Chapter 7

Ecology of Snowshoe Hares in Southern Boreal and Montane Forests

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Abstract—Snowshoe hares occur in many of the montane and sub-boreal forests of the continental United States, as well as throughout the boreal forests of Canada and Alaska. Population dynamics in their southern range were previously thought to be noncyclic, in contrast to the strong 10-year fluctuation that typifies boreal populations of snowshoe hares. Time series data and studies of hare demography indicate that northern and southern populations of hares may instead have similar population dynamics. Hares in southern areas appear to experience two- to 25-fold fluctuations in numbers with peaks eight to 11 years apart. Peak and low densities may be lower in southern areas than in northern ones; in the south, peak densities are commonly one to two hares/ha, whereas northern hare populations commonly have peak densities up to four to six hares/ha. Demographically, survival estimates (30-day) range from approximately 0.65-0.95 in Wisconsin, with lowest survival occurring as populations decline; these values parallel those of cyclic hares in Yukon. Annual reproductive output may vary regionally, but interpretation of this pattern is hindered by noncomparable methodologies.

The southern range of snowshoe hares is roughly delineated by the range of suitable forested habitats. Along the eastern seaboard, hares use spruce/fir and deciduous forests as far south as Tennessee and the Virginias. Around the Great Lakes, hares occur throughout the sub-boreal coniferous forests. In the Rockies and westward, hares mainly use the coniferous forests that extend along the mountains down into New Mexico and California. Throughout their range, hares are predominantly associated with forests that have a well-developed understory that provides protection from predation and supplies them with food. Such habitat structure is common in early seral stages but may also occur in coniferous forests with mature but relatively open overstories or in eastern deciduous forests.

Introduction

Snowshoe hares occur throughout much of North America and have a regular 10-year population cycle in the northern part of their range. Dynamics of southern hare populations, in contrast, have been described as cyclic, cyclic with reduced amplitude, noncyclic but fluctuating, and noncyclic (Howell 1923; Chitty 1950; Finerty 1980; Bittner and Rongstad 1982; Smith 1983; Keith 1990). During the northern hare cycle, hares have both regular numeric changes and regular changes in survival, reproduction, and possibly dispersal (Cary and Keith 1979; Bittner and Rongstad 1982; Keith 1990; Krebs et al. 1995; Hodges et al. in press). The habitats in which hares occur in northern and southern forests vary in terms of species composition, stand structure, and amount of disturbance (from fire or from harvest), leading to speculation that hare dynamics are related to habitat structure and degree of interspersion of different habitat types (Dolbeer and Clark 1975; Wolff 1980, 1981; Buehler and Keith 1982; Sievert and Keith 1985; Keith 1990).

In this chapter, I therefore examine the demography and numeric patterns of southern hare populations, describe patterns of habitat use by hares in southern areas, and discuss the linkages between hare demography and habitat. Throughout, I compare results from southern areas to patterns in northern hare populations. I compile the information with explicit reference to methodology, to ensure that comparisons among regions are made using comparable data. I ask first whether hares display numeric cycles in the southern parts of their range. Second, I examine demographic parameters (reproduction, survival, and dispersal) to see if they show cyclic fluctuations in southern hare populations. Third, I address the dietary and habitat associations of snowshoe hares. I conclude with a discussion of the relationship of hare population dynamics to habitats, and whether refugia, habitat fragmentation, and increases in numbers of facultative (multiple-prey)

predators can explain the variation in demographic parameters observed among hare populations.

Distribution and Population Trends

Hares in "the south" occur in four general areas—through the western mountains of Washington and Oregon down into California, through the Rockies into New Mexico, around the Great Lakes, and from the Maritimes down through the Alleghenies and Appalachians into Virginia and West Virginia (Bittner and Rongstad 1982; Fies 1993, unpublished; Hoefler and Duke 1996, unpublished; G. Schmidt, personal communication; J. Rieffenberger, personal communication) These four areas are biologically and climactically diverse (Bailey 1997), so there is good reason to expect that hares might display differing dynamics in each of these regions. With the exception of the mixed deciduous and coniferous forests that cover the nonmountainous areas from the Great Lakes eastward through the Maritimes, most areas containing snowshoe hares in the United States are montane. In contrast, the boreal forests—where hares display a clear population cycle—provide a more contiguous and less mountainous swath of hare habitat (Keith 1990; Bailey 1997).

We have extremely limited knowledge about hares in many of the states where they occur. Distribution records exist for hares in Maryland, Rhode Island, New Jersey, Delaware, Virginia, Tennessee, North Carolina, Ohio, Oregon, California, and New Mexico (Keith 1963; Godin 1977; Bittner and Rongstad 1982; Nagorsen 1985), but I am not aware of any harvest or other time series data for these states. The status and distribution of hares in these states are not well known (Bailey 1971; Godin 1977; Verts and Carraway 1998; G. Schmidt, personal communication), but snowshoe hares are thought to be extirpated from Ohio (D. Scott, personal communication), and in Virginia and California snowshoe hares are a species of special management concern (Handley 1978; Williams 1986, unpublished; Fies 1991; Hoefler and Duke 1996, unpublished; Brylski et al. 1997).

In areas for which time series exist, it is possible to address the issue of cyclicity. There are four possibilities for hare population dynamics: *cyclic,* like northern populations, which display cycles with amplitudes of five to 25 and eight to 11 years between peak populations (Chapter 6); *reduced-amplitude cyclic*, demonstrating the eight- to 11-year periodicity but with amplitudes lower than five-fold; *fluctuating*, with amplitudes similar to those in northern populations, but lacking an eight- to 11-year periodicity; or *noncyclic*, lacking both high-amplitude fluctuations and the eight- to 11-year periodicity in numeric change.

Empirically, applying these definitions requires arbitrary decisions, such as defining the amplitudes at which cyclic populations become cyclic with reduced amplitude or fluctuating populations become noncyclic. It is similarly difficult to know what to do with interpeak durations of less than eight or greater than 11 years, especially in time series recording only two or three peaks. Because even long time series record only a few potential cycles, the power to determine differences in amplitude and duration among time series is low. This difficulty is compounded by the use of indices of abundance (tracks, sightings, harvest records) for which the relationship to actual hare densities is unknown. Because of these problems, I simply present the time series and describe the observed amplitude and interpeak durations of each, but I do not analyze these values statistically (Table 7.1). I consider peaks to be local maxima separated by at least two years and lows are similarly local minima. I calculated amplitudes by dividing each peak value by the subsequent low value, and I present the range of these amplitudes.

Table 7.1—Snowshoe hare population trends in southern parts of their range. Amplitude is rounded to the nearest whole number. Amplitude was calculated by dividing peaks by subsequent lows. I also present the total amplitude for the entire series (max/min) because some series show large overall fluctuations. If only amplitude is given, max/min was the same; if only max/min is given, it was impossible to match peaks and lows. Peak years are given only for series >5 years long, but peaks for series <10 years long should be regarded with suspicion, as should peak years that occur at the beginning or end of a study. Most of these rubrics indicate overwinter estimates; for peak year, I indicate the year that started the winter (e.g., 1990 implies winter 1990-1991).

Location	Survey period (# of years)	Amplitude (max/min)	Years between peaks	Peak years	Reference
Fecal pellet plots (n/plot)[a]					
Montana	1986-1998 (13)	2	7	1990 1997	J. Malloy, unpublished
Utah[b]	1974-1978 (5)	2	—	—	Wolfe et al. 1982
Washington	1986-1989 (3)	2[c]	—	—	Koehler 1990a, 1990b
West Virginia	1942-1953 (12)	10	9	1942 1951	Brooks 1955
Quebec (southern)	1991-1996 (6)	4	—	1991	Ferron et al. 1998
(% plots with pellets)					
Minnesota	1969-1984 (16)	3	—	1978	Fuller & Heisey 1986
Live trapping					
Minnesota	1932-1942 (11)	15	—	1933	Green & Evans 1940a Keith 1963
New Brunswick	1967-1970 (4)	7	—	—	Wood & Munroe 1977
Harvest records					
Nova Scotia (Long Island)	1950-1964 (14)	4	9	1951 1960	Dodds & Thurber 1965
Nova Scotia	1990-1998 (8)	(4)	—	1996	M. Boudreau, unpublished
New Brunswick	1984-1990 (7)	(40)	—	1984	K. Eagle, unpublished

(con.)

Table 7.1—(Con.)

Location	Survey period (# of years)	Amplitude (max/min)	Years between peaks	Peak years	Reference
Maine	1955-1983 (29)	2 (4)	7 to 9	1948 1957 1966 1973 (1972)[d] 1981 (1982)[d]	C. McLaughlin, unpublished Keith 1963
New York	1932-1951 (19) 1960-1968 (7) 1982-1998 (16)	2-6 (24)	8 to 13	1932 1940 1950 1963 (no data) 1982 1995	Keith 1963 G. Batchelar & A. Jacobson, unpublished
Massachusetts	1958-1986 (15)	(12)	—[e]	—[e]	J. Cardoza, unpublished
Pennsylvania	1930-1997 (64)	4-12 (48)	7 to 11	1931 1942 1949 1959 (1967)[f] 1982 (1992)[f]	Diefenbach 1998, unpublished
Connecticut	1923-1955 (32)	2-3 (3)	9 to 10	(1933)[g] 1942 1952	Sondrini 1950 Keith 1963
Ontario (southern, one trapline)	1931-1943 (13)	(17)	9	1933 1942	Hess 1954
Michigan	1937-1997 (61)	1.5-4 (7)	5 to 12	1939 1949 (1954)[h] 1959 1964 1976 1988	G. Karasek, unpublished Keith 1963
Harvest records					
Wisconsin	1931-1997 (57)	3-11 (30)	8 to 10	1932 1941 1949 1957 (no data) 1978 1988	B. Dhuey, unpublished
Minnesota	1941-1997 (56)	2-24 (29)	8 to 11	1941 1952 1960 1971 1980 1991	Berg 1998, unpublished
Colorado	1955-1960 1968-1970 (9)	(2)	—	1956	Dolbeer 1972a, 1972b
Washington	1988-1997 (9)	(6)	—	1988	D. Ware, unpublished
Idaho	1986-1992 (7)	(5)	—	1988	C. Harris, unpublished
Harvest/area					
Quebec	1979-1997 (19)	3-9 (14)	7 to 9	1980 1989	R. Lafond, unpublished Fortin and Huot 1995, unpublished

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Table 7.1—(Con.)

Location	Survey period (# of years)	Amplitude (max/min)	Years between peaks	Peak years	Reference
Harvest/hunter					
Prince Edward Island	1971-1984 1993-1997 (19)	2 (4)	—	1978	R. Dibblee, unpublished
Harvest/hunter-day					
Utah	1975-1996 (22)	3 (5)	12	1978 1990	D. Mitchell, unpublished
Hare sighting indices					
Minnesota	1974-1996 (23)	14-70 (70)[i]	9	1980 1989	B. Berg 1998, unpublished
Minnesota	1946-1959 (13)	(75)	—	1950	Marshall 1954 Keith 1963
Michigan (Isle Royale)	1974-1997 (24)	9-27 (38)[i]	8	1980 1988	Peterson 1998, unpublished
Ontario (Manitoulin Island)	1959-1962	—	—	1959	Newson & de Vos 1964
Manitoba (southeastern)	1974-1979 (5)	9	—	1978	Leonard 1980; Raine 1987
Track transects[j]					
Wisconsin (%)	1977-1998 (21)	2-17 (17)	12	1977 1989	Glenzinski & Dhuey 1998, unpublished
Maine (%)	1994-1997 (4)	2	—	—	C. McLaughlin, unpublished
Montana (#)	1992-1998 (7)	10	—	1991	D. Dziak, unpublished
Wyoming (#)	1987-1996 (10)[k]	(45)[k]	—	—	L. Ruggiero, unpublished

[a]Densities from pellet plots were calculated using a regression equation derived from hare density information from 1976 to 1996 (C.J. Krebs unpublished): ln(hares/ha)=0.888962*ln(pellets)-1.203391, corrected for bias by multiplying with 1.57 following Sprugel (1983). Pellets is pellets/0.155m^2. The methodology and rationale were derived in Krebs et al. (1987), and the current equation simply uses more information.

[b]This time series is for pellet counts in Douglas-fir stands.

[c]Values are based on pellet counts in fall; values for fall 1997 were calculated by summing values for two sampling periods within the year.

[d]From 1972 through 1983, there were also estimates of numbers of hunters. Harvest per hunter indicates the peak years given in parentheses.

[e]The years that have data are sporadic, making it impossible to determine peak years.

[f]Harvest estimates from 1967-1970 were 6,000, 4,000, 5,000, 5,000; although I've given the peak as 1967, it could have been later. From 1982 through 1997, hare harvests have generally declined, with a higher harvest in 1992 than in the preceding two years or subsequent five years.

[g]The early peak is not as clear as the others; for several years, high and low values alternated.

[h]One method of harvest estimation was used from 1937 to 1953, and another from 1954 forward. Although the 1954 harvest estimate represents a local peak, it is difficult to interpret because it lies on the cusp of the two methods.

[i]The amplitudes and max/min ignore one 0 value.

[j]Each track transect methodology is somewhat different; I present them in two broad classes: counts of number of tracks (#) and proportions of transect segments containing any hare tracks (%).

[k]These numbers were derived from transect J, including only years when the transect was run ≥2 times; the amplitude reflects just maximum/minimum rather than trying to match a low to its preceding peak.

The most reliable time series are from live-trapping data or counts of fecal pellets, because density estimates can be derived from these methods (Table 7.1). Based on short time series (three to 13 years), fecal pellet plots have shown density differences of two-fold in Montana, Utah, and Washington (J. Malloy, unpublished; Wolfe et al. 1982; Koehler 1990a,b), four-fold in southern Quebec (Ferron et al. 1998), and 10-fold in West Virginia (Brooks 1955). These surveys indicate peak hare densities of approximately 1-2 hares/ha (see also Table 7.5), which is considerably

lower than observed peak densities of approximately 4-6 and sometimes higher in northern areas (Chapter 6). The two longest pellet plot time series showed nine years between peaks in West Virginia (Brooks 1955) and seven years in Montana (J. Malloy, unpublished). Live-trapping in Minnesota and New Brunswick have indicated fluctuations of seven- to 15-fold, with peak densities of approximately 1.6 hares/ha (Green and Evans 1940a; Wood and Munroe 1977).

Most southern time series for snowshoe hares are harvest data. Harvest data are unlikely to indicate either amplitude or peak and low density years accurately. Harvest data provide a true reflection of population dynamics if and only if the same proportion of hares are caught in each year, which almost certainly does not occur because of socioeconomic as well as biological reasons. Furthermore, the harvest data we have reflect various survey techniques (phone and mail surveys, hunter licensing, pelt or carcass sales) and are often based on a small proportion of the hunters (e.g., 5-10%), hence calling into question the ability of the data to record the actual harvest.

As an additional complication, several of the harvest time series show an overall fluctuation of approximately 20-50-fold, but have distinct periods of low or high average harvest. For example, in Pennsylvania, harvests ranged between 8,600-26,200 from 1930 to 1935; 550 to 6,000 from 1937 to 1979; and 1,400-21,800 from 1980 to 1997 (Diefenbach 1998, unpublished). The entire time series has an amplitude of 48, but matching lows to their previous peaks yields amplitudes of four- to 12-fold. It is difficult to partition that variation into anthropogenic versus hare demographic changes without additional information such as area exploited or hunter effort. As an example of the effect of knowing hunter effort: 22 years of Utah harvest data showed a high correlation between total hare harvest and hares per hunter ($r = 0.87$ $p < 0.05$), but the magnitude of difference over the entire time series for total harvest was 20-fold whereas for hares per hunter it was only 4.3-fold (D. Mitchell, unpublished). Furthermore, these two indices showed the same peak year, but were off by a year for their lows. Harvest data should therefore not be relied upon for determining the population dynamics of hares. Regular 10-year cycles are unlikely to arise in the harvest data solely because of anthropogenic factors, however; so if harvest data show cycles, they probably reflect hare population dynamics even if absolute duration and amplitude cannot be correctly inferred.

Harvest records from New England, southeastern Canada (Quebec eastward through the Maritimes), and the eastern seaboard show amplitudes ranging from two to 12, with 78% of the interpeak lengths between eight and 10 years (Table 7.1, Fig. 7.1A-D). These data may be confounded by programs of stocking hares for hunters, which has occurred in at least Connecticut, New York, Massachusetts, Pennsylvania, West Virginia, and

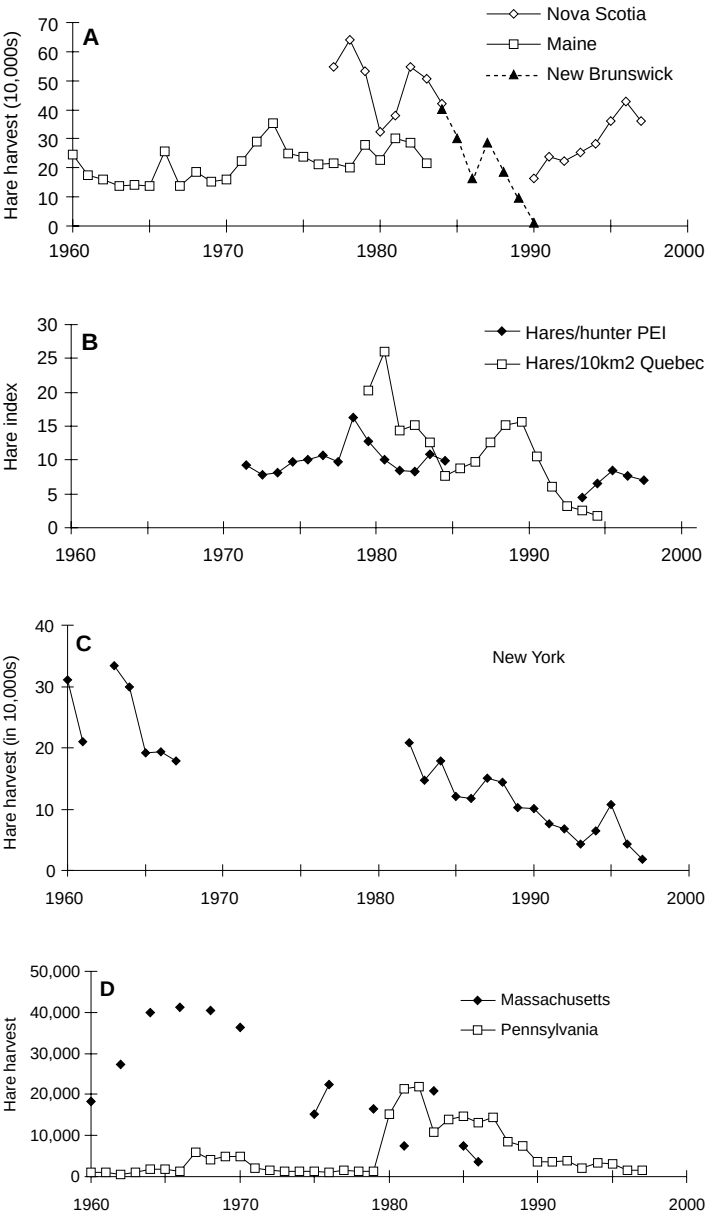

Figure 7.1—Records of snowshoe hare population trends. All records are from sources cited in Table 7.1. (A) Hare harvests from the Maritimes and Maine. (B) Hares per hunter and hares killed per unit area from Prince Edward Island and Quebec. (C) Hare harvests from New York. (D) Hare harvests from Massachusetts and Pennsylvania. (E) Hare harvests in the Midwest. (F) Hare sighting indices in the Midwest. (G) Pellet and track records of hares in the Midwest. (H) Hare harvests and hares per hunter-day in the western states.

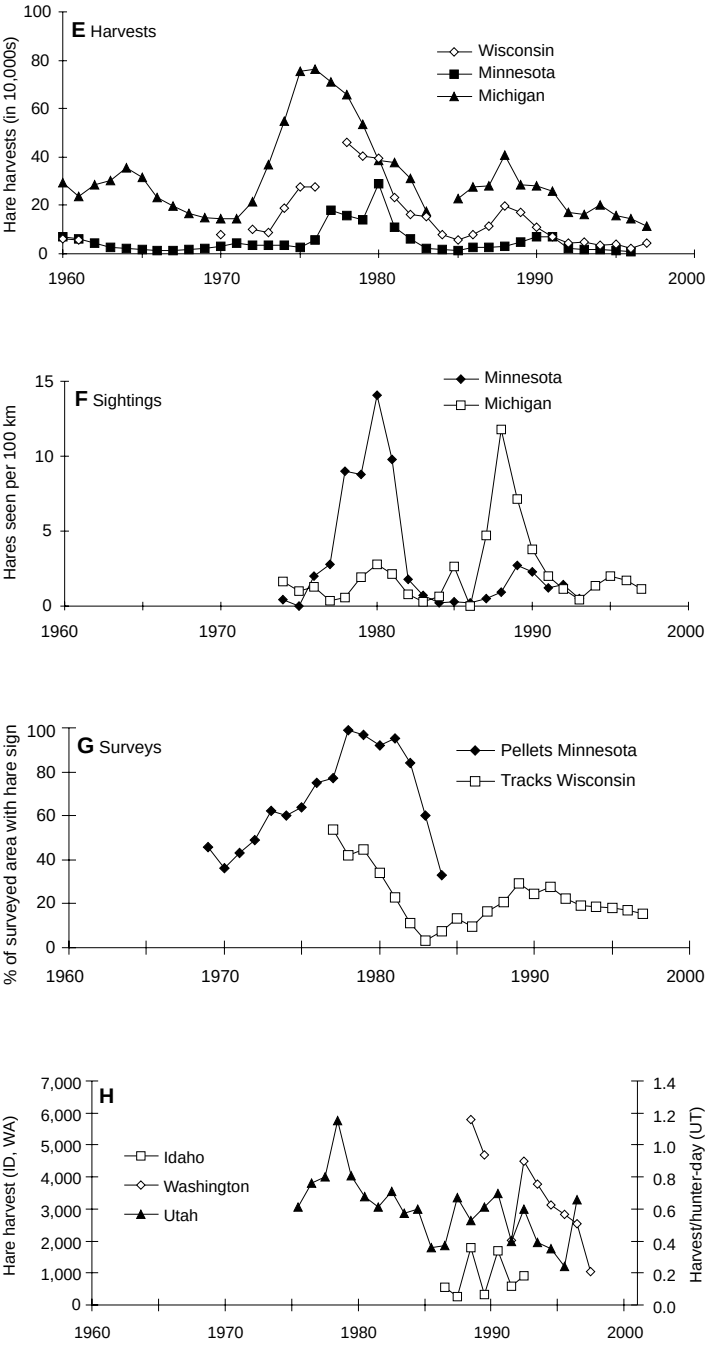

Figure 7.1 (Con.)

Virginia (Brooks 1955; Boyle 1955; Fitzpatrick 1957; Behrend 1960, unpublished; August 1974; Richmond and Chien 1976; Schultz 1980; Brown 1984). Analyses of these programs indicate that <10% of the stocked hares are actually killed by hunters (Fitzpatrick 1957; Schultz 1980), but it is unknown what demographic effects the stocking programs have had.

Around the Great Lakes, harvest data show eight- to 10-year fluctuations of two- to 25-fold amplitude (Table 7.1, Fig. 7.1E-G; see also Keith 1990). These cyclic patterns are confirmed by records of hare sightings in Minnesota (B. Berg, unpublished) and Michigan (Peterson 1998, unpublished; see also Johnson 1969). Pellet plots in Minnesota (Fuller and Heisey 1986) and tracking surveys in Wisconsin (Glenzinski and Dhuey 1998, unpublished) show roughly the same pattern of highs and lows as the harvest data do. Keith (1963, 1990; Buehler and Keith 1982; Sievert and Keith 1985) has argued that hares have become noncyclic in Wisconsin since the 1950s, but the tracking surveys and harvest records are equally suggestive that the cycles have continued.

Population trends of hares from the Rockies westward are not well known (Fig. 7.1H). The harvest records from Idaho, Colorado, and Washington are short compared to the 10-year cycle (i.e., seven to nine years of records), making it difficult to tell if the harvests have the typical 10-year periodicity (Dolbeer 1972b; D. Ware, unpublished; C. Harris, unpublished). Within those years, the amplitudes of fluctuation are two- to six-fold. In Utah, harvest per hunter-day had an amplitude of three-fold and an interpeak duration of 12 years through 22 years of data (D. Mitchell, unpublished). Pellet plots in Utah, Montana, and Washington show two-fold fluctuations in hare density (J. Malloy, unpublished; Wolfe et al. 1982; Koehler 1990a, b). In Wyoming, track counts showed 45-fold variation (L. Ruggiero, unpublished), while Montana track counts showed four- to 10-fold variation (D. Dziak, unpublished; Giddings 1998, unpublished).

The existing time series do not show a strong synchrony. For example, five time series showed a peak in 1988, three in 1989, two in 1990, and two in 1991 (Table 7.1). Throughout the century, there tend to be three- to four-year clusters of peak densities, typically close to the turn of each decade. There are occasional time series that miss peaks or show peaks in years that no other series matches (e.g., New York, which shows a peak in 1995). Southern hare populations may therefore be genuinely asynchronous or the synchrony may only be at a scale of three to four years. As another possibility, the harvest data in particular may be off a year or two relative to the actual hare densities, which would make detection of synchrony difficult.

There are likely to be differences of opinion about how deviant hare populations have to be in amplitude and interpeak duration in order to disqualify them as cyclic or to class them as reduced-amplitude cyclic. In my

opinion, the existing evidence is strongly suggestive that southern hare populations are cyclic—amplitudes in the various indices vary from two to 70, and in the longer time series (>10 years) approximately 75% of interpeak intervals are between eight and 11 years. At a minimum, these patterns suggest that studies of hares in southern areas should explicitly address population dynamics. Additional analyses of the existing time series data are unlikely to resolve the cyclicity debate because of the methodological difficulties; we require more time series that are density estimates rather than harvests or other indices.

Snowshoe Hare Demography

Reproduction

Female snowshoe hares can have up to four litters in a season, with one to 14 young per litter; they breed synchronously, leading to distinct litter groups (Cary and Keith 1979; O'Donoghue and Boutin 1995; Stefan 1998). Regionally, there has been some suggestion that hares in southern populations have more but smaller litters than do hares in northern populations, leading to a lower total annual natality (Rowan and Keith 1956; Keith et al. 1966; Ernest 1974; Keith 1981, 1990). Many of the data used to infer this latitudinal pattern were derived using Green and Evans' (1940c) method—calculating average number of litters from the number of females observed to be pregnant throughout the summer corrected for days of observable pregnancy, and calculating mean litter size from all litters combined (often with uneven sampling effort across litter groups). This method has three problems: the average number of litters has often been calculated on a multiyear basis thus conflating cyclic phase, and both pregnancy rates and litter sizes are not calculated independently for each litter group. A much more reliable approach derives pregnancy rate and litter size estimates for each litter group separately, and then sums the litter groups for total annual natality (e.g., Dolbeer and Clark 1975; O'Donoghue and Krebs 1992).

Much of the variation in total annual natality actually seems to be better explained by cyclic phase than by latitude, especially when methodological issues are considered. In Figure 7.2, the dark symbols indicate estimates derived from assessment of each litter group; these show a strong effect of cyclic phase on hares' natality. Data collected using Green and Evans' (1940c) method (open symbols and crosses) do not pick up this cyclic pattern, except in short-term studies, which are less biased by conflation of years. Additionally, this method is likely to bias estimated annual natality downward, because first litters are smaller than later litters (Keith 1990; Stefan

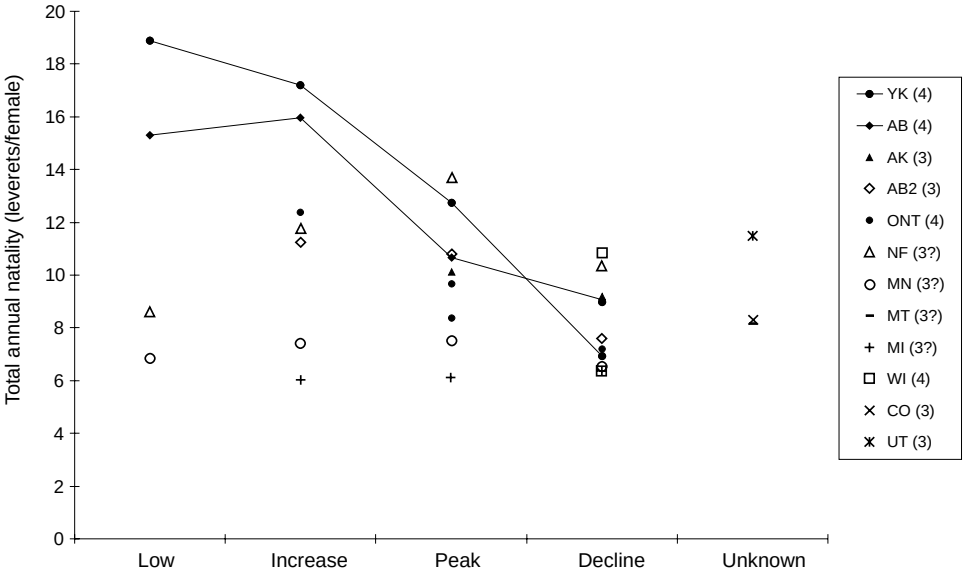

Figure 7.2—Annual reproductive output of snowshoe hares at different phases of the population cycle. Filled symbols are for natalities analyzed as percent pregnant x mean litter size, summed for each litter group. Open symbols are for natalities calculated by Green & Evan's (1940c) method, as mean litter size (litter groups not distinguished) x average litter number (often calculated from many years of data, with phase not distinguished). The first method is much more reliable. When a study had more than one year of data for a phase, annual values were averaged. The number given with each region indicates the maximum number of litter groups observed in that area; ? indicates that the number of litters was not specified in the reference. Wisconsin and Michigan data were assigned to cyclic phases based on trend data from Glenzinski and Dhuey (1998, unpublished) and Karasek (unpublished), while the other references provided information on the population trends in different years. The unknown cyclicities are from Montana, Utah, and Colorado. Sources: YK, Stefan 1998, Hodges et al. in press; AB, Keith & Windberg 1978, Cary & Keith 1979; AK, Ernest 1974; AB 2, Rowan & Keith 1956; ONT, Newson 1964; WI, Kuvlesky & Keith 1983; NF, Dodds 1965; MN, Green & Evans 1940b; MT, Adams 1959; CO & UT, Dolbeer & Clark 1975; MI, Bookhout 1965a.

1998). Thus the smaller and less cyclic annual natalities shown for southern populations are probably due to methodological biases rather than to a true latitudinal gradient. The two strongest data sets, from Alberta and Yukon (symbols with lines) (Cary and Keith 1979; Stefan 1998), offer weak support to the latitudinal pattern, in that Alberta hares tended to have four litters whereas Yukon hares had two to four, but larger litter sizes in Yukon yielded slightly larger total annual natalities in all phases except the decline. Hares in Alaska show trends similar to those of Yukon hares (Ernest 1974). The largest annual natality is approximately 2.5 times greater than the lowest for hares in Yukon and Alberta. The southern hare studies that have calculated annual natality on a per litter basis have been too short to assess

the range of reproductive values through a cycle (Newson 1964; Dolbeer and Clark 1975), but three six- to seven-year studies using Green and Evans' (1940c) method show approximately 1.5-fold fluctuation in annual natality (Green and Evans 1940c; Bookhout 1965a; Dodds 1965).

The Alberta and Yukon data sets (Cary and Keith 1979; Stefan 1998) also show that hares consistently have smaller first litters than later litters, and that first litters have a smaller range of variation through the cycle (approximately 0.5 leverets/litter; Chapter 6). If regional differences in litter size exist, they may therefore be easier to detect in the first litter than in later litters, especially if the variation among regions is higher than 0.5 leverets/litter. Additionally, we currently have more data on first litters than on later litter groups. For populations that are known to be cyclic, there does appear to be a latitudinal gradient in the size of the first litter (Fig. 7.3). Within each phase of the cycle, hares in southern populations have smaller first litters (by up to approximately 1.5 leverets) than do hares in northern populations. Hares in Utah and Colorado do not fit this pattern, however; their first litter sizes of approximately 3-4 (Dolbeer and Clark 1975) are comparable to those of hares in Yukon, Alaska, and central Alberta (Ernest 1974; Windberg and Keith 1978, Stefan 1998).

There is a weak latitudinal difference in the dates when hares have their litters (Keith 1981). The onset of hare reproduction is affected by gonadotropin levels, which are affected by daylength (Davis and Meyer 1972, 1973). The beginning of reproduction is also affected by the beginning of spring (Meslow and Keith 1971; Keith 1990), so hares in northern latitudes begin breeding somewhat later than do hares in more southerly latitudes. Nonetheless, most hares have their first litter of the season in May (Keith 1981; Keith 1990; Hodges et al. in press), and the number of litters per season does not seem to depend on when the first litter is born (Stefan 1998; Hodges et al. in press). Additionally, within a region, parturition dates can vary by two to three weeks among years (Cary and Keith 1979; Stefan 1998), which is as great as the purported difference among regions (Keith 1981, 1990).

Survival and Causes of Death

Our estimates of snowshoe hare survival have come from trapping and radiotelemetry, and both of these types of data have been analyzed using various statistical methods (Fig. 7.4). Inferring patterns of regional and even cyclic differences in survival is therefore complicated because the data are not truly comparable. Boutin and Krebs (1986) compared two trapping and two radiotelemetry estimates of 28-day survival using five years of Yukon hare data and found that the radiotelemetry estimates were consistently higher than both trapping estimates, sometimes by as much as 30%. Radio-

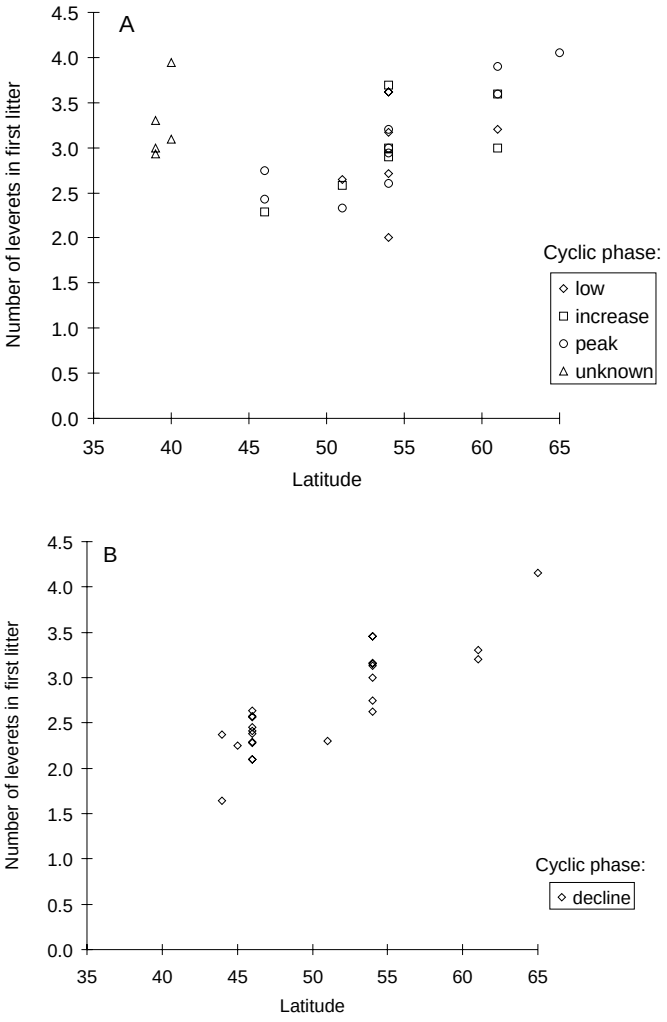

Figure 7.3—The correlation between size of first litter and latitude. Each point represents mean first litter size in one year. Cyclic phases are shown separately because of evidence from Alberta and Yukon that litter size varies through the cycle (Cary and Keith 1979; Stefan 1998). Wisconsin data were assigned to cyclic phases based on trend data from Glenzinski and Dhuey (1998, unpublished) and Karasek (unpublished), and the other references provided information on the population trends in different years; the "unknown" points are for Colorado and Utah (Dolbeer and Clark 1975). Sources: AB, Keith & Windberg 1978, Windberg & Keith 1978, Cary & Keith 1979, Keith et al. 1984; MB, Criddle 1938; ONT, Newson 1964; NB, Wood and Munroe 1977; YK, O'Donoghue and Krebs 1992, Stefan 1998; AK, Ernest 1974; WI, Kuvlesky and Keith 1983; UT, Dolbeer & Clark 1975; and CO, Dolbeer & Clark 1975. The regression of litter size during the decline phase on latitude is highly significant ($F_{1,23} = 71.4$, $p < 0.001$, $r^2 = 0.76$).

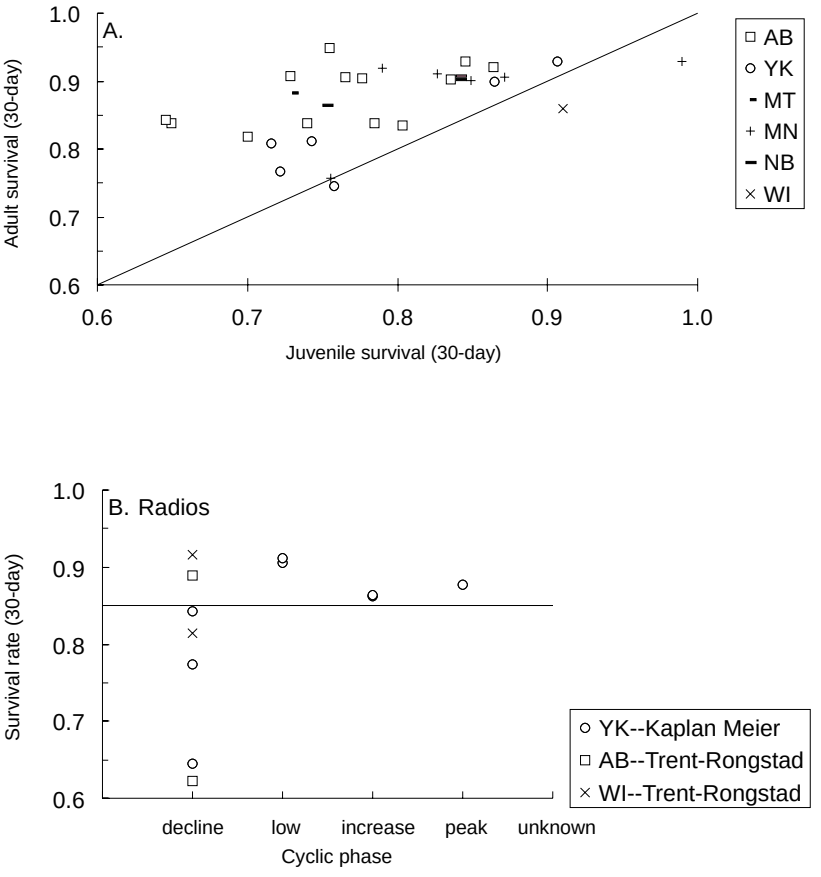

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Figure 7.4—Snowshoe hare survival estimates. Wisconsin data were assigned to cyclic phases based on trend data from Glenzinski and Dhuey (1998, unpublished), and the other references provided information on the population trends in different years. Panel A shows studies in which juvenile survival (from birth through the following spring, or overwinter) was contrasted with adult annual (or overwinter) survival. The diagonal line indicates identical 30-day survival rates. Each point represents one overwinter or annual period. Sources: AB, Keith & Windberg 1978; YK, Krebs et al. 1986; MT, Adams 1959; MN, Green & Evans 1940b; NB, Wood and Munroe 1977; and WI, Keith et al. 1993. Panels B (radiotelemetry) and C (trapping) show adult overwinter or annual survival broken down regionally and methodologically. Lines are given at 0.85 for comparative purposes. Kaplan-Meier and Trent-Rongstad refer to survival calculated following methodologies in Pollock et al. (1989) and Trent & Rongstad (1974) respectively. Jolly-Seber estimation is described in Krebs (1989), recatch estimation in Keith & Windberg (1978), and age ratios in Green and Evans (1940b). Minimum estimation simply calculates individuals caught at time t that are recaught at time t+1. Sources for panel B: YK, Hodges et al. in press; AB, Keith et al. 1984; and WI, Sievert & Keith 1985. Data for panel C: YK, Krebs et al. 1986; AB, Keith & Windberg 1978; BC, Sullivan & Moses 1986, Sullivan 1996; MN, Green & Evans 1940b; MT, Adams 1959; NB, Wood & Munroe 1977; WI, Kuvlesky & Keith 1983; CO, Dolbeer 1972a; and OR, Black 1965.

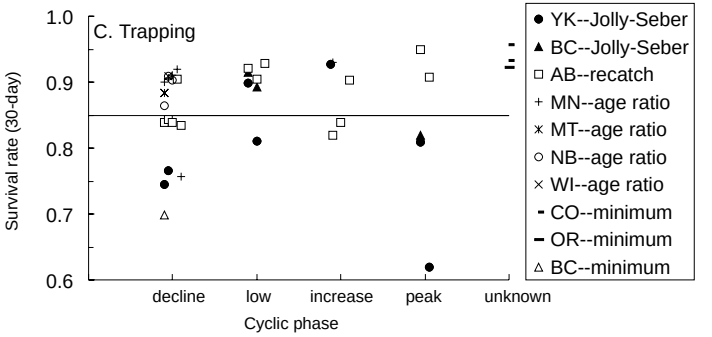

Figure 7.4 (Con.)

telemetry estimates are more likely to be accurate (Chapter 6); survival estimates based on trapping are hampered by the low trappability and potentially high dispersal rates of hares, both of which vary with season, sex, age, phase of cycle, and possibly region and habitat (Trapp 1962; Boutin et al. 1985; Boulanger 1993; Sullivan 1994; Gillis 1997; Hodges 1998).

Trapping studies suggest that juvenile survival is lower than adult survival (Fig. 7.4). This pattern may not be always true, however; using radiocollars, Gillis (1997) found that post-weaning juveniles survived as well as adults during an increase year in Yukon, and Keith et al. (1993) found that juvenile survival was comparable to or higher than adult survival during winter in Wisconsin. Within any given locality, both adult and juvenile survival are lower during population declines (Green and Evans 1940b; Keith and Windberg 1978; Krebs et al. 1986; Hodges et al. in press).

For regional comparisons, I consider only radiotelemetry estimates because of methodological concerns with the trapping data (Table 7.2). Hares

Table 7.2—Survival rates of hares, assessed from radiotelemetry. Where several values are given, they indicate the range among study sites and/or years.

Location	Phase & years	30-day survival rate	Reference
Virginia[a]	unknown 1989-1990	0.63 (>14 days[a]) 0.86 (>60 days[a])	Fies 1993 unpublished
Wisconsin	decline 1988-1991	0.66-0.95	Keith et al. 1993[b] Keith & Bloomer 1993[b] Bloomer et al. 1995[b]
Wisconsin	decline (Dec-Feb) 1994-1995	0.93	Cox et al. 1997
Wisconsin	decline 1982-1983	0.86	Sievert & Keith 1985

[a]Hares were released in a reintroduction program. Estimates are for days post-release.
[b]Approximately half of these hares were treated with antihelminthic drugs, and hares were distributed among seven patches of habitat ranging in size from five to 28 ha. I present survival rates recalculated from Table 5 of Keith et al. 1993.

in Wisconsin had 30-day survival rates ranging between 0.66 and 0.95, with lowest survival occurring as the population declined (Sievert and Keith 1985; Keith et al. 1993; Cox. et al. 1997). These 30-day survival estimates are similar to those from a cyclic population of hares in Yukon, where the lowest monthly survival (0.64) occurred during the decline phase and highest survival (0.91) occurred as the population increased (Hodges et al. in press). In Virginia, imported hares were released in a restocking program; their survival in the first two weeks was low (17 of 26 died), but their survival rates thereafter were similar to those of hares in Wisconsin and Yukon (Fies 1993, unpublished). These results are comparable to those of Sievert and Keith (1985) and evaluations of stocking programs for hunters (Fitzpatrick 1957; Schultz 1980), all of which conclude that transplanted hares have much higher mortality rates within the first several weeks after release.

Most hares in southern populations are killed by predators (Table 7.3) (Fies 1993, unpublished; Sievert and Keith 1985; Keith et al. 1993; Cox et al. 1997; Murray et al. 1997). These studies indicate that predation is responsible for >90% of all hare deaths, a figure comparable to the predation rates found for northern hare populations (Boutin et al. 1986; Krebs et al. 1995; Hodges et al. in press). Both studies of hare mortality patterns and studies of predators indicate that southern hares are preyed upon by lynx, coyotes, bobcat, grey fox, great-horned owls, red fox, weasels, mink, marten, fisher, and goshawks (Zielinski et al. 1983; Litvaitis 1986; Halpin and Bissonette 1988; Giuliano et al. 1989; Kuehn 1989; Dibello et al. 1990; Koehler 1990a; Erdman et al. 1998). Southern forests also contain predators such as raccoons, skunks, feral cats and dogs, and snakes, but the extent to which these predators prey upon hares is unknown. In boreal forests, very young hares are also susceptible to predation by small predators such as red and ground squirrels and some of the smaller hawks (O'Donoghue 1994; Rohner et al. 1995; Stefan 1998; F. Doyle, unpublished), but the southern predators on young hares are unknown.

Dispersal

Radiotelemetry provides the most reliable assessment of dispersal rates (Boutin et al. 1985; Gillis 1997; Chapter 6). There are few such estimates for southern hare populations, but during a population decline in Wisconsin, 2.6% of the hares dispersed and another 5.2% were found dead far enough away from their original locations to suggest possible dispersal (Keith et al. 1993). During a decline in Yukon, 2.7% of hares dispersed (Boutin et al. 1985). Keith et al. (1993) argue that the dispersal rate is higher from smaller habitat patches, but their sample size of dispersers is small (five known dispersers plus 10 animals found dead).

Table 7.3—Causes of mortality for snowshoe hares. Values are % of deaths due to each cause.

Location	Phase & years	Avian	Mammalian	Unknown predator	Non-predation	Unknown	n dead	Observed predators	References
Virginia[a]	unknown 1989 & 1990	8.3	41.7	33.3	16.7[a]	0	24	bobcat grey fox great-horned owl	Fies 1993, unpublished
Manitoba (southern)	decline 1991-1993	32.3	33.3	29.2	5.0	0	318	—	Murray et al. 1997
Wisconsin	decline 1982-1983	26.7	48.3	16.7	8.3	0	60[b]	red fox coyote long-tailed weasel mink great-horned owl goshawk	Sievert & Keith 1985
Wisconsin	decline 1988-1991	10	55	31	4	0	122	—	Keith et al. 1993[c] Keith & Bloomer 1993[c] Bloomer et al. 1995[c]
Wisconsin	decline 1994-1995	14	64	0	7	14	14	coyote	Cox et al. 1997

[a]Hares were relocated from West Virginia into Virginia during January-April in each year. Most died within two weeks of release, and deaths in this period are thought to be related to handling and release into unfamiliar habitat.
[b]I excluded deaths from handling, hunting, and dogs.
[c]Approximately half of these hares were treated with antihelminthic drugs, and hares were distributed among seven patches of habitat ranging in size from five to 28 ha.

Experiments in which hares are transplanted show that hares have reduced survival immediately following release (Schultz 1980; Sievert and Keith 1985; Fies 1993, unpublished), which Sievert and Keith (1985) interpreted to mean that dispersers suffer higher mortality than non-dispersers. Although both transplanting and dispersal lead to habitat unfamiliarity, the process of catching, transporting, and releasing hares is very different than what occurs as hares disperse naturally, making it hard to judge from these experiments what factors lead to the higher mortality rate.

Comparative Demography Between Northern and Southern Hare Populations

The available evidence suggests that demographic patterns are largely similar between hares in northern and southern areas. Most hares are killed by predators and the limited data we have on survival in southern areas (Sievert and Keith 1985; Keith et al. 1993; Fies 1993, unpublished; Cox et al. 1997) suggest that northern and southern hares have similar survival. Because the southern regions potentially have a larger suite of predators, particularly for young hares, it is possible that there are regional differences in leveret and juvenile survival rates. Although there appear to be differences in reproduction, with northern hares having larger litters but sometimes not as many litters in a season, it is unclear what effect this variation has on the cycle. Analyses of snowshoe hare population dynamics suggest that juvenile and adult survival have more impact on the numeric change than does natality (Keith 1990; Krebs 1996; Haydon et al. 1999). More long-term studies of demography and modeling of the effects of variable survival and reproductive rates would help in our understanding of why hare populations display different lengths and amplitudes of fluctuation.

Snowshoe Hare Behavior

Diets

Hares eat many plant species (Table 7.4). The variability in number of species eaten in the different regions is an amalgam of how speciose the different areas are, hares' likings for the different species, and sampling effort.The short list for the north reflects fewer species in boreal forests than in temperate ones, whereas the relatively short western list may be due instead to less intensive sampling. Although many species preferences have been identified (e.g., Telfer 1972; Bryant and Kuropat 1980; Scott and Yahner 1989; Thomas et al. 1997, unpublished), these depend on the plant

Table 7.4—Food plants used by snowshoe hares in different regions. Because of the variety of analytic techniques and the different floristic communities, I have not attempted to separate species into degrees of utilization or preference.

Conifers	Deciduous trees	Shrubs	References
Maritimes & Maine			
Abies balsamea	Acer pensylvanicum	Corylus cornuta	Telfer 1972 (NB)
Picea spp.	Acer rubrum	Gaylussaccia baccata	Litvaitis 1984 (ME)
Picea rubens	Acer saccharum	Hamamelis virginiana	
Pinus strobus	Acer spicatum	Kalmia spp.	
Thuja occidentalis	Alnus rugosa	Myrica gale	
Tsuga canadensis	Alnus crispa	Nemopanthus mucronata	
	Betula alleghaniensis	Rhododendron canadense	
	Betula papyrifera	Vaccinium spp.	
	Betula populifolia	Viburnum spp.	
	Comptonia peregrina		
	Fagus grandifolia		
	Quercus rubra		
Eastern: Appalachians & Alleghanies			
Picea glauca	Acer pensylvanicum	Juniperus communis	Rogowitz 1988 (NY)
Picea rubens	Acer rubrum	Kalmia latifolia	Cook & Robeson 1945 (NY)
Pinus resinosa	Acer saccharum	Rhododendron lapponicum	Brooks 1955 (VA)
Pinus strobus	Betula alleghaniensis	Rubus alleghaniensis	Scott & Yahner 1989 (PA)
Pinus sylvestris	Betula lenta	Rubus hispidus	Walski & Mautz 1977 (NH)
Thuja occidentalis	Betula lutea	Vaccinium erythrocarpum	Brown 1984 (PA)
Tsuga canadensis	Betula papyrifera	Viburnum dentatum	
	Fagus grandifolia		
	Fraxinus americana		
	Populus tremuloides		
Midwest: Great Lakes			
Abies balsamea	Acer pensylvanicum	Amelanchier spp.	Bider 1961 (Que)
Larix laricina	Acer rubrum	Chamaedaphne calyculata	Grange 1932 (WI)
Picea abies	Acer saccharum	Corylus cornuta	Bookhout 1965b (MI)
Picea glauca	Acer spicatum	Juniperus communis	Conroy et al. 1979 (MI)
Picea mariana	Alnus crispa	Ledum groenlandicus	De Vos 1964 (ONT)
Pinus banksiana	Alnus rugosa	Lonicera spp.	Grigal & Moody 1980 (MN)
Pinus divaricata	Betula alba	Rhamnus alnifolia	Johnson 1969 (MI)
Pinus resinosa	Betula papyrifera	Rosa spp.	Bergeron & Tardif 1988 (Que)
Pinus strobus	Betula pumila	Rubus spp.	
Thuja occidentalis	Fagus grandifolia	Salix spp.	
Tsuga canadensis	Ostrya virginiana	Shepherdia canadensis	
	Populus grandidentata	Viburnum spp.	
	Populus pensylvanica		
	Populus tremuloides		
	Populus virginiana		
	Prunus pensylvanica		
	Prunus serotina		
	Prunus virginiana		
	Pyrus malus		
	Quercus rubra		
	Sorbus americana		
	Ulmus americana		
Western: Rockies, Cascades & Intermountain West			
Pinus contorta		Amelanchier alnifolia	Adams 1959 (MT)
Pinus ponderosa		Arctostaphylus uva-ursi	Koehler 1990a (WA)
Pseudotsuga menziesii		Ceanothus spp.	Radwan & Campbell 1968 (WA)
Tsuga heterophylla		Juniperus scopulorum	Thomas et al. 1997, unpublished (WA)
		Mahonia repens	Sullivan and Sullivan 1983 (BC)
		Rosa spp.	Borrecco 1976 (WA)
		Rubus spp.	Black 1965 (OR)
		Salix coulteri	
		Symphoricarpus albus	
		Vaccinium spp.	
North: Boreal Forests			
Picea glauca	Alnus crispa	Amelanchier alnifolia	Smith et al. 1988 (YK)
Picea mariana	Alnus rugosa	Betula glandulosa	Wolff 1978 (AK)
	Betula papyrifera	Corylus cornuta	Bryant 1981 (AK)
	Populus balsamifera	Ledum decumbens	
	Populus tremuloides	Rosa spp.	
		Salix spp.	
		Shepherdia canadensis	

community where each study is conducted. Hares also eat many nonwoody species (Adams 1959; Radwan and Campbell 1968; Thomas et al. 1997, unpublished; Hodges 1998).

Browse damage by hares can slow regeneration of conifers after logging, especially if hares eat the bark of the young trees (Cook and Robeson 1945; Borrecco 1976; Krefting 1975, unpublished; Sullivan and Sullivan 1986; Bergeron and Tardif 1988). When hares are at high density, they are more likely to eat bark and large twigs than during years when hare densities are lower (de Vos 1964; Lloyd-Smith and Piene 1981, unpublished; Fox and Bryant 1984). Hares can affect young trees by slowing their growth rate, destroying the apical meristem, and even killing them (Corson and Cheyney 1928; Cook and Robeson 1945; Krefting 1975, unpublished; Black et al. 1979).

In the north, food availability has been addressed because of its potential role in the generation of cycles (Vowles 1972; Pease et al. 1979; Bryant 1981; Keith 1983; Smith et al. 1988). In the south, more effort has been placed on describing potential competition for food between hares and deer or moose (Dodds 1960; Dodds 1962, unpublished; Bookhout 1965b; Telfer 1972; Krefting 1975, unpublished). These studies have generally agreed that these herbivores often eat the same plants but do not appear to be limiting each other's numbers, although this pattern has not been thoroughly examined. There is at present no evidence suggesting food limitation in southern hare populations.

Analyzing Snowshoe Hare Habitat Use

In the following discussion, I focus on describing the habitats hares use. I avoid using the terms "habitat needs" and "habitat requirements." These terms are designed to address whether particular habitats are so critical to a species that without them the species cannot survive (these may be "source" habitats [sensu Pulliam 1988] or they may be habitats critical to a particular life-stage, such as habitat for lambing). For a species like the snowshoe hare that uses many habitat types, it is difficult to know what criteria to employ to designate a habitat as "required." Density may not be a good index because in some cases higher densities can occur in "sink" habitats (Van Horne 1983), and hares have no obvious need for particular habitats for reproduction. I similarly avoid discussing "habitat quality" because this phrase does not have a precise definition. In all of these cases, it is more valuable to discuss and to quantify habitat-specific demography.

Hare habitat use patterns have been measured by estimates of density (from trapping or from pellet counts; e.g., Litvaitis et al. 1985b; Krebs et al. 1987; Eaton 1995), direct estimates of relative use (from trapping or radiotelemetry locations of marked hares; e.g., Dolbeer and Clark 1975; Ferron

and Ouellet 1992), and indirect estimates of relative use (from browsing intensity or hare tracks; e.g., Monthey 1986; Rogowitz 1988). Of these, density estimates are the most informative, because they can indicate amplitude of change through time or magnitude of difference among habitats. Direct estimates of relative use can be valuable for showing how individuals split their time among different habitats (Manly et al. 1993). Indirect estimates of relative use (indices) are difficult to interpret, because the amplitudes of difference among habitats or years have an unknown relationship to the actual differences in hare densities (Hartman 1960; Thomas et al. 1997, unpublished). Additionally, different protocols (e.g., how to count hare runways) make it difficult to compare results from different studies.

Patterns of Habitat Use by Snowshoe Hares

Density estimates show that hares use certain seral stages more than others, and this pattern appears to be most correlated with horizontal understory cover from approximately 1 to 3 m (Table 7.5). Newly clear-cut areas are essentially not used (Ferron et al. 1998). In Washington, younger lodgepole pine stands support higher densities of hares than do older stands, which is associated with the higher stocking density of the younger stands (Koehler 1990a, b). Typically, forest stands that are densely stocked support higher hare densities than do lightly stocked stands (Litvaitis et al. 1985b; Brocke et al. 1993, unpublished). Similarly, stands with dense understory cover tend to be used more by hares than are stands with little understory cover (Orr and Dodds 1982; Wolfe et al. 1982). Deciduous forests can support reasonable densities of hares, especially if they have well-developed understories (Orr and Dodds 1982; Wolfe et al. 1982; Reed et al. 1999, unpublished).

These patterns of habitat use by hares are supported by studies that employed direct or indirect estimates of relative use (Tables 7.6 and 7.7). The most consistent finding is that hares' use of habitats is correlated with understory cover—stands with shrubs, stands that are densely stocked, and stands at ages where branches have more lateral cover are more heavily used by hares (Black 1965; Dolbeer and Clark 1975; Wolfe et al. 1982; Litvaitis et al. 1985a, b; Monthey 1986; Parker et al. 1983; Koehler 1990a; Swayze 1994, unpublished; Thomas et al. 1997, unpublished). Overstory cover is sometimes correlated with hare habitat use patterns, but typically in cases where it is also significantly correlated with understory cover (Richmond and Chien 1976; Orr and Dodds 1982; Parker et al. 1983; Rogowitz 1988). The species composition in a stand appears to be less correlated with hare habitat use than is understory structure (Ferron and Ouellet 1992; Thomas et al. 1997, unpublished). Stand age per se does not appear to be critical, again

Table 7.5—Snowshoe hare densities in different habitat types. Density estimates are derived either from pellet plots[a] or from live-trapping data.

Location	Year/season	Method	Habitat type	Hare density (hares/ha)	Reference
Stand age/height					
Nova Scotia	1976	pellet plots	forests with ≥50% spruce-fir. height classes (m):		Orr & Dodds 1982
			4.5-9.2	0.59	
			4.5-15	0.52	
			9.4-12.3	0.60	
			12.5-15.2	0.36	
Quebec (southern)	1993-1996	pellet plots	uncut black spruce forest	0.12-0.25	Ferron et al. 1998
			clear-cut black spruce forest	0.01-0.02	
Washington	1986-1989	pellet plots[b]		1986 /1987 /1989	Koehler 1990a, b
			~25-yr-old lodgepole pine	1.04 / 1.79 / 0.99	
			~45-yr-old lodgepole pine	0.86 / 0.45 / 0.39	
			>80-yr-old lodgepole pine	0.43 / — / 0.22	
			>100-yr-old Englemann fir-subalpine spruce	0.09 / 0.27 / 0.12	
Species Composition					
Nova Scotia	1976	pellet plots	spruce-fir	0.49	Orr & Dodds 1982
			maple/birch	0.22	
			alder	0.69	
Utah	1976-1978[c]	pellet plots	aspen—sparse understory	0.01	Wolfe et al. 1982
			aspen—dense understory	0.22	
			aspen-conifer edge	0.17	
			Douglas-fir	0.57	
			subalpine fir	0.99	
			Engelmann spruce	0.19	
Utah	1976-1978	live-trapping	Englemann spruce-subalpine fir		Andersen et al. 1980
			July 1976	1.0	
			July 1977	1.8	
			May 1978	2.7	
Colorado	1998	pellet plots[d]	aspen	0.26	Reed et al. 1999, unpublished
			Douglas-fir	0.37	
			subalpine fir	0.37	
			lodgepole pine	0.35	
			Gambel oak	0.05	
			Ponderosa pine	0.18	
			Engelmann spruce	0.46	
% cover					
Nova Scotia	1976	pellet plots	forests with ≥50% spruce-fir. canopy cover classes:		Orr & Dodds 1982
			10-40	0.62	
			41-60	0.49	
			61-100	0.38	
New Hampshire	1990	pellet plots[e]	spruce-fir-birch-ash-maple		Brocke et al. 1993, unpublished
			9,221 stems/ha (90% conifer)	1.34	
			26,028 stems/ha (99% conifer)	1.27	
			8,512 stems/ha (82% conifer)	0.74	
			6,533 stems/ha (90% conifer)	0.40	
Maine	1982-1983 spring	live-trapping	total understory stems/ha (total conifer stems/ha):	1982 / 1983	Litvaitis et al. 1985b
			31,490 (2,580)	0.4 / 0.6	
			20,350 (16,150)	1.2 / 1.7	
			18,980 (8,580)	0.6 / 0.5	
			16,440 (4,360)	0.2 / 0.1	

[a]Densities from pellet plots were recalculated from the original papers using a regression equation derived from hare density information from 1976 to 1996 (C.J. Krebs, unpublished): ln(hares/ha)=0.888962*ln(pellets)-1.203391, corrected for bias by multiplying with 1.57 following Sprugel (1983). Pellets is pellets/0.155m^2. The methodology and rationale were derived in Krebs et al. (1987), and the current equation simply uses more information.

[b]Fall 1987 pellet values were calculated from Koehler 1990a by adding the winter and summer counts.

[c]Values are from the three years in which all habitats were sampled; the values given are averages across years.

[d]Only cover types with >15 pellet plots are shown here.

[e]Pellet counts were transformed to hare densities using the Krebs (1998, unpublished) equation rather than reporting the densities in this reference, which were calculated according to another formula.

Table 7.6—Proportional occurrence of snowshoe hares in different habitat types. The data in this table show the proportion of locations of hares in each habitat type, from locations gathered via radiotelemetry or live-trapping. Live-trapping data are included here instead of in Table 7.5 if the data were presented as number of captures of animals in each habitat type.

Location	Year/season	Method	Habitat type	Proportional use by hares	Reference
Species composition					
Quebec (southeastern)	1987 summer	radiotelemetry (feeding and resting observations combined)	overstory composition:		Ferron and Ouellet 1992
			conifer	19	
			deciduous	37	
			mixed	29	
			none	15	
			understory composition:		
			conifer or none	4	
			deciduous	80	
			mixed	16	
Oregon	1960-1962	trapping[a]	~15-yr Douglas-fir stands	78.3 / 74.4[a]	Black 1965
			open (clear-cut and fire)	21.7 / 25.6	
% cover					
Nova Scotia (Cape Breton Island)	1977-1979	trapping[b]	fir/spruce/birch forests:		Parker et al. 1983
			open mature	47.2	
			closed mature	9.3	
			regeneration (16-30 yr)	22.3	
			regeneration (5-15 yr)	21.2	
Maine	1981-1983 October-May	trapping[c]	understory density:		Litvaitis 1984
			< 700 stems/ha	0 / 6.8[c]	Litvaitis et al. 1985a
			700-7,000 stems/ha	13.7 / 15.6	
			7,000-20,000 stems/ha	30.1 / 27.9	
			>20,000 stems/ha	56.3 / 49.7	
Colorado	1969-1971 July-August	trapping	open (scattered trees)	9.7 (A) / 25.5 (J)[d]	Dolbeer 1972a
			forested (spruce-fir-pine)	90.3 (A) / 74.5 (J)	Dolbeer & Clark 1975

[a]Values are for the same sites but for periods with different numbers of traps.
[b]Values are % of live captures/1,000 trap nights.
[c]Values are for two sites.
[d]A refers to adults, J to juveniles.

because of the importance of stand structure, but several studies have indicated that younger stands may support more hares than do older mature stands (C. Grove, unpublished; Johnson 1969; Koehler 1990a,b; Byrne 1998, unpublished).

Fires and harvesting both return land to early seral stages but may differ in their effects on hares. Spatial scale of the two disturbances may differ, and whereas fire often leaves some standing trees, both dead and alive, clear-cuts and even some selective cuts remove much of the overstory and often understory as well (Chapter 3). Several authors have argued that fire contributes to the cyclicity of hares, by providing regenerating areas rich in food and cover (Howell 1923; Grange 1965; Fox 1978), but there are comparatively few studies of hares' use of burned stands of various ages. In Colorado, pellet plots showed that hares used an eight-year-old burn of lodgepole pine forest much less than the adjacent unburned forest (Roppe and Hein 1978). In Michigan, hares used a 30-year-old burned site

Table 7.7—Indices of relative use by hares of different habitat types. Statistical significance (at $p < 0.05$) is taken directly from the analyses performed by the authors: > shows statistical significance, ≥ shows a trend but no statistical significance, = shows no trend and no statistical significance. In cases where no statistics were performed, the comparable symbols ⊃, ⊇, and ≈ are used to indicate trends. (0) indicates little or no sign of hares in the habitat.

Location	Year/season	Methods[a]	Snowshoe hare habitat use	Reference
Stand age/height				
Maine	1974-1977 winter	tracks (%)	conifer regrowth: 12-15 yr > 7-9 yr > 1-3 yr	Monthey 1986
Vermont	winter	tracks	deciduous: stands younger than 60 yr ⊃ stands older than 60 yr[b]	C. Grove, unpublished
New York	1972-1974 March	tracks (#)	saw timber ⊃ seedling/sapling ⊇ pole timber ⊃ old field (0)	Richmond and Chien 1976
Pennsylvania	1984-1985 winter	tracks (%)	successful deciduous regeneration > unsuccessful deciduous regeneration[c]	Scott & Yahner 1989
Colorado	1997-1998 winter	tracks (#)	mature ⊇ sapling/pole ⊇ old-growth ⊃ shrub/seedling ⊃ open	Byrne 1998, unpublished
Stand composition				
Maine	1974-1977	tracks (%)	spruce/fir > mixed > maple/beech/birch	Monthey 1986
Maine	1981	tracks (#) pellets	deciduous > spruce/fir > mixed	O'Donoghue 1983
Vermont	winter	tracks	conifer ≈ deciduous ≈ mixed ≈ open[d]	C. Grove, unpublished
Connecticut	1958-1959 winter	tracks trapping[e]	conifer plantation = deciduous > mixed > old field	Behrend 1960, unpublished
New York	1972-1974 March	tracks (#)	Norway spruce ≈ white pine ⊃ stands without these species	Richmond and Chien 1976
New York	1980 January/March	food offerings pellets	spruce > pine-shrub, spruce-shrub > deciduous (0), open (0)	Rogowitz 1988
Pennsylvania	1977 Feb-March	tracks (#)	deciduous regeneration (8 yrs old) ⊃ laurel ⊃ hemlock	Brown 1984
Michigan	1976 Jan-March	browsing intensity	cedar/fir ⊃ ash/elm ⊇ alder ⊃ oak/pine ⊃ clear-cut	Conroy et al. 1979
Michigan (Isle Royale)	1963-1968	pellets	1936 burn > conifer, deciduous > 100-yr-old burn (0)[f]	Johnson 1969

(con.)

Table 7.7 (Con.)

Location	Year/season	Methods[a]	Snowshoe hare habitat use	Reference
Stand composition				
Wisconsin	1978-1979 winter	tracks (#)	spruce-cedar-tamarack > pine-oak, alder, aspen-birch, pine-maple, maple-basswood (0) spruce-pine plantations > pine-oak, alder, maple-basswood (0) spruce-pine plantations ≥ aspen-birch, pine-maple	Buehler & Keith 1982
Utah	1972-1973 June-July	pellets	spruce/fir ≥ lodgepole pine > aspen	Clark 1973
Montana	1977	tracks (#)	lodgepole ⊃ grass islands in lodgepole stands ⊃ subalpine fir-Engelmann spruce ⊃ conifer islands in grassland	Koehler et al. 1979
Colorado	1974	pellets	unburned lodgepole > 8-yr-old burned lodgepole	Roppe & Hein 1978
Colorado	1997-1998 winter	tracks (#)	lodgepole ≈ white fir ≈ limber pine ⊇ Douglas-fir ⊇ Engelmann spruce ≈ ponderosa pine ⊃ aspen ⊃ willow ⊃ oak ⊃ open	Byrne 1998, unpublished
% cover				
Maine	1981-1983	tracks (%) pellets	understory density: 20,000+ stems/ha > 7,000-20,000 > 700-7,000 > below 700 stems/ha	Litvaitis 1984 Litvaitis et al. 1985a
Maine	1981	tracks (#) pellets	understory density: dense > moderate > open > sparse	O'Donoghue 1983
New York	1970-1974 fall-winter	tracks (#) trapping	fir/spruce: 20,900 stems/ha ⊃ 5,900 stems/ha	Brocke 1975
Connecticut	1958-1959 winter	tracks trapping[e]	understory cover from 0-6 ft: 61-100% > 21-60%	Behrend 1960, unpublished
Washington	1994	pellet plots	23-yr-old lodgepole pine regeneration stand density: ~100,000 stems/ha > ~20,000 stems/ha = ~1000 stems/ha	Swayze 1994, unpublished
Washington	1974-1975	damage to seedlings (live-trapping)	sites with Douglas-fir regeneration: clearcuts > clear-cuts treated with herbicides to eliminate herbaceous growth	Borrecco 1976

[a]For methods, tracks (%) means track counts where the proportion of transect segments with tracks was calculated, tracks (#) means tracks were actually counted along transects, pellets indicates pellet plots where the collection design or the presentation do not allow for conversion to density estimates, and browsing intensity and food offerings indicate observations of browse use.

[b]Stands were evaluated for presence/absence of hares only. For this analysis, I excluded stands containing trees of ages overlapping these two groups.

[c]Successful regeneration: >70% of 20 1.83-m radius plots containing ≥2 stems that are ≥1.5 m tall.

[d]Stands were evaluated for presence/absence of hares only. 82-86% of deciduous, mixed, and coniferous stands contained hare sign; 100% of open sites did as well, but only four open sites were sampled compared to 37-99 stands of the other types.

[e]Behrend presented tracks and live captures together in the analysis of habitat use.

[f]The 1936 burn had a variety of habitat types within it, including alder, jack pine, white birch, aspen.

more than a 100-year-old burned site (Johnson 1969). In the Northwest Territories, hares used a burned site during the first winter post-fire, to eat the bark of the burned black spruce trees (Stephenson 1985).

Hares may show seasonal shifts in habitat use, using more or denser coniferous cover in winter than in summer, which suggests that winter cover may be more important than summer cover (O'Donoghue 1983; Parker et al. 1983; Litvaitis et al. 1985b; Swayze 1994, unpublished). Additionally, hare habitat use may vary with regional density; in Minnesota, hares' use of areas with little cover was higher when population densities were high, even though the rank order of hare habitat use remained basically the same as at low densities (Fuller and Heisey 1986). Juvenile hares may use more open habitats than do adult hares (Dolbeer and Clark 1975), and there may be differences in habitat use between males and females (Litvaitis 1990).

Regionally, hares appear more likely to use deciduous forests in the east than in the west (Tables 7.5 through 7.8). On the east coast, where both deciduous and coniferous stands are present, hares may use the coniferous stands more (Richmond and Chien 1976; Orr and Dodds 1982; Rogowitz 1988), but in some cases hares make equal or more use of the deciduous

Table 7.8—Habitat survey results. Forest managers were requested to indicate the top two habitats in which they would find hares. The numbers indicate responses for different national forests; in some cases, one forest manager responded for multiple forests. Clearly, some forest types occur only in one of the regions; the more valuable comparison is within a region to see which habitat types managers consider to contain more hares.

Forest type	Oregon & Washington	Intermountain West	Great Lakes & eastern U.S.
Engelmann spruce-subalpine fir	2	15	–
Interior Douglas-fir	6	4	–
Western larch	1	3	–
Grand fir	5	3	–
White fir	3	–	–
Balsam fir	–	–	5
Mountain hemlock	3	–	–
Coastal fir-hemlock	2	–	–
Red cedar-hemlock	2	1	–
Western red cedar	–	1	–
White cedar	–	–	2
Lodgepole pine	7	14	–
Whitebark pine	–	1	–
Red pine	–	–	2
Jack pine	–	–	1
Ponderosa pine	1	–	–
Red spruce	–	–	1
White spruce	–	–	1
Spruce-tamarack	–	–	1
Spruce-birch	–	–	1
Cottonwood/willow	1	1	–
Aspen	1	4	2
Birch	–	–	2

stands (Behrend 1960, unpublished; O'Donoghue 1983; Brown 1984; Litvaitis et al. 1985b). On the east coast, many deciduous forests have dense understories of shrubs and immature trees and these forest types are commonly used by hares (Tompkins and Woehr 1979; O'Donoghue 1983; Brown 1984; Scott and Yahner 1989; Ferron and Ouellet 1992). Western deciduous forests—such as aspen or poplar stands—may lack this understory growth, and these stands do not show as much use by hares (Clark 1973; Wolfe et al. 1982; Byrne 1998, unpublished; Reed et al. 1999, unpublished). This pattern again highlights the association between hares and understory cover. On the west coast, lodgepole pine, Douglas-fir, and Englemann-spruce/subalpine fir stands are common habitats for hares. On the east coast, the common cover types for hares are spruce/fir, pine, and deciduous.

Habitat interspersion may be valuable to hares by providing them access to habitats with different protective abilities and food availabilities (Conroy et al. 1979; Krenz 1988; Koehler and Brittell 1990; Beauvais 1997; Thomas et al. 1997). Krenz (1988) found that hares in Minnesota were more likely to use deciduous shrub cover if it was clumped (at a scale of circles of 168 m radius), whereas hares were more likely to use coniferous cover that was more evenly distributed. Additionally, the size of habitat patches can affect hare densities. In Washington, stands ≥32 ha had roughly double the number of hare pellets as occurred in stands <16 ha (Thomas et al. 1997), and in Wisconsin there was a trend for larger forest stands to be more likely to have hares present within them (Buehler and Keith 1982). Thomas et al. (1997, unpublished) also found that the amount of disturbed habitat (talus, meadows, or heavily thinned mature forest) in a 600 m strip around each habitat patch was negatively correlated with the number of hare pellets within the patch. In Maine, an area managed with clear-cutting had higher track counts than did areas that were partially harvested or entirely uncut, suggesting that the habitat matrix affects hare abundance (Monthey 1986). In Minnesota, hare habitat use was more correlated with habitat interspersion than with stand type, and hares used the edges more than centers of the heavily used stand types (Conroy et al. 1979). In Wyoming, snowshoe hare presence in stands was correlated with the degree of interspersion with clear-cuts and riparian areas (Beauvais 1997).

The bulk of evidence suggests that habitats affect hares' survival rates because vulnerability to predation and predator density vary among habitats (O'Donoghue 1997; Murray et al. 1994, 1995). Fecundity may possibly vary with habitat as well, perhaps mediated by dietary differences (Hik 1994) or the effects of predation risk on stress levels (Boonstra et al. 1998). At a stand level, then, demography is likely to vary with cover and food availability. At the level of multiple stands, however, hares may be able to switch back and forth between different types of stands (Conroy et al. 1979;

Krenz 1988; Hik 1994), or different age classes of hares may use different stand types (Dolbeer and Clark 1975; Boutin 1984). Hare dynamics within the set of stands will therefore depend on the densities of hares within each stand as well as the survival and fecundity rates typical of each stand type. The size of each stand and the degree of interspersion are likely to affect hare dynamics as well—an array of large stands may have different overall dynamics than a quilt of small stands because the movement of hares between stands is easier when each stand is smaller. Additionally, if certain predators require large stands of particular habitat types, they may not occur in landscapes where the same amount of habitat is dispersed in smaller patches.

The habitat use patterns of southern snowshoe hares are similar to those of hares in northern boreal forests. Hares in northern forests also are often associated with early seral forests, again with understory cover or stand density as good correlates with hare habitat use patterns (Wolff 1980; Sullivan and Sullivan 1982a,b, 1983; Hik 1994, 1995; O'Donoghue 1997). Northern forests are predominantly coniferous, and the deciduous aspen and poplar stands typically do not support a thick shrub understory; hares in northern forests do not use these deciduous stands extensively (Hodges 1998).

Discussion

The predominant snowshoe hare story in this century has been that snowshoe hares are strongly cyclic in the north but show reduced or no cycles in their southern distribution (Howell 1923; MacLulich 1937; Criddle 1938; Keith 1963, 1990; Grange 1965; Finerty 1980; Bittner and Rongstad 1982; Smith 1983). This paradigm has arisen from two main fronts: analyses of time series data (mainly harvest records) and comparisons of demographic patterns among regions. I have so far presented time series that support the possibility that hares are cyclic in southern areas, although with peak and low densities lower than those in northern areas. I have similarly argued that the comparable data we have from southern and northern hare populations indicate similar demography among regions. In this final section, I argue that it is time to emphasize analyses that address why snowshoe hare fluctuations vary in amplitude, maximum density, and duration both within and among regions. There is an extensive literature discussing the linkages of hare behavior, habitats, and demography, and this framework may prove useful for evaluating the mechanisms leading to different dynamics and densities in different times or areas.

The dominant model of the effect of hare habitat use patterns on their demography has been used to explain both cyclic dynamics and the previ-

ously hypothesized noncyclicity in the southern range of hares (Keith 1966, 1990; Dolbeer and Clark 1975; Wolff 1980, 1981; Buehler and Keith 1982; Sievert and Keith 1985; Hik 1994, 1995). The refugium model was most clearly articulated by Wolff (1980, 1981) as follows: hares selectively use dense, safe habitats until high hare densities force some hares into poor habitats, which exposes them to higher predation risk, thus contributing to the numeric and functional responses of predators and the cyclic decline. The habitats with densest cover, meanwhile, provide refugia to hares, thus allowing a source population during the low phase. In this model, reproductive declines are thought to originate because food supply in the densest habitats is lower, or poorer quality, leaving hares with a trade-off between nutrition and survival (Hik 1994, 1995). Alternatively, recent evidence suggests that reproductive declines may be due to the stress of encounters with predators, which is highest as hare populations decline (Boonstra and Singleton 1993; Boonstra et al. 1998).

The refugium model has also been used to explain the putative lack of cycles in the south (Dolbeer and Clark 1975; Wolff 1980, 1981). In this case, the basic argument is that southern habitats are more patchy due to being montane (and with greater human impacts). The implication is that hares that disperse from refugia are even less likely to survive, especially since there are noncyclic facultative predators able to prey on the hares. Within each southern habitat patch, therefore, cyclic dynamics are liable to be subdued because of the smallness of the patch and the survival sink awaiting dispersers from the patch.

This refugium model can be broken down into a number of testable components:

(1) refuge habitats exist, in which hares have higher survival than in other habitat types;

(2) the distribution of hares relative to habitats changes through the cycle, with a higher proportion of hares in refugia during the low phase;

(3) hare reproduction varies with habitat, with hares in refugia showing the lowest reproductive output.

If hares in southern populations have dynamics that differ from those of hares in northern populations, then two additional propositions are relevant:

(4) hares in southern populations have lower survival in non-refuge habitats than do hares in northern non-refuge habitats (or in the north refugia comprise a larger proportion of the habitat available than in the south); and

(5) hares in southern populations have lower survival overall than do hares in northern populations, thus stabilizing the cycle.

A similar model has been proposed for Fennoscandian microtine cycles that emphasizes the role of facultative predators in the southern noncyclic range of microtine rodents (Erlinge et al. 1983; Hansson and Henttonen 1985; Hansson 1987; Erlinge 1987; Hanski et al. 1991; Lindström 1994). This model is similar to the refugium model in that a critical element is the increased mortality that occurs in noncyclic prey populations relative to cyclic ones. Habitat is invoked more in the role of enabling facultative predators and alternative prey to be present, rather than in the role of changing the accessibility of the cyclic prey species to the predators. The same argumentation could be applied to the snowshoe hares: if the facultative predation model is true, we would expect to see (A) overall higher mortality rates of snowshoe hares in their southern range, and (B) a higher proportion of deaths by facultative predators in southern populations than in northern populations. Although both models need higher hare mortality in the southern populations (requirements 5 and A), it is possible that hares could have higher mortality rates in the south without the other requirements of either model being upheld, in which case other hypotheses would need to be constructed to explain why the mortality rates differed. It is also possible that per capita predation rates on hares may be similar among regions, but that the predators are compensatory with each other (Stenseth et al. 1997; Hodges et al. in press), thus making the proportion of kills due to each predator interesting from a community organization perspective but irrelevant to the dynamics of hares.

At present, our evaluation of these two predation models can be little more than conjectural (Table 7.9). We have limited data that address only requirements 1 and 2 of the refugium model. A few studies have indicated small differences in hare survival (measured with radiotelemetry) among habitats (Sievert and Keith 1985; Keith and Bloomer 1993), and predators choose particular habitat types and may have differential success rates in each type (Hik 1994; Murray et al. 1994, 1995; Rohner and Krebs 1996; Cox et al. 1997). There is, however, no clear cyclic pattern in snowshoe hares' use of the available habitat types (Fuller and Heisey 1986; Chapter 6), counter to the refugium hypothesis. Experimental work in Yukon has shown that hares protected from predators still prefer dense cover and do not show much greater use of open cover than unprotected hares (Hik 1994; Hodges 1998), which argues against the idea that high predation pressure forces hares into dense habitats.

To evaluate the roles of habitat structure and predation on hare cycles among regions properly, we need precise definitions of refugia and nonrefugia and our data from hare populations in different regions need to be comparable. Given the evidence from Alberta and Yukon that shows that both food and predation are necessary components of the cycle (Keith 1990;

Table 7.9—Evaluation of the refugium and facultative predation hypotheses for snowshoe hare cycles. Requirements 1-5 belong to the refugium hypothesis, and A-B to the facultative predation hypothesis. Support for any of 4a-4c would be adequate; only one is needed to support that requirement of the refugium model. If requirements 1 & 2 are met, but 4 & 5 are not, refugia can help explain northern cyclicity but cannot explain dynamics in southern populations. Requirement 3 is not strictly necessary, but would support the argument that habitat affects hare demography.

Model requirements	Evidence	Questions that need to be resolved
1. differential survival in different habitat types	see chapter 6; 2 Wisconsin studies found differential survival	What magnitude of difference is necessary?
2. hare distribution in habitats varies cyclically (higher % of hares in refuges during low phase)	see chapter 6; no clear cyclicity in hare habitat use	What magnitude of difference is necessary? Does the % of mortalities/hare/habitat vary? (is a refugium a physical place?)
3. differential reproduction in different habitat types	no data available	Is habitat a proxy for nutrition or maternal stress?
4a. survival in southern non-refuges < survival in northern non-refuges	no comparable data available	Critical to define well and make comparable between regions.
4b. survival in southern refuges < survival in northern refuges	no comparable data available	Critical to define well and make comparable between regions. Can "refuge" habitats be defined by vegetation type and/or structure or are they defined by having higher survival within them?
4c. lower % of refuge habitat in south than in north	"refuge" habitat needs definition first	Critical to define well and make comparable between regions. Can "refuge" habitats be defined by vegetation and/or structure or are they defined by having higher survival within them?
5 & A. lower survival rate in south than in north	comparable data suggest similar survival rates	What period of the cycle should be used for comparison? What magnitude of difference is necessary? Is it sufficient if survival differs in only one age class or season?
B. higher % of deaths by facultative predators in south than in north	no comparable data available	Definitions needed of facultative vs. obligate for N. American predators of hares. Is it sufficient if this requirement applies to only one age class? What magnitude of difference is necessary?

Krebs et al. 1995), it is distressing that the dominant models for explaining cycles and potential regional differences in cycles focus on predation. Reproductive changes occur cyclically and possibly regionally yet are given only minor attention in these models of hare dynamics. Even though hare survival appears to have more effect on numeric changes, explicit hypotheses should be developed that incorporate hares' food supply and reproductive changes. Furthermore, the degree of interspersion and the size of each habitat patch may matter as much to hare demography as does the actual proportion of each habitat type, so spatially explicit analyses need to be conducted.

Conclusions

Currently, our knowledge of snowshoe hares in their southern range is dominated by information on distribution and habitat use patterns. Our knowledge of hare numeric patterns is derived mainly from harvest records, and our knowledge of hare demographic patterns in their southern range tend to come from short-term studies (<5 years). All of these data sets are stronger in the northeast and around the Great Lakes than in the southern and western range of snowshoe hares. Time series of snowshoe hare density will be valuable throughout the range of snowshoe hares, but especially in the western and southern regions where few time series exist. The existing demographic studies suggest that patterns may be similar from north to south, but southern records tend to be shorter in duration; it will be valuable to assess the range of variation in demography in southern sites across a range of densities and population trends. The consensus of many studies from north to south is that hares utilize habitats with dense understories and many overstory species, but we do not yet have a complete understanding of how the degree of interspersion or spatial scale of fragmentation affect hare densities and population dynamics. Our future research should emphasize the interrelationship between habitats—at multiple scales and in various spatial arrays—and snowshoe hare population dynamics.

Acknowledgments

I wish I had more space to acknowledge the consistent and patient support of G. Koehler and C.J. Krebs; this chapter is much better than it would have been sans their support and their insightful comments. Three anonymous reviewers and members of the Lynx Science Team offered comments on the manuscript that have greatly strengthened it. S. Clark was indispensible: she was incredibly useful in contacting people and acquiring references for me, an effort that L. Moffatt additionally aided. This chapter relies on the generosity of many people who were willing to provide me with their unpublished, reports, and observations. I am extremely grateful to the following people for doing so: M. Boudreau, C. McLaughlin, K. Eagle, D. Dziak, G. Batchelar, A. Jacobson, J. Cardoza, G. Karasek, D. Ware, R. Lafond, R. Dibblee, D. Mitchell, J. Malloy, L. Ruggiero, G. Schmidt, C. Harris, J. Rieffenberger, C. Krebs, and D. Scott. I additionally benefitted from seeing an unpublished manuscript by D. Murray.

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