Movements, activity patterns, and habitat use of snowshoe hares (*Lepus americanus*) in interior Alaska

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Snowshoe hares (*Lepus americanus*) are generally sedentary, but are likely to move among habitats frequently to gain access to spatially segregated food and cover. We investigated movement patterns of hares from 2 characteristic boreal habitats using very-high-frequency radio collars (*n* = 300) monitored weekly and global positioning system (GPS) collars (*n* = 18) programmed to record locations at 30–120-min intervals. We used collar recoveries (*n* = 203) to estimate distance from capture to mortality site. Approximately 90% of collars were recovered within 1 km of their deployment locations, the greatest distances being recorded in winter. We used locations of GPS-collared hares to estimate seasonal home range sizes, habitat use, and diel patterns of movement among and within habitats. Seasonal home ranges were 3–6 ha in size, depending on season and habitat. Hares used multiple habitat types on a daily basis. Movement rates, based on animal locations recorded every 2 h, varied 4-fold between peak and nadir. The majority of movements between habitat types coincided with times when hares were most active. Our findings show that hares may use 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 in dense cover in a different location.

Key words: boreal forest, GPS telemetry, habitat use, home range, predation, radiotelemetry

The snowshoe hare (*Lepus americanus*) is a foundational prey species in the boreal forests of North America (Krebs et al. 2001) that faces drastically different weather conditions, food availability, and predation pressure throughout the year. In response to changing environmental challenges, hares shift their seasonal ranges to habitats with denser cover when more predators are present (Wolff 1980; Boutin 1984), apparently sacrificing access to preferred browse for safety (Keith et al. 1984; Sievert and Keith 1985). 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), then expanding or shifting their ranges to include mixed-vegetation stands in the summer when deciduous browse is available (Wolff 1980; Pietz and Tester 1983; Beaudoin et al. 2004), 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) and to forage near cover (Hodges and Sinclair 2005), but their use of habitat edges (Ferron and Ouellet 1992) suggests that they benefit from being in proximity to open areas or early seral stands where preferred food species are typically more abundant (Hodson et al. 2011). Hares in a landscape with fine-scale habitat heterogeneity are likely to move among habitats on a daily basis to capitalize on differences in food availability and cover; the dramatic seasonal changes in these environmental parameters should, in turn, affect movement rates and habitat use.

We investigated diel movement patterns of snowshoe hares among different habitat types in interior Alaska in summer and winter, using global positioning system (GPS) collars to measure movements 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 movements among habitats would then result in larger home ranges. Snowshoe hares primarily
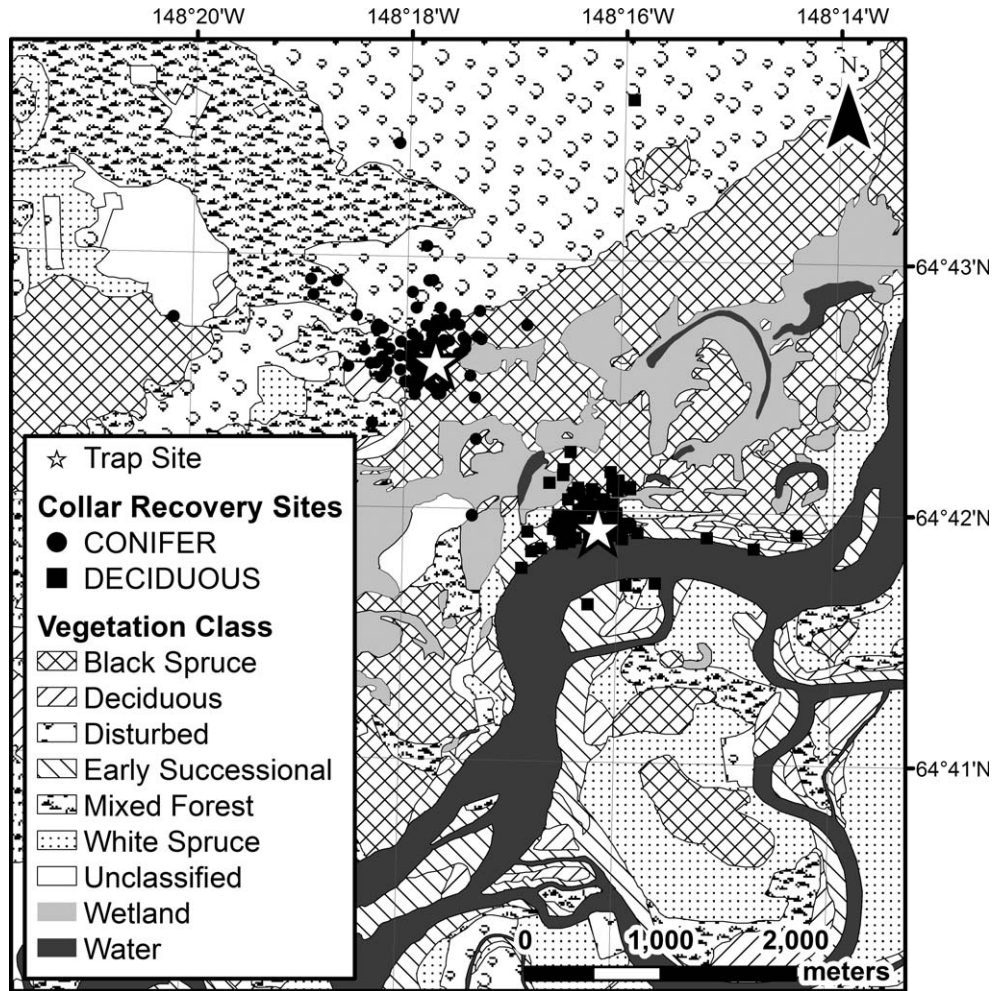
Fig. 1.—Collar recovery locations for snowshoe hares (*Lepus americanus*) collared in the CONIFER (*n* = 113) and DECIDUOUS (*n* = 90) trapping grids in the Bonanza Creek Experimental Forest near Fairbanks, Alaska, from June 2008 to January 2013. Ten collars were recovered beyond the boundaries of the map.

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 very-high-frequency (VHF) transmitters after they had died. By understanding the frequency and timing of these fine-scale movements, we gained insight into the importance of habitat heterogeneity to hares and the indirect impact it may have on closely associated predators.

MATERIALS AND METHODS

Study area.—This study took place in the Bonanza Creek Long-Term Ecological Research site and Bonanza Creek Experimental Forest (65°N, 148°W), located approximately 20 km southwest of Fairbanks, Alaska. Snowshoe hare populations have been monitored at 2 sites here since 1998 (Kielland et al. 2010), exhibiting cyclic peaks in the fall of 1999 and 2009. Habitat type differed between the 2 sites. One

site was located in a floodplain early successional community adjacent to the Tanana River (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* spp. The other site was located in a mature black spruce (*Picea mariana*) community (hereafter referred to as the CONIFER site) with an understory composed of *Ledum* spp., *Rosa acicularis*, *Vaccinium vitis-idaea*, *Salix* spp., *Chamaedaphne calyculata*, mosses, and lichens. Other forested habitats in the area included floodplain white spruce (*Picea glauca*), poplar, mixed white spruce and birch (*Betula neoalaskana*), and aspen (*Populus tremuloides*). Recently disturbed areas included small forest-manipulation plots and parts of the 1983 Rosie Creek Burn, which were dominated by regenerating birch and aspen, as well as an area of sparse shrub cover directly north of the CONIFER site (Fig. 1).

Snowshoe hare capture and collaring.—Within each site, we used an established 9-ha trapping grid with 50 traps spaced

50 m apart in a 5 × 10 pattern. The 2 trapping grids were separated by 1.5 km. We captured hares in #3 Havahart live traps (model 1085, Lititz, Pennsylvania) and aged, sexed, weighed, and sized them. We marked each study animal with Monel ear tags (National Band and Tag Co., Newport, Kentucky) 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 conservative. Traps were baited with alfalfa, carrots, and snow (when available) for moisture. Traps were opened during midday and checked the following morning. Trapping sessions were conducted once every 3 months; sessions ranged in length from 1 to 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 et al. 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 collared a subset of trapped hares with VHF radiotransmitters. Collars weighed between 20 and 26 g (models M1555, M1565, M1575, Advanced Telemetry Systems, Isanti, Minnesota) and were equipped with a mortality switch activated by a lack of movement over 6 consecutive hours. Collars were only put on hares weighing > 900 g so that they did not exceed 3% of the hare's body weight; this restricted our study to adult and older juvenile hares.

We redeployed collars on new hares as mortalities occurred in an attempt to maintain at least 25 collared individuals in each site at any given time, conducting additional trapping sessions as needed. Collared hares represented 20–90% of the estimated hare population on each trap grid, depending on the time of year. On the basis of an ongoing mark–recapture study, hare densities peaked at 5.4 and 3.3 hares/ha in the CONIFER and DECIDUOUS sites, respectively, in autumn of 2009. Densities fell to approximately 2 hares/ha on both trap sites in autumn of 2011, and by spring of 2012 were < 1 hare/ha. 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 17 individual adult hares with GPS loggers and VHF transmitters (model G30L, Advanced Telemetry Systems; model Quantum 4000, Telemetry Solutions, Concord, California). Only females were collared in DECIDUOUS: 6 between May and September 2010, 4 between May and August 2011, and 1 that was collared in both years on separate occasions, yielding a total sample of 12 trials in DECIDUOUS. We collared 4 females and 2 males in CONIFER between February and April 2012. We were unable to collar hares with GPS loggers in both trapping grids in all seasons, so the effects

of site and season were not separable. GPS loggers were programmed to take fixes at half-hour ($n = 3$) or 1.5-h ($n = 4$) intervals in 2010, 1-h ($n = 3$) or 2-h ($n = 2$) intervals in 2011, and 2-h ($n = 6$) intervals in 2012 (we used different fix intervals for the 2 different collar models to determine battery life of the collars before settling on 2-h 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 et al. 2011).

We monitored VHF-collared hares (including those with GPS) every 1–7 days using a directional Yagi antenna and handheld receiver (model R1000; Communications Specialists Inc., Orange, California) to detect movements of hares off the trapping grids and locate mortalities. When transmitter signal strength or location suggested that a hare had moved > 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.

Data analysis.—For VHF-collared hares, we calculated the linear distance between the location of initial collaring and the site where the 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. In most cases, we could not be sure if collars were moved by predators or scavengers after a hare had died, but any movement was assumed to take place in a random direction and measurements should therefore be unbiased. There was no indication from our telemetry data that any of the retrieved collars had been moved long distances since the hare was last known to be alive. In addition, the proximity of recovered collars to kill sites, recent hare tracks, and hare remains suggested that any movement of collars was small relative to the distance from the collaring sites. We used a 3-factor analysis of variance (ANOVA) 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 nonwinter seasons, we pooled data for spring (May), summer (June–August), and fall (September–October), and compared these with winter (November–April). 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 *t*-test.

We estimated seasonal home range sizes for GPS-collared hares in summer (late May to late September) and late winter (late February to mid-April) using Brownian bridge movement models (BBMM—Horne et al. 2007). This method is preferable to kernel density estimation when relocation intervals are short and likely to be autocorrelated (Walter et al. 2011), and BBMM incorporates GPS location error and a mobility parameter unique to each individual on the basis of its movements over the sampling period. Thus, BBMM should provide a more realistic representation of the utilization distributions (UDs) for hares in our study than would kernel density estimation (Worton 1989). 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. The standard deviation of fix locations for 2 stationary collars placed in the field was 8.0–10.6 m beneath both dense cover ($n = 264$) and open sky ($n = 128$). Therefore, we used an estimated location error of 10 m when calculating the UD. We censored animal locations that were obviously incorrect, such as those occurring in the Tanana River during summer. We used all remaining fixes ($\bar{X} = 433 \pm 92$, range: 78–1,802) from all days that fixes were obtained ($\bar{X} = 30 \pm 5$, range: 6–54). Although the number of fixes and the time during which fixes were obtained were highly variable, there was no correlation between the number of fixes and seasonal home range sizes ($r^2 = 0.05$, $P = 0.37$) or between the number of fix days and seasonal home range sizes ($r^2 < 0.01$, $P = 0.84$). Further, subsampling of animal locations has been shown to underestimate home range sizes (Blundell et al. 2001), so we used all available fixes in home range estimation. We calculated UD using the kernelbb function (adehabitat package) in R (R Development Core Team 2011) and extracted isopleths using geospatial modeling environment (Beyer 2012). Home-range boundaries were defined by 90% isopleths (Börger et al. 2006), which usually delineated a single, continuous area. Core use areas were defined by isopleths that divided intensively used areas from peripheral areas of less intense use. This was done by fitting an exponential regression to a plot of UD area against UD volume (i.e., isopleth value) and identifying the UD volume for which the slope of the regression line was equal to 1 (Vander Wal and Rodgers 2012). Core use isopleths ranged from 32% to 38% ($\bar{X} = 36$, $SD = 2$) and did not differ between trapping sites or seasons. Because of an inability to incorporate physical boundaries into range estimation using BBMM, estimated home ranges for hares collared in DECIDUOUS often included open water, either from the Tanana River or from wetlands. These portions, which represented 0–38% ($\bar{X} = 13$, $SE = 3$) of any home range area, were removed before calculating the home range sizes reported here.

To understand fine-scale habitat use, we used a vegetation layer in ArcGIS 10.0 (ESRI 2010) for the Bonanza Creek Experimental Forest to determine composition of the vegetation within seasonal home ranges on the basis of floristic classifications (Baird 2011). Habitat use was quantified at the home range scale using the number of GPS locations in each vegetation community. We also calculated the relative proportion of each vegetation community represented in the core use areas. To investigate diel patterns of habitat use, we compared the proportion of GPS locations in each habitat type used in 2-h periods throughout the day, beginning at midnight (2400–0200 h, 0200–0400 h, 0400–0600 h, etc.).

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

We quantified diel patterns for hare movements among habitats over the same 2-h periods by calculating the number of times an individual was located in different habitats at the beginning and end of each time 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 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-h intervals were assigned to the 2-h period with which they overlapped most.

Statistical analyses were conducted using program JMP version 10 (SAS Institute 2012). Means are reported with standard errors 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 1). We recovered 203 transmitters from mortality events, 23% of which were within 100 m of their deployment locations (Fig. 1). Transmitter recoveries tapered off dramatically at 500 m (82% of recoveries), with 91% and 95% of transmitters recovered within 1 and 2 km, respectively. Hares died as far as 8.7 km from their capture locations, 8 of them crossed the frozen Tanana River, and 1 live hare was last estimated at a linear distance of > 14 km from its initial capture point after crossing at least 2 major roads in the process. In general, we documented greater movements of collared hares off the trapping sites in winter than in other seasons; 18 of 21 transmitters located > 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 (825 $\pm$ 147 m) than in nonwinter (321 $\pm$ 58 m) seasons ($F_{3,196} = 5.9$, $P < 0.001$), but did not differ between sites or sexes (Table 2); however, adult female distances were > 2 times larger than those for adult males. Mean distances were similar in spring (208 $\pm$ 36 m), summer (385 $\pm$ 119 m), and fall (336 $\pm$ 97 m), but did not differ between juveniles and adults ($t_{201} = 0.12$, $P = 0.91$).

Seasonal home range sizes.— Seasonal home ranges for GPS-collared hares varied from 0.67 to 10.27 ha and core use areas ranged from 0.07 to 1.49 ha. Hares from CONIFER

TABLE 1.—Sex, age class, and fate of snowshoe hares (*Lepus americanus*) collared in the CONIFER and DECIDUOUS trapping grids in the Bonanza Creek Experimental Forest near Fairbanks, Alaska from 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 mortality	102	67
Starvation mortality	4	4
Trapping-related mortality	15	6
Unknown mortality	20	32
Censored (e.g., lost transmitter signal)	14	21
Alive when the study ended	5	0

averaged considerably larger home ranges and core use areas than hares from DECIDUOUS in 2010, but not in 2011 (Table 3). Home ranges for males from CONIFER averaged 4.26 ± 0.43 ha (range: 3.83–4.69, $n = 2$) and females averaged 6.59 ± 0.89 ha (range: 3.98–7.93, $n = 4$). Core use areas represented 15% ± 1% of seasonal home ranges, regardless of site. The only hare that carried a GPS collar in consecutive years occupied the same areas in both years.

Habitat use.—The space use patterns of GPS-collared hares from DECIDUOUS varied greatly among individuals. All hares from this site primarily used early successional forest (82% of locations, 83% of core use area), but half also used adjacent habitat types such as black spruce forest (11% of locations) and white spruce forest (12% of core use area). 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. Four hares had pairs of core areas with centers about 100–250 m apart that incorporated different habitats, and another hare had a home range comprised of 3 discontinuous areas with centers about 500 m apart.

Hares from CONIFER spent most of their time in black spruce forest (68% of locations, 77% of core use area), but all hares from this site also regularly used other habitat types including mixed forest (12% of locations, 6% of core use area) and burned areas characterized by shrubs and regenerating birch and aspen trees (19% of locations, 17% of core use area). Half of the hares from CONIFER had multiple core areas located in different habitats.

TABLE 3.—Seasonal home range (90% isopleths) and core use area (32–36% isopleths) sizes ($\bar{X} \pm SE$) derived from GPS locations for snowshoe hares (*Lepus americanus*) collared on the CONIFER and DECIDUOUS trapping grids in the Bonanza Creek Experimental Forest near Fairbanks, Alaska.

Trapping grid/season	Sampling period	Home range (ha)	Core use area (ha)	n
DECIDUOUS/summer	May–Oct. 2010	2.94 ± 1.23	0.38 ± 0.12	7
DECIDUOUS/summer	May–Oct. 2011	5.14 ± 1.53	0.76 ± 0.26	5
CONIFER/winter	Feb.–April 2012	5.81 ± 0.75	0.85 ± 0.08	6

Hares from CONIFER 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 (Fig. 2). By contrast, hares from DECIDUOUS exhibited no change in habitat use during the day.

Hares from both sites also repeatedly made extensive movements among habitats over short time periods. For example, traveling > 1 km while moving rapidly among 3 distinct locations that were used for as little as 1.5 h, or moving a similar distance through black spruce forest to a small stand of birch before returning 48 h later, making each trip in 4 h.

Diel movement patterns.—GPS-collared hares showed peak movement rates between 1800 and 0800 h (Fig. 3). 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.

Interhabitat movements.—GPS-collared hares from CONIFER moved among habitats several times per day ($\bar{X} = 2.0 \pm 0.4$, 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. Half of the hares from DECIDUOUS rarely moved among habitats, whereas the other half did so with the same frequency as hares from CONIFER ($\bar{X} = 2.0 \pm 0.5$, range: 0.3–4.3). Regardless of site, movements between habitats generally took place at times when hares were most active, which was during the darkest hours of the day (Fig. 4).

DISCUSSION

Snowshoe hares living in a variable landscape with many available habitat types could optimize food intake and safety

TABLE 2.—Linear distance ($\bar{X} \pm SE$) between capture location and mortality site for snowshoe hares (*Lepus americanus*) collared in the CONIFER and DECIDUOUS trapping grids in the Bonanza Creek Experimental Forest near Fairbanks, Alaska from June 2008 to January 2013.

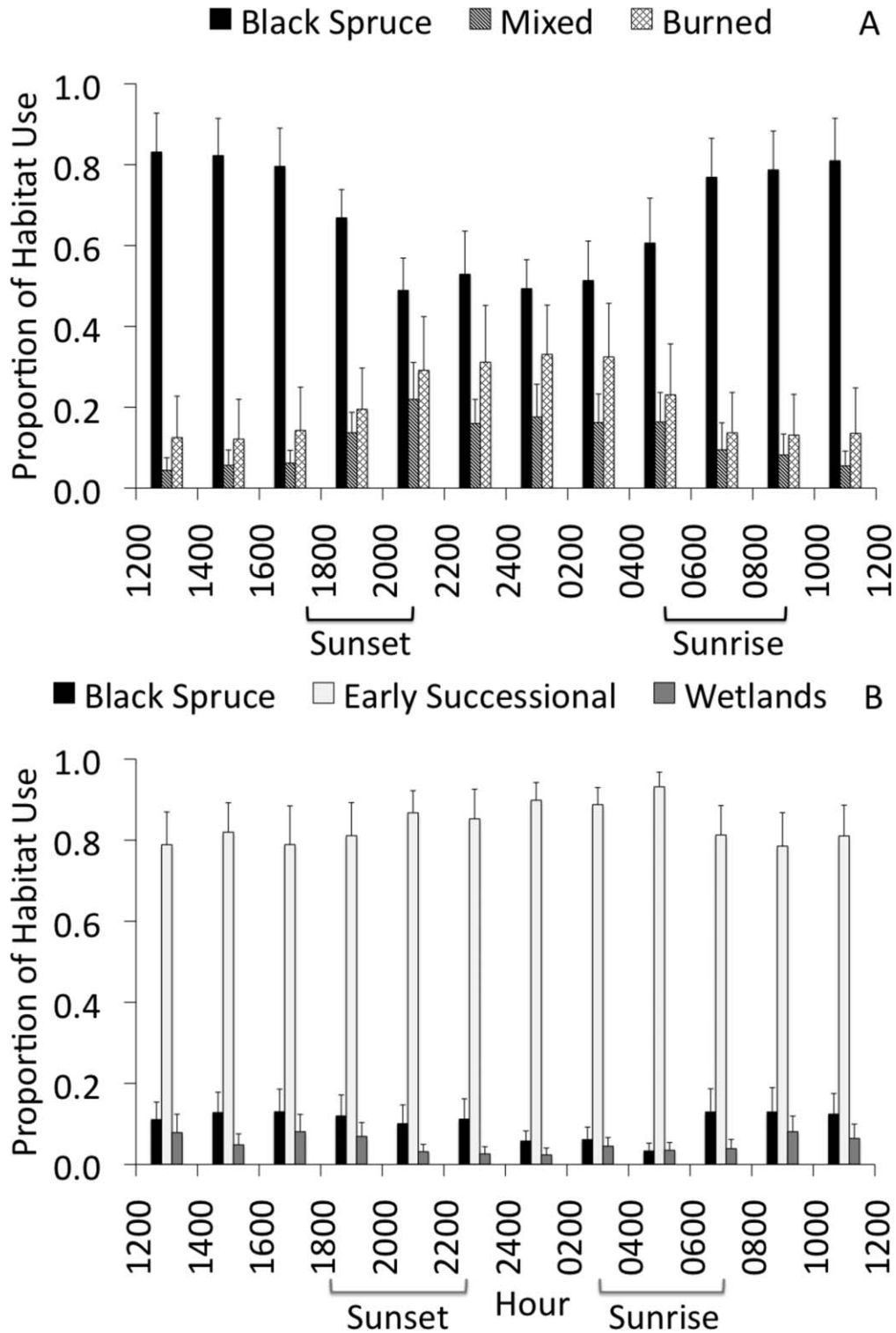|	CONIFER				DECIDUOUS			
	Nonwinter		Winter		Nonwinter		Winter	
	M	F	M	F	M	F	M	F
n	25	22	29	36	16	29	9	34
Distance (m)	192 ± 30	396 ± 162	475 ± 160	959 ± 254	294 ± 36	391 ± 133	674 ± 403	1,088 ± 354
Range	15–572	15–3,602	51–4,598	15–6,438	60–546	33–3,987	35–3,880	25–8,792

FIG. 2.—Proportion of habitat used in 2-h intervals for snowshoe hares (*Lepus americanus*) 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 the Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ±1 *SE*. Sunrise and sunset are indicated for winter (black) and summer (gray) sampling periods.

by foraging in productive open areas and seeking refuge from predators in denser vegetation nearby. Such opportunities abound in much of the Alaskan boreal forests due to habitat heterogeneity resulting from frequent wildfires (Kasischke and

Turetsky 2006). We found that hares captured in black spruce forests and early successional habitats moved among habitat types approximately twice per day, which generally corresponded with movement between disparate core use areas.
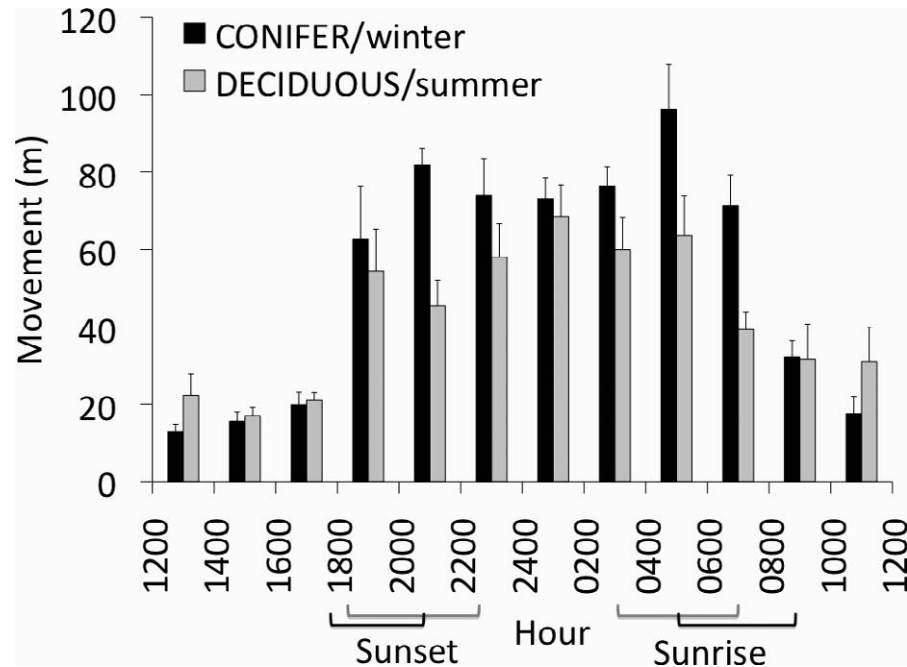
Fig. 3.—Linear distance moved (m) in 2-h intervals for snowshoe hares (*Lepus americanus*) collared in the CONIFER trapping grid from February to April 2012 ($n = 6$) and DECIDUOUS trapping grid from May to October 2010 ($n = 7$) and 2011 ($n = 5$) in the Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ± 1 *SE*. Sunrise and sunset are indicated for winter (black) and summer (gray) sampling periods.

Black spruce forests offer dense cover to hares throughout the year but lack an abundance or variety of preferred browse, especially during winter. Early successional forests typically offer an abundance of browse species preferred by hares, especially during summer, but they often lack the dense cover that is typically available in older conifer forests. Thus, hares that moved from black spruce forest to mixed forest, regenerating birch and aspen stands, or shrubby areas during the winter may have been seeking species of deciduous browse such as *R. acicularis*, *Salix* spp., and *Betula* spp., which are preferred by hares (Wolff 1978), to supplement a diet dominated by black spruce (Bonanza Creek Long-Term Ecological Research 2013). In contrast, hares that moved from early successional forest to conifer forest during summer may have sought safer or cooler resting sites, some of which were used repeatedly by several study animals.

Hares in our study area had smaller home ranges and lower movement rates in summer than in winter, which likely resulted from greater use of singular core areas located in early successional habitat during summer. Because of confounding factors, we cannot directly compare home range sizes between sites or seasons, but we speculate that a higher availability of leafy browse in summer and in early successional forests contributed to reduced home range sizes. Increased food availability has been shown to reduce home range sizes in snowshoe hares (Boutin 1984), as has preferred browse in mountain hares (Dahl 2005; Kauhala et al. 2005), and early successional forests in summer undoubtedly offered more preferred and higher-quality browse to hares in our study area

than did other habitats in winter. Additionally, females with litters must visit the same nursing site each night (O'Donoghue and Bergman 1992), which may constrict home range sizes during the summer (Jekielek 1996). This may further explain why adult females, which comprised our entire sample of hares in early successional habitat in summer, had smaller home ranges there than in black spruce forest in winter.

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). Hares may disperse in any season (Windberg and Keith 1976), although populations in Montana exhibited seasonally high emigration rates during fall and winter (Griffin and Mills 2009). Likewise, we recovered transmitters at greater distances from capture sites in winter than in other seasons, which suggests that hares are more mobile and potentially dispersing at higher rates in the winter than in other seasons. These movements followed peak hare and predator densities in the fall when deciduous habitats no longer offered significant cover, and the diets of hares in conifer forests became 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 1984; Boutin et al. 1985) and for mountain hares in boreal Sweden (Dahl and Willebrand 2005). It was also not uncommon for GPS-collared hares in our study to make linear
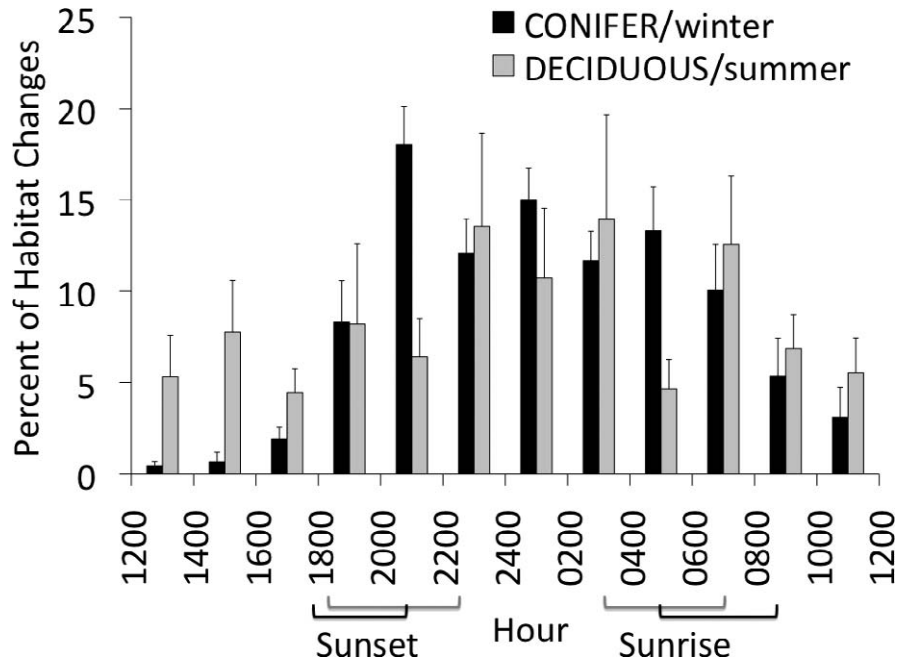
Fɪɢ. 4.—Percentage of movements between 2 habitat types occurring in 2-h intervals throughout the day for snowshoe hares (*Lepus americanus*) collared in the CONIFER trapping grid between February and April 2012 (*n* = 6) and DECIDUOUS trapping grid between May and October 2010 (*n* = 7) or 2011 (*n* = 5) in the Bonanza Creek Experimental Forest near Fairbanks, Alaska. Error bars are ±1 *SE*. Sunrise and sunset are indicated for winter (black) and summer (gray) sampling periods.

movements of up to 500 m in a range as small as 3 ha, and at least 1 hare repeatedly moved up to 1 km from parts of its seasonal range. Despite being characteristically sedentary, snowshoe hares can clearly move considerable distances without actually shifting their home ranges.

Due to their crepuscular/nocturnal nature, it is not surprising that snowshoe hares moved among habitats primarily at night when movement rates were highest. However, hares may respond to changes in photoperiod by further restricting their activity to dark hours of the day in fall and winter (Keith 1964; Mech et al. 1966), remaining crepuscular in spring and summer (Mech et al. 1966; Foresman and Pearson 1999), or maintaining diurnal activity in midsummer with periods of rest during peak afternoon temperatures (Théau and Ferron 2001). Such behavioral changes are likely to be most pronounced at high latitudes like those of interior Alaska, where the change in daylight among seasons is extreme. Thus, the seasonal differences in activity we observed, with changes in movement rates near sunrise and sunset being more dramatic during winter than summer, may, at least in part, be a consequence of changing photoperiod. In winter, hares 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. The proximity and availability of adjacent habitat types likely played a large role in the differences observed, so further investigation is needed to distinguish between the effects of season and habitat on hare activity.

Movements among habitats were common for hares in our study, but the diel movement rates, behavior, and selection of habitats were highly variable among individuals. A landscape with fine-scale habitat heterogeneity, such as our study area, 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 (Kasischke and Turetsky 2006), if dense conifer refuges persist among an increasing diversity of young, regenerating deciduous communities.

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