windberg and Keith 1976). We recovered transmitters at distances that indicate dispersal (>1.5 km from capture sites, ~3 times the radius of the largest home ranges in our study) with no observable difference between age classes, suggesting that juvenile and adult snowshoe hares were equally likely to disperse, although we could not reliably distinguish between ages when hares were first captured after mid-September. We tended to recover transmitters from adult females farther from the trapping grids than collars from adult males, despite the fact that males disperse farther and more frequently than females in most mammal species (Greenwood 1980). Large movements were not always indicative of dispersal though: it was not uncommon for GPS-collared hares in our study to make linear movements up to 500 m in a range as small as 3 ha, and at least one hare repeatedly moved up to 1 km from parts of its seasonal range. Despite being characteristically sedentary, snowshoe hares clearly move considerable distances without shifting their home ranges. Such movements appear to be exceptional, but without monitoring an individual's movements for more than a month it may be difficult to distinguish between dispersal and temporary exploration.

Hares in our study moved among habitats mostly at night when general movement rates were highest, as would be expected for a crepuscular/nocturnal animal. However, changes in photoperiod could be expected to have an effect on diel activity patterns. Between June and September, snowshoe hares in Alberta, Canada, exhibited activity patterns similar to those of hares using early successional forest in summer in our study, showing a sharp symmetrical peak around 2300, but nearly doubling the percent of activity taking place between 2030 and 0130 as photoperiod shortened over the study (Keith 1964). Mech et al. (1966) found that snowshoe hares exhibited nocturnal activity patterns during winter, but became more crepuscular in spring and summer; this pattern was also suggested by Foresman and Pearson (1999). Hares in our study confined their movement to times of darkness more in winter than in summer, but exhibited a more crepuscular pattern during winter when movement rates sharply increased around sunset and rapidly declined following sunrise. Hares may respond less strongly to photoperiod in mid-summer, especially at high latitudes where daylight extends for nearly 24 hours, remaining active diurnally and resting primarily during peak afternoon temperatures. Activity of snowshoe hares in Quebec, Canada, suggested this pattern (Théau and Ferron 2001), although daylight was not as extensive as it is in interior Alaska. An alternative explanation for the seasonal differences we observed is that hares in winter routinely made large movements between discontinuous core areas around sunset and sunrise, whereas fewer hares in summer moved between separate core areas on a daily basis and those that did moved shorter distances on average. Once again, we cannot disentangle the effects of site, season, and sex for our data, so the behavior we observed in winter may not be representative of male and female hares in early successional forest at that time or for hares in black spruce forest in other seasons.

To conclude, movement among habitats was common among our GPS-collared hares, but the diel movement rates, behavior, and selection of habitats was highly variable among individuals. A landscape with fine-scale habitat heterogeneity, such as the one in our study, probably enhances variation in hare activity by providing numerous routes for meeting nutritional and safety requirements. In light of the potential advantages of using multiple habitat types, snowshoe hares may thrive with increasing wildfire frequency, which is projected for interior Alaska, if dense conifer refuges persist among an increasing diversity of young, regenerating deciduous communities.

ACKNOWLEDGMENTS

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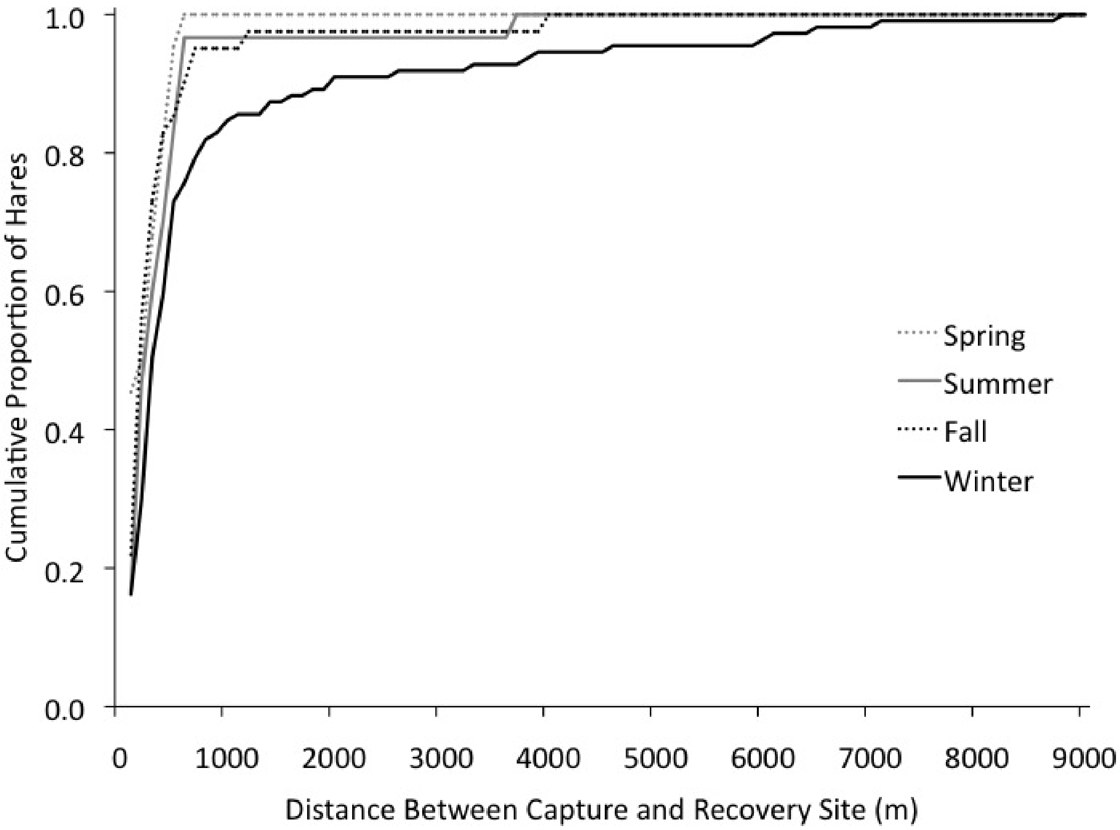

Figure 2.1 Cumulative proportion of snowshoe hares by distance (m) between initial capture site and recovery location for hares (*n* = 203) collared in Bonanza Creek Experimental Forest near Fairbanks, Alaska, June 2008 to January 2013.

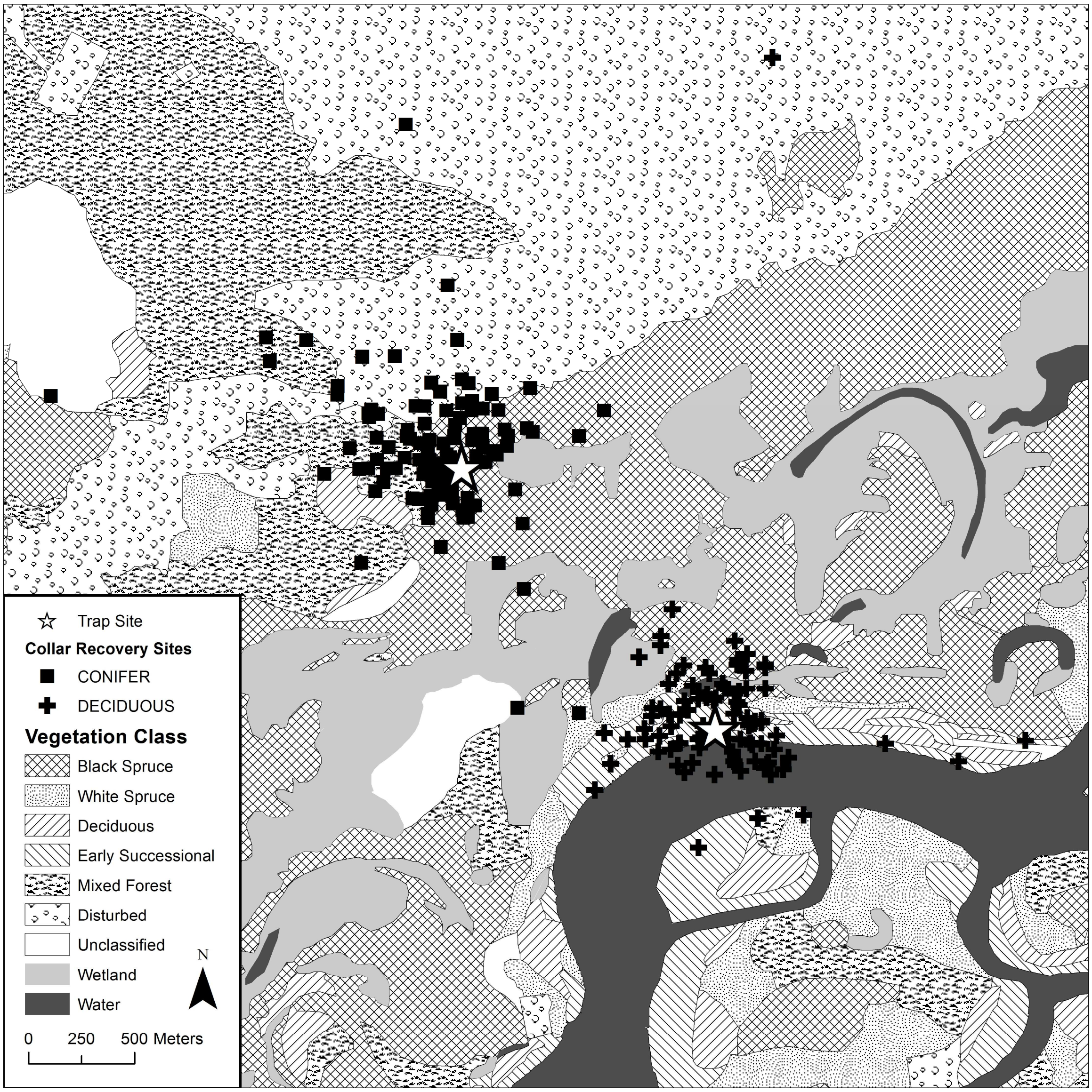

Figure 2.2 Collar recovery locations for snowshoe hares collared in the CONIFER (*n* = 113) and DECIDUOUS (*n* = 90) trapping grids in Bonanza Creek Experimental Forest (68° N, 148° W) near Fairbanks, Alaska, June 2008 to January 2013. Ten collar recovery locations are beyond the boundaries of the map.

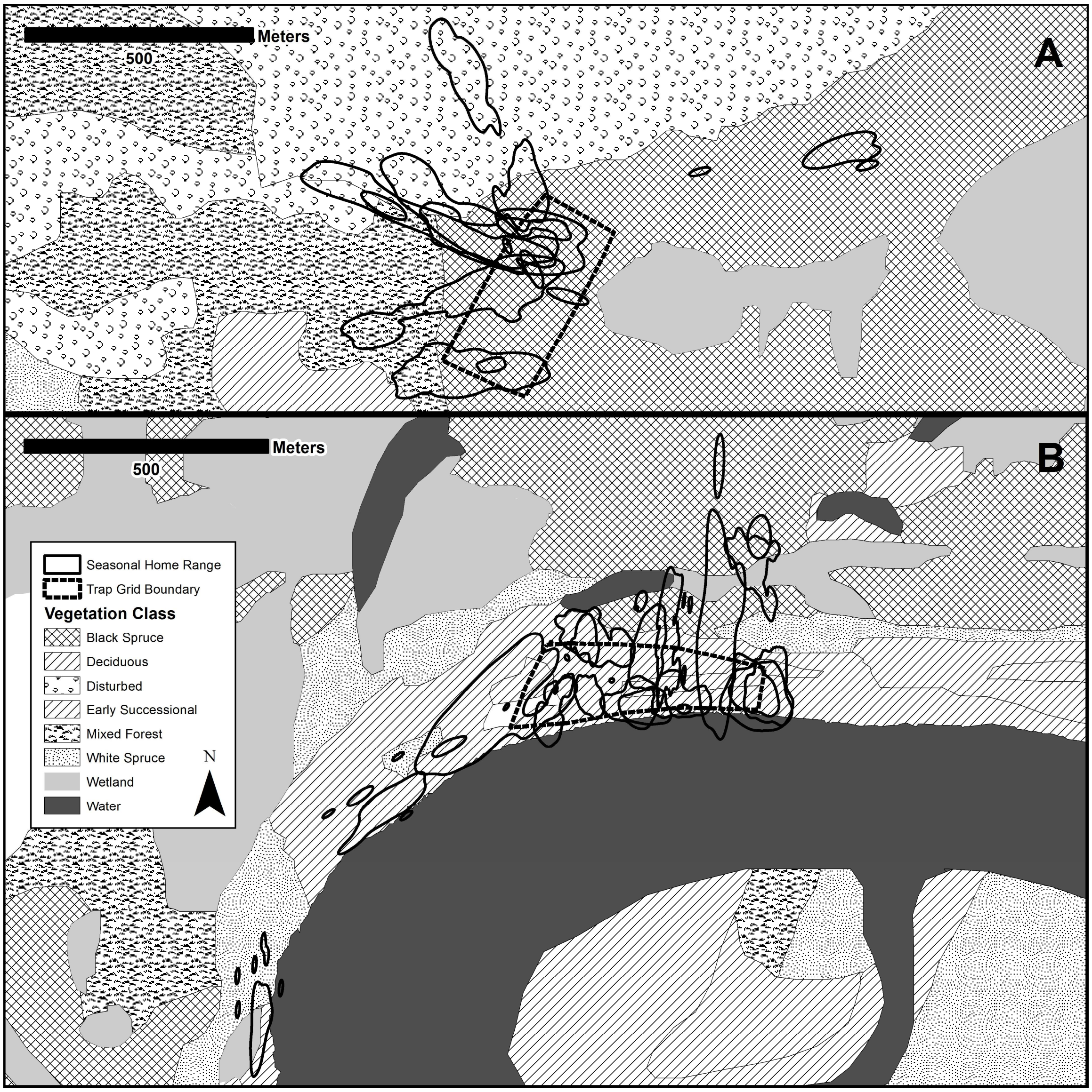

Figure 2.3 Seasonal home ranges (90% isopleths) for snowshoe hares collared in the (A) CONIFER trapping grid from February to April 2012 (*n* = 6) and (B) DECIDUOUS trapping grid from May to October 2010 (*n* = 7) and 2011 (*n* = 5) in Bonanza Creek Experimental Forest near Fairbanks, Alaska.

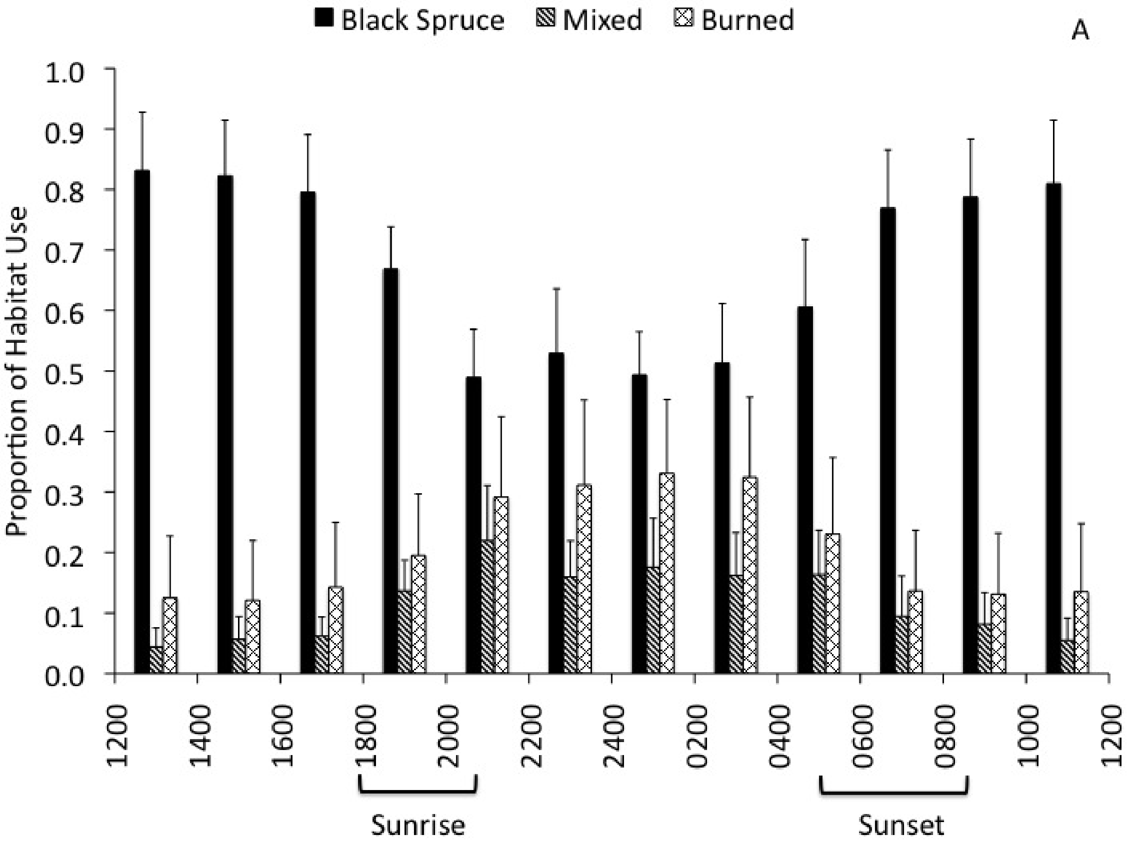

Figure 2.4 Proportion of habitat used in 2-hour intervals for snowshoe hares collared in the CONIFER trapping grid from February to April 2012 (*n* = 6) and DECIDUOUS trapping grid from May to October 2010 (*n* = 7) and 2011 (*n* = 5) in Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ± 1 SE. Sunrise and sunset are indicated for winter (black) and summer (grey) sampling periods.

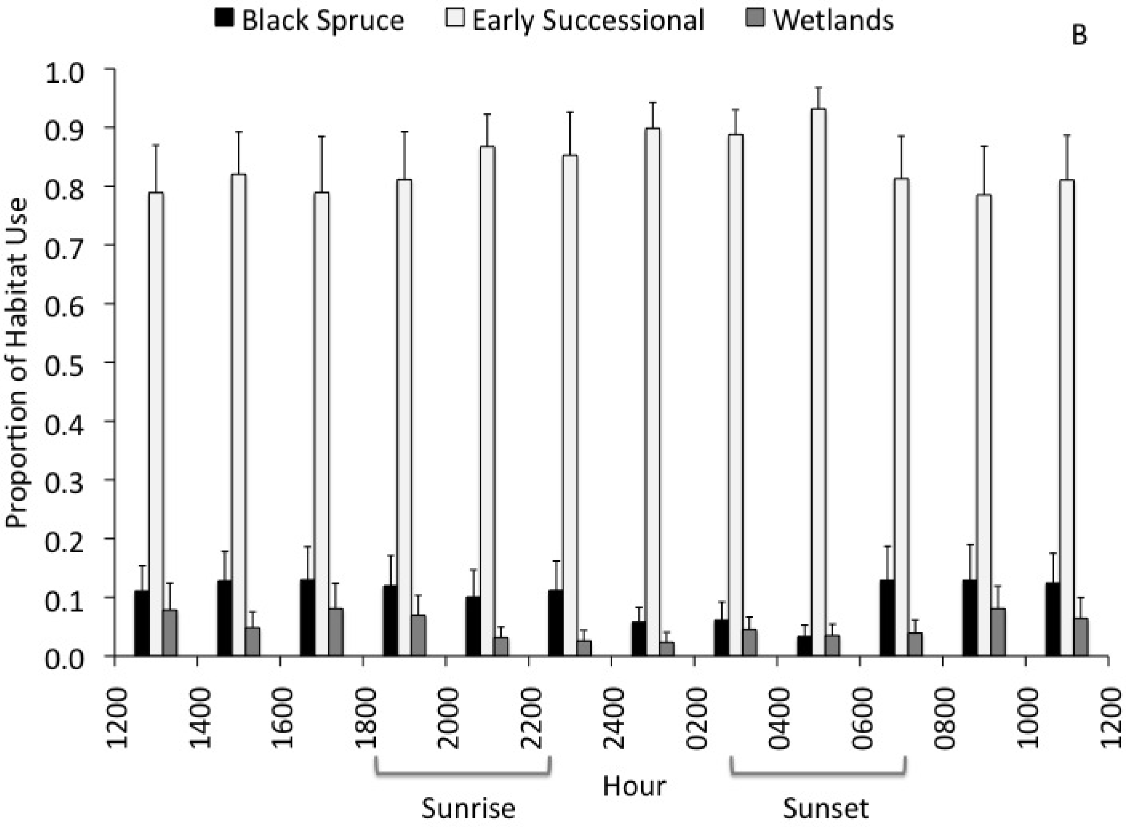

Figure 2.4 Continued…Proportion of habitat used in 2-hour intervals for snowshoe hares collared in the (A) CONIFER trapping grid from February to April 2012 (*n* = 6) and (B) DECIDUOUS trapping grid from May to October 2010 (*n* = 7) and 2011 (*n* = 5) in Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ± 1 SE. Sunrise and sunset are indicated for winter (black) and summer (grey) sampling periods.

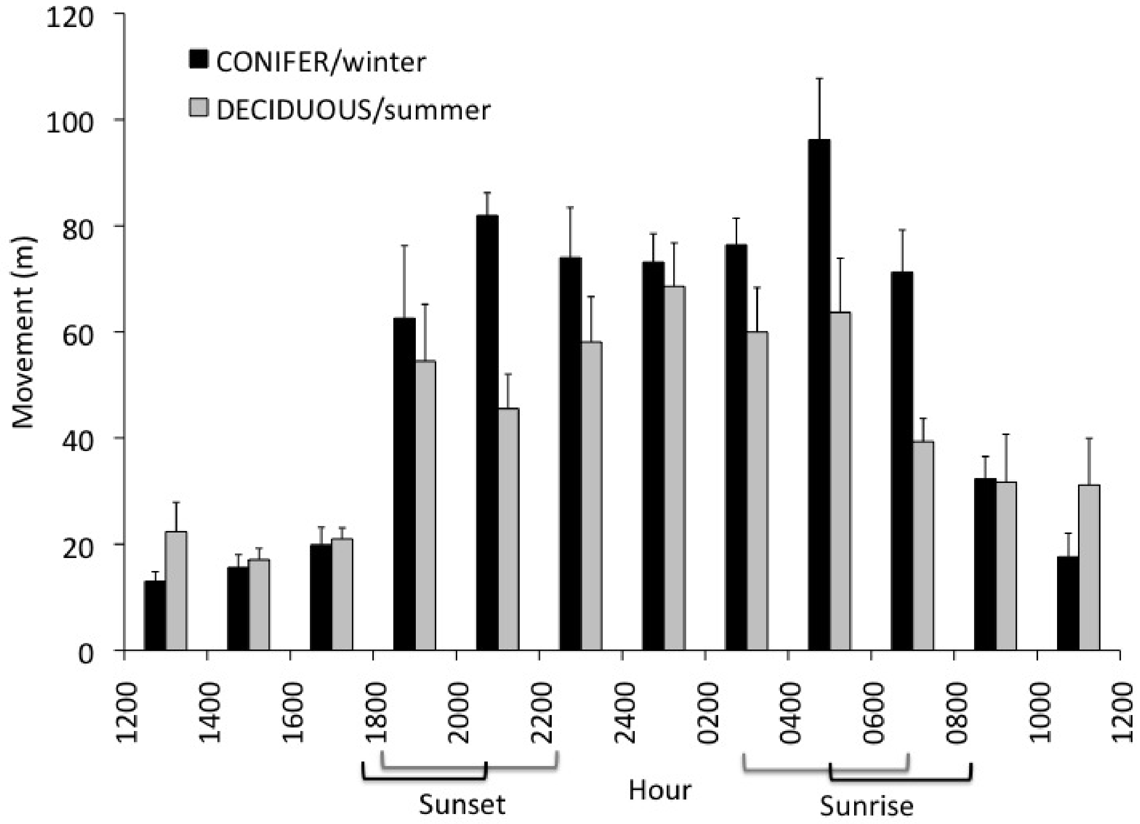

Figure 2.5 Linear distance moved (m) in 2-hour intervals for snowshoe hares collared in the CONIFER trapping grid from February to April 2012 (*n* = 6) and DECIDUOUS trapping grid from May to October 2010 (*n* = 7) and 2011 (*n* = 5) in Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ± 1 SE. Sunrise and sunset are indicated for winter (black) and summer (grey) sampling periods.

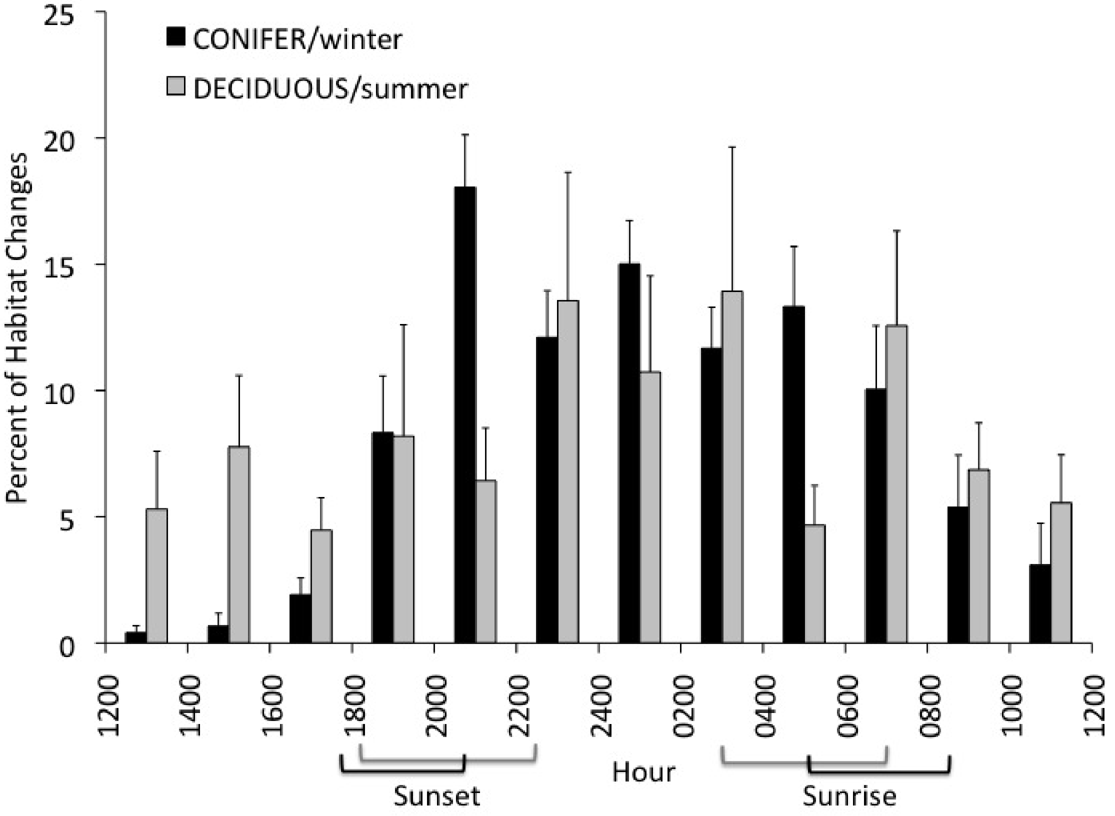

Figure 2.6 Percent of movements between 2 habitat types occurring in 2-hour intervals throughout the day for snowshoe hares collared in the CONIFER trapping grid between February and April 2012 (n = 6) and DECIDUOUS trapping grid between May and October 2010 (n = 7) or 2011 (n = 5) in Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ± 1 SE. Sunrise and sunset are indicated for winter (black) and summer (grey) sampling periods.

Table 2.1 Classification and fates of radio-tagged snowshoe hares in the CONIFER and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska, June 2008 to January 2013.

	CONIFER	DECIDUOUS
Total Collared	170	130
Male / Female / Unknown	79 / 88 / 3	37 / 89 / 4
Adult / Juvenile / Unknown	121 / 13 / 36	72 / 16 / 42
Fate		
Predation	102	67
Non-predation (i.e. Starvation)	4	4
Unknown Mortality	20	32
Censored (i.e. Lost Transmitter Signal)	14	21
Trapping Related Mortality	15	6
Remaining Alive at End of Study	5	0

Table 2.2 Distance (mean ± SE) between capture location and mortality site for snowshoe hares collared in the CONIFER and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska, June 2008 to January 2013.

	CONIFER				DECIDUOUS			
	Non-winter		Winter		Non-Winter		Winter	
	M	F	M	F	M	F	M	F
n	25	22	29	36	16	29	9	34
Distance (m)	192 ± 30	396 ± 162	475 ± 160	959 ± 254	294 ± 36	391 ± 133	674 ± 403	1088 ± 354
Range	15-572	15-3602	51-4598	15-6438	60-546	33-3987	35-3880	25-8792

Table 2.3 Seasonal home range (90% isopleths) and core use area (50% isopleths) sizes (ha, mean ± SE) for snowshoe hares collared with GPS units on the CONIFER and DECIDUOUS trapping grids in Bonanza Creek Experimental Forest near Fairbanks, Alaska.

Capture Site	Sampling Period	Home Range	Core	n
DECIDUOUS/Summer	May-Oct 2010	1.25 ± 0.27	0.34 ± 0.09	7
DECIDUOUS/Summer	May-Oct 2011	2.30 ± 0.60	0.58 ± 0.14	5
CONIFER/Winter	Feb-Apr 2012	3.70 ± 0.49	0.87 ± 0.07	6

GENERAL CONCLUSIONS

In this study I examined the effects of biological and environmental variables on the survival and movement of snowshoe hares at different temporal scales in interior Alaska. Habitat greatly influences the degree to which these variables affect the survival of hares. I focused my research in black spruce and early successional forests, both of which can sustain high densities of hares but which differ markedly in the availability of vegetative cover and preferred browse species. Estimated hare survival differed among habitats and months in the year, but there was no clear relationship between vegetative cover and predation. However, sources of predation differed significantly among habitats between which hares moved on a daily basis, implicating vegetative cover in the vulnerability of hares to different predators.

Estimated survival rates of adult and older juvenile hares were highest in July and generally highest in summer, probably due to a combination of increased cover from predators provided by deciduous foliage, abundant forage, and availability of alternative seasonal prey for hare predators. Estimated survival was lowest in May and November, or more generally during the shoulder seasons when deciduous foliage was largely absent. Hares undergo seasonal changes in pelage color at these times and begin to seek mates in late-winter, making them more visible to predators. An addition of juveniles to the sample population in September may also have depressed survival rates, as juveniles often have lower survival than adults (Gillis 1998, Kielland et al. 2010). Hares transition to a winter diet of woody browse in the fall as air temperatures drop, which negatively affects their body condition at a time when it most influences survival. Despite monthly differences, there was a high degree of variability in survival within each month across the four study years. I found little support for an effect of air temperature, precipitation, or snow depth on hare survival, and considering the low number of non-predatory deaths observed, I propose that variability in the presence or successful hunting of predators may be a primary cause of variation in hare survival among months.

I found higher estimated survival rates of hares in black spruce than in early successional forest and this difference was most pronounced when deciduous leaves were absent. Black spruce offered more lateral cover throughout the year, providing a consistent refuge from predators, whereas early successional forest was most suitable for hares in summer when abundant deciduous leaves provided considerable lateral and canopy cover and an excellent source of food. Hares also regularly used mixed forest, which had a seasonal abundance of deciduous forage but offered very little lateral cover during most of the year. The higher survival of hares in black spruce forest suggests that the dense lateral cover there benefited survival more than the scarcity of preferred browse species may have hindered it.

As in other studies, the vast majority of deaths (95%) for which the cause was known were due to predation. Lynx, goshawks, and great horned owls were the dominant predators, but the magnitude of their depredation varied in space and time. For example, despite the dense cover in black spruce forest, lynx killed more hares there than in other habitats and exhibited highest predation rates in winter. Predation rates by great horned owls were also highest in winter, but hares were killed primarily in mixed forest and open areas with shrubs. Goshawks killed hares in a variety of habitats including black spruce and mixed forest with predation rates being highest in spring and fall. Contrary to my predictions, predation often took place in sites with more than average cover. I surmise that lynx may have benefited from dense lateral cover when stalking or ambushing hares, but it was surprising to find goshawks killing hares in black spruce forest where thick foliage at ground level would have made aerial attacks difficult.

Most hares (90%) remained within 1 km of their capture site. When hares dispersed, it was usually during winter and adult females traveled farther than adult males. This runs counter to the majority of mammal species in which juvenile males disperse most frequently and to the greatest distances. Some hares traveled away from the trapping sites in early winter and returned months later, apparently settling into the same area from which they had left. Seasonal home ranges were small (0.6-5.5 ha) with core areas typically < 1 ha, and hares spent most of their time using the habitat in which they were captured. However, the home ranges of most hares spanned multiple vegetation communities and often contained multiple core areas located in different habitats. These habitats probably served different purposes such as providing refuge from predators, efficient foraging opportunities, or thermal refugia. GPS-collared hares that we captured in black spruce forest moved regularly to and from an adjacent mixed forest, probably to gain access to deciduous leaves and stems, especially during the winter when food availability in black spruce forest was largely limited to evergreens. Signals from VHF-collared hares located in mixed forest, along with the large number of hares dying in mixed forest, further emphasize the extent to which this habitat was used in all seasons. GPS-collared hares occupying early successional forest also used nearby coniferous forest and shrubby forest edges, possibly for day resting sites rather than foraging. We also found VHF-collared hares from this site in many other habitats throughout the year, suggesting that the use of multiple habitats is common even in early successional forest where preferred food species are usually abundant. Frequent movement away from trapping grids could result in severe underestimation of hare abundance on those grids if hares remain away for the duration of a trapping session. To accurately assess densities in a particular habitat, trapping grids may need to be placed well away from habitat edges to buffer from hare movement across habitat boundaries. This is assuming that hares move less in larger habitat patches due to the homogeneity of vegetation. If the goal is to measure abundance in an area containing a mosaic of habitats, such as the area in which my study took place, trapping will need to be conducted in many adjacent habitats simultaneously, much like the concurrent measurements made here in black spruce and early successional forests. Densities of hares varied greatly between early successional and black spruce forest among seasons and years, which also suggests that a measure for the amplitude of hare cycles will need to incorporate multiple habitat types.

I documented considerable variation in daily habits among individual snowshoe hares, even among those with home ranges concentrated in the same vegetation type. A complex mosaic of habitats such as that in my study area probably benefits hares by putting into close proximity areas of dense cover and open areas with higher productivity of preferred food items such as young willows and birches. While the relative homogeneity of the boreal forest at a large spatial scale may facilitate the synchronous fluctuations of hare populations across the continent, habitat patchiness occurs at smaller spatial scales here much like it does at the southern edge of the snowshoe hare’s range. This patchiness likely leads to similar, if subtler and more localized, source-sink dynamics like those observed in Wisconsin (Keith et al. 1993) and Idaho (Wirsing et al. 2002), and promotes not only seasonal home range shifts and/or expansion (Wolff 1980), but also daily use of multiple habitats. In Alaska, mature black spruce forest appears to act as a refuge for hares throughout the population cycle, but is also an important habitat for lynx, as was indicated by the disproportionate number of hares killed by lynx in this forest type. Early successional forest provides a more seasonal habitat for hares, supporting very high densities in summer and fall, and probably benefits hares most when denser cover is available nearby. Management for hare and lynx populations should consider the benefits of maintaining a patchy landscape incorporating dense conifer and young deciduous forest. In interior Alaska, this landscape arises naturally from the frequency of wildfires that return older forests to early seral stages. Fires are becoming more frequent with a changing climate (Kasischke and Turetsky 2006) and the predicted progression from a landscape dominated by conifers to one dominated by deciduous trees (Rupp et al. 2000) may sustain higher hare densities for a short time. However, as patches of dense coniferous forest become less common, hares may have fewer refuges from predators and populations of both prey and predator may permanently decline. Ultimately, this could lead to population dynamics similar to those at the southern end of the snowshoe hare’s range where cycles are highly irregular and dampened (Dolbeer and Clark 1975), if present at all.

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