Chapter 6

The Ecology of Snowshoe Hares in Northern Boreal Forests

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Abstract—Snowshoe hares exhibit eight to 11 year population fluctuations across boreal North America, typically with an amplitude of 10 to 25 fold. These fluctuations are synchronous across the continent, with the most recent peak densities occurring in 1990 and 1991. The numeric cycle is driven by changes in survival and reproduction, with annual survival of adults ranging from approximately five to 30% and annual natality ranging from approximately six to 20 leverets/female. These parameters show cyclic changes because of functional and numerical responses of predators and changes in food supply. Predator densities show approximately two to 10 fold fluctuations during the hare cycle. The cyclicity of hares may be partly explained by regular behavioral shifts, with repercussions on their physiology, availability to predators, reproduction, and survival. However, this hypothesis needs more empirical support before it can be accepted.

Introduction

In this chapter, I discuss the ecology of cyclic populations of snowshoe hares in the boreal forests of North America. I emphasize the demographic changes leading to changes in numbers of hares, the habitats that hares use, the impacts of nutrition, physiology, and parasite loads on hares' susceptibility to predation, and the effects of disturbance (fire, logging, fragmentation, and regeneration) on snowshoe hares' behavior and demography. I address what is known about the causes of the cycle and cyclic synchrony among regions. For demographic data, I focus on data sets that show variation through a cycle in one location; I use demographic results from shorter studies to examine the factors that influence demography, rather than trying to infer cyclic or geographic patterns from them.

Magnitude and Synchrony of Northern Hare Cycles

Snowshoe hares show cyclic fluctuations in density across northern North America, with peak densities every eight to 11 years. It was thought that only northern populations of hares cycle (Green and Evans 1940; Finerty 1980; Smith 1983; Keith 1990), but recent evidence suggests that hare in their southern range—through the Cascades, Rockies, and Alleghenies to California, New Mexico, and Virginia—may also cycle (Chapter 7). Hares were introduced into Newfoundland in the 1860s and 1870s. Their numbers increased rapidly, crashed, and have since shown a 10-year cycle (Bergerud 1983).

During the last four decades, the cycle has been largely synchronous across Canada and into Alaska (Table 6.1). Cyclic peaks have occurred roughly at the turn of each decade (1960 to 1961, 1970 to 1971, 1980 to 1981, 1990 to 1991), with lowest densities typically occurring three years later (1963 to 1964, 1973 to 1974, 1983 to 1984, 1993 to 1994). These patterns support previous surveys that concluded that the cycle is synchronous (MacLulich 1937; Keith 1963; Finerty 1980; Smith 1983; Sinclair et al. 1993; Sinclair and Gosline 1997). In the last four decades, peak and low density years have been synchronous across the continent, whereas cycles in the early and middle parts of the century were synchronous at peak densities but not necessarily at low densities (Sinclair and Gosline 1997). There have also been debates about whether hares in the central part of Canada (i.e., Alberta, Saskatchewan, and Manitoba) reach peak densities earlier than in other locations, followed by a wave of peaks that extends north, west, and east (Bulmer 1974; Smith 1983; Ranta et al. 1997). The data from the last three cycles do not support this idea.

There are a few areas in which hares may not cycle in synchrony. The hunting data from Newfoundland suggest that cyclic peaks are asynchronous with those in mainland Canada (S. Mahoney, unpublished). Harvest

Table 6.1—The snowshoe hare cycle: synchrony, densities, and amplitude. Peak or low years coinciding with the beginning or termination of a study should be viewed with skepticism because of the inability to see what the hare population did in the previous or subsequent years. Density estimates are not comparable because of different field and statistical techniques applied to their generation; they and cyclic amplitude are presented to give an order of magnitude. Cyclic amplitude is rounded to the nearest 5. The data collated into this table are roughly post-1960 and most are within the taiga provinces of the polar domain (Bailey 1997). (S) is spring enumeration. (F) is fall enumeration. No data are indicated by —.

Location	Years of study	Peak	Low	Peak density (hares/ha)	Low density (hares/ha)	Amplitude	Methods	Reference
Newfoundland	1990-1993	1990	1993	—	—	—	Track counts	Thompson & Curran 1995
Newfoundland	1954-1998	1960, 1969, 1976, 1983, 1998[a]	—	—	—	—	Harvest records[a]	Dodds 1965; S. Mahoney, unpublished
Manitouwadge, Ontario	1980-1985	1980	1984	—	—	—	Track counts	Thompson & Colgan 1987; Thompson et al. 1989
Narcisse Wildlife Mgmt Area, Manitoba	1991-1993	—	—	—	0.3-0.4	—	Live-trapping	Murray et al. 1998
Narcisse Wildlife Mgmt Area, Manitoba	1971-1973	—	1973 (S)	—	—	—	Sightings along transects	Rusch et al. 1978
Long Point Peninsula, Manitoba	1971-1987	1971 (F) 1980 (F)	1974 (F) 1985 (F)	4.4	0.2	25	Live-trapping	Koonz 1988, unpublished
Saskatchewan	1958-1987	1960 1970 1980	1963 1973 1984	—	—	—	Observation[b]	Houston 1987; Houston & Francis 1995
Rochester, Alberta	1961-1984	1962 (S) 1971 (S) 1981 (S)	1966 (S) 1975 (S)	5.9-11.8 (F)	0.13-0.26 (S)	25 (S)	Live-trapping	Keith & Windberg 1978; Keith 1983; Keith et al. 1984
Westlock, Alberta woodlot fragments	1970-1974	1970 (F)	1973 (F)	5.6 (F)	0.8 (F)	5	Live-trapping	Windberg & Keith 1978
Prince George, B.C.	1979-1983 1988-1991	1979 (F) 1990 (F)	—	16.4 (F) 4.2-5.2 (F)	—	—	Live-trapping	Sullivan & Sullivan 1988b; Sullivan 1994
Mackenzie Bison Sanctuary, NWT	1989-1996	1989-1990	1992-1993	4.6	0.34	15	Pellet plots[c] Track counts	Poole 1994; K. Poole, unpublished
Ft. Simpson, NWT	1993-1996	—	1994-1995	—	0.17	—	Pellet plots[c]	Poole & Graf 1996; K. Poole, unpublished
Ft. Smith, NWT	1989-1996	1989-1990	1992-1993	2.0	0.09	20	Pellet plots[c]	Poole & Graf 1996; K. Poole, unpublished
Norman Wells, NWT	1989-1997	1989-1990	1992-1993	1.9	0.14	15	Pellet plots[c]	Poole & Graf 1996; K. Poole, unpublished
Yellowknife, NWT	1989-1996	1989-1990	1993-1994	3.4	0.28	10	Pellet plots[c]	Poole & Graf 1996; K. Poole, unpublished

(con.)

Table 6.1—Con.

Location	Years of study	Peak	Low	Peak density (hares/ha)	Low density (hares/ha)	Amplitude	Methods	Reference
Inuvik, NWT	1989-1996	1995-1996	1988-1989	2.0	0.43	5	Pellet plots[c]	K. Poole, unpublished
Dawson, Yukon	1988-1991	1989-1990	—	1.3-4.3[d]	—	—	Pellet plots[c] Track counts	Mowat et al. 1997, unpublished
Whitehorse, Yukon	1988-1991	1990-1991	—	0.9-4.4[d]	—	—	Pellet plots[c] Track counts	Mowat et al. 1997, unpublished
Snafu Lake, Yukon	1988-1993	1990-1991	1986-1987 1993-1994	7.5	0.8-1.1	5-10	Pellet plots[c]	Mowat et al. 1997, unpublished; Slough & Mowat 1996
Kluane Lake, Yukon	1976-1998	1980-1981 1989-1990	1984-1985 1993-1994	2.9 (S) 1.5 (S)	0.16 (S) 0.08 (S)	20	Live-trapping	Krebs et al. 1986b; Krebs et al. 1995; Hodges et al., in press; C. J. Krebs, unpublished
Tanana Valley & s. of Fairbanks, Alaska	1995-1998	—[e]	1994-1995[e]	—	—	—	Aerial surveys	M. McNay, unpublished[e]
Wrangell-St. Elias, Alaska	1991-1998	1990-1991	1993-1994	2.9-5.5[f]	0.12-0.43[f]	20-25[f]	Pellet plots[c]	C. D. Mitchell, unpublished
Fairbanks, Alaska	1986-1996	1988-1989	1992-1993	0.5	0.02	25	Pellet plots[c]	L.A. Viereck & P.C. Adams Bonanza Creek LTER, unpublished
Fairbanks, Alaska	1971-1977	1971 (F)	1975 (F)	~5.9[g]	0.12	50[g]	Live-trapping Pellet plots	Wolff 1980
Fairbanks, Alaska	1955-1961	1961	1955	—	—	—	Live-trapping Pellet plots	Trapp 1962; O'Farrell 1965
Fairbanks, Alaska	1970-1973	1971	—	6.0-6.5	—	—	Live-trapping	Ernest 1974
Kenai Peninsula, Alaska	1971-1974	1973-1974	—	—	—	—	Observations	Oldemeyer 1983
Kenai Peninsula, Alaska	1983-1998	1984-1985	1989-1992	0.8-3.0[h]	0-0.4[h]	5-25[h]	Live-trapping[h]	Bailey et al. 1986; Staples 1995; T. Bailey, unpublished

[a] There does not appear to have been a distinct peak in the late 1980s. Lows are difficult to infer from the data because of variation in hunter effort. (M. O'Donoghue, personal communication).

[b] Peaks are from Houston 1987 and generally correspond to the next to the last year of "high" densities in Houston & Francis (1995). Low values are the 4th of the "low" years from Houston & Francis (1995).

[c] Densities from pellet plots are 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). The current equation uses more information.

[d] The range of values is the range that occurred in five different habitat types.

[e] M. McNay also reports that hare populations were highest in 1988 to 1989 or 1989 to 1990, and may have been at their lowest densities in 1993 to 1994.

[f] For most years, four sites were surveyed and ranges of values indicate sites. In 1991, only two sites were surveyed.

[g] The peak density was inferred from 1971 peak densities in similar habitats in interior Alaska by Ernest (1974).

[h] Density estimates are for adult hares only, trapped in summer. Ranges indicate the extreme values for the five study sites.

data and observations suggest that there may not have been a cyclic peak in the late 1980s or early 1990s (M. O'Donoghue, personal communication), although track surveys in western Newfoundland showed a pronounced decline from 1990 to 1993 (Thompson and Curran 1995). Human impacts on hares are severe in Newfoundland and probably influence hare dynamics (M. O'Donoghue and T. Joyce, personal communication).

The hare population around Inuvik, NWT, is asynchronous. The highest densities were in 1995 and 1996 and the lowest densities were in 1988 and 1989 (out of eight years of collecting pellet-plot data) (K. Poole, unpublished). The Kenai Peninsula in Alaska also is asynchronous, with hares reaching peak densities in 1984 and 1985 with low densities from 1989 to 1992 (Oldemeyer 1983; Bailey et al. 1986; Staples 1995; T. Bailey, unpublished). There has been speculation that hare populations are out of phase throughout Alaska, which allows predators to travel the state in search of locally abundant hares. The available data suggest that is not the case. With the exception of the Kenai Peninsula, hares cycle in synchrony in Alaska (H. Golden, unpublished; Chapter 9).

It has been hypothesized that synchrony is modulated by sunspot activity (Sinclair et al. 1993; Sinclair and Gosline 1997). Sunspot activity is correlated with weather patterns, fire, snowfall, and, potentially, plant growth. Regular changes in one or several of these patterns at a continental scale could synchronize population cycles that are occurring because of biological interactions (Meslow and Keith 1971; Fox 1978; Finerty 1980). The Inuvik and Kenai populations of hares are at the edges of snowshoe hare distribution, and both are coastal. The coastal influence has pronounced effects on the weather patterns, which may change the synchrony in these populations.

The question of whether there is geographic variation in peak and low densities is more difficult to answer because of the array of field and statistical methodologies used for density estimation and the problem of determining what area of land was sampled. There is no obvious north-south or east-west gradient in densities; indeed, during the 1990 to 1991 peak, Yukon had the lowest (1.4 hares/ha at Kluane Lake) (Krebs et al. 1995) and the second-highest (7.3 hares/ha at Snafu Lake) (Slough and Mowat 1996) recorded peak densities. Estimates of low densities range from <0.1 to 1.0 hares/ha. Most estimates of amplitude are five to 25 fold, which is somewhat lower than those inferred by Keith (1990). Hare densities vary within different habitat types (Fuller and Heisey 1986; Koonz 1988, unpublished; Mowat et al. 1997, unpublished; Chapter 7), so estimates may also reflect sampling effort in different habitats.

Natural History of Snowshoe Hares

Adult snowshoe hares range in weight from approximately 1,200 to 1,800 g (Rowan and Keith 1959; Newson and de Vos 1964; C. J. Krebs, unpublished). Sex ratios are fairly even at all ages (Dodds 1965; Keith 1990; Hodges et al., in press). Hares do not breed until the summer following their birth, with very rare exceptions (Keith and Meslow 1967; Vaughan and Keith 1980). Breeding is restricted to the summer, and each female has one to four litters per summer (Keith et al. 1966; Cary and Keith 1979). Anywhere from one to 14 leverets are born per litter; the first litter of the summer has a mean of approximately three leverets, the second litter is largest with a mean of five to six, and the later litters are intermediate in numbers (Cary and Keith 1979; O'Donoghue and Krebs 1992; Jardine 1995; Stefan 1998). Females breed synchronously, perhaps to reduce leveret mortality (O'Donoghue and Boutin 1995). Mating occurs immediately post-partum and gestation lasts 35 to 37 days (Meslow and Keith 1968; Stefan 1998). The early litters are weaned at about 24 to 28 days of age, but the last litter of the season may be nursed for up to 40 days (O'Donoghue and Bergman 1992). The young are precocial; they hide together under deadfall, at the base of a bush, in tangled grasses, or under lupines for the first three to five days, and then hide separately, coming together for their once-a-day nursing (Rongstad and Tester 1971; Graf and Sinclair 1987; O'Donoghue and Bergman 1992; O'Donoghue 1994).

Most North American predators eat snowshoe hares, and most hares die of predation (Keith 1990; Hodges et al., in press). Boreal predators display size selection for hares. Small predators, such as Harlan's hawks, hawk owls, kestrels, and weasels, eat leverets and small juveniles (Stefan 1998; Rohner et al. 1995; F. I. Doyle, unpublished), while larger predators, such as lynx and coyotes, eat large juveniles and adult hares (Keith 1990; Hodges et al., in press). Great horned owls and goshawks eat hares of all sizes (Hodges et al., in press). Most mortality occurs before hares reach breeding age, and leveret survival is lower than juvenile survival. Although wild hares can reach five to six years of age, typically over 70% of the spring breeding population is composed of yearlings (Keith 1990; Hodges et al., in press).

In summer, hares eat forbs, grasses, leaves of shrubs, and some woody browse (Wolff 1978; Grisley 1991; P. Seccombe-Hett, unpublished). In winter, they mainly eat twigs and some bark of bushes and trees (de Vos 1964; Wolff 1978; Keith 1990), but they will also dig through shallow snow for forbs and grasses (Gilbert 1990; Hodges 1998). Hares usually select smaller twigs and are selective about which species they browse (Wolff 1978; Pease et al. 1979; Rogowitz 1988; Smith et al. 1988). Diet selection may be based on protein or fibre content, secondary compounds, energy content, or digestibility (Bryant 1981a; Schmitz et al. 1992; Rodgers and Sinclair 1997; Hodges 1998).

The Community Cycle

Many snowshoe hare predators also display cyclic dynamics, often with a lag of one to three years behind the hare cycle (Keith et al. 1977; Keith 1990; Royama 1992; Boutin et al. 1995). Lynx, coyotes, goshawks, and great horned owls display numerical and functional responses to the changes in hare densities, with numeric responses of two to 10 fold (Brand et al. 1976; Adamcik et al. 1978; Brand and Keith 1979; Todd et al. 1981; Parker et al. 1983; Poole 1994; Doyle and Smith 1994; Houston and Francis 1995; Slough and Mowat 1996; Rohner 1996; O'Donoghue et al. 1997, 1998). Other predators, such as red foxes, marten, fisher, eagles, wolverine, wolves, bobcats, hawk owls, and Harlan's hawks, may show functional responses to hare densities (Keith 1963; Bulmer 1974; Litvaitis et al. 1986; Raine 1987; Kuehn 1989; Theberge and Wedeles 1989; Dibello et al. 1990; Rohner et al. 1995; Hodges et al., in press; F. I. Doyle, unpublished). Foxes, wolverine, marten, and fisher may also exhibit numeric responses to the snowshoe hare cycle (Bulmer 1975; Thompson and Colgan 1987; Kuehn 1989; Slough et al. 1989; Poole and Graf 1996).

Other small herbivores in the boreal forest also demonstrate cyclic dynamics, perhaps resulting from competition with hares for limited food or from being the alternate prey when hares densities are low (Keith 1963; Boutin et al. 1995). Spruce grouse and ruffed grouse show a 10-year fluctuation (Rusch et al. 1978; Keith and Rusch 1988; Boutin et al. 1995), while red squirrels do not (Keith and Cary 1991; Boutin et al. 1995; Boonstra et al., in press), and Arctic ground squirrels may cycle in part of the boreal forest (Boonstra et al., in press). Mice and voles do not have regular 10-year fluctuations (Krebs and Wingate 1985; Boutin et al. 1995), even though several predators prey more heavily on small mammals when hares are scarce (Raine 1987; Giuliano et al. 1989; O'Donoghue et al. 1998).

Hares affect their woody browse species in several ways through the cycle. At peak densities, hares may eat a large proportion of the standing shrub biomass (Pease et al. 1979; Keith 1983; Smith et al. 1988), which will not necessarily kill the plants. Hares also girdle the woody stems of trees and shrubs (Sullivan and Sullivan 1982a; Hodges 1998), which will kill the trees. However, some shrubs resprout from the ground, and girdling may stimulate new growth (Smith et al. 1988). Browsing by hares may affect successional dynamics (Bryant 1987; Rossow et al. 1997), disrupt attempts at reforestation (Sullivan and Moses 1986; Radvanyi 1987, unpublished), and influence the amount of secondary compounds that plants produce and their palatability to hares (Bryant 1981a, 1981b; Fox and Bryant 1984; Bryant et al. 1985).

Demographic Changes Through the Cycle

The numeric hare cycle results from demographic changes. The main demographic changes in order of importance are post-weaning juvenile survival, adult survival, and leveret survival (Krebs 1996; Haydon et al. 1999; Hodges et al., in press). Leveret survival and dispersal contribute the least to cyclic dynamics (Haydon et al. 1999), even though they also vary through the cycle (Boutin et al. 1985; Keith 1990; Stefan 1998).

Reproduction

Two long-term studies in Yukon and Alberta have shown that snowshoe hares have the highest reproductive output during the early increase phase of the cycle (16 to 19 leverets/female) and the lowest reproductive output during the decline phase (six to eight leverets/female), with maximum annual reproductive output about 2.5 fold higher than the lowest reproductive output (Fig. 6.1a,b) (Cary and Keith 1979; O'Donoghue and Krebs 1992; Krebs et al. 1995; Stefan 1998). This pattern is the result of changes in the proportion of females pregnant for each litter group, the number of litters that females have in the summer, and the number of leverets per litter (Table 6.2). In Yukon, hares had only two litters during the decline phase, but had four in the early increase phase (Stefan 1998). In Alberta, in contrast, at least a few hares had a fourth litter in every year of the cycle, but during decline years most hares had only three litters (Keith and Windberg 1978; Cary and Keith 1979). Hares in Alaska had a higher pregnancy rate for the third litter during the peak than during the decline (Ernest 1974). In both Yukon and Alberta, litter size varied more for litters two to four than for litter one; mean size for the first litter varied by approximately 0.5 leverets per litter through the cycle. Means for later litter groups varied by one to two leverets per litter through the different phases.

The factors influencing hares' reproductive output are not well known. Snowshoe hares exhibit cyclic changes in stress levels, indexed by several blood chemistry traits such as cortisol and testosterone concentrations (Boonstra and Singleton 1993; Boonstra et al. 1998a). Stress might cause reproductive changes either by affecting females' reproductive output directly or through maternal effects on the offspring (Boonstra et al. 1998b). Reproduction does not seem to be affected by levels of parasitic infestation (Bloomer et al. 1995; Sovell and Holmes 1996; Murray et al. 1998). Physically, mass, skeletal size, and body condition (indexed by mass corrected for skeletal size) do not appear to affect number of litters or litter size (Hodges et al. 2000, in press; Hodges et al., in press). Older, heavier individuals may have higher ovulation rates than younger, lighter hares (Newson 1964), but

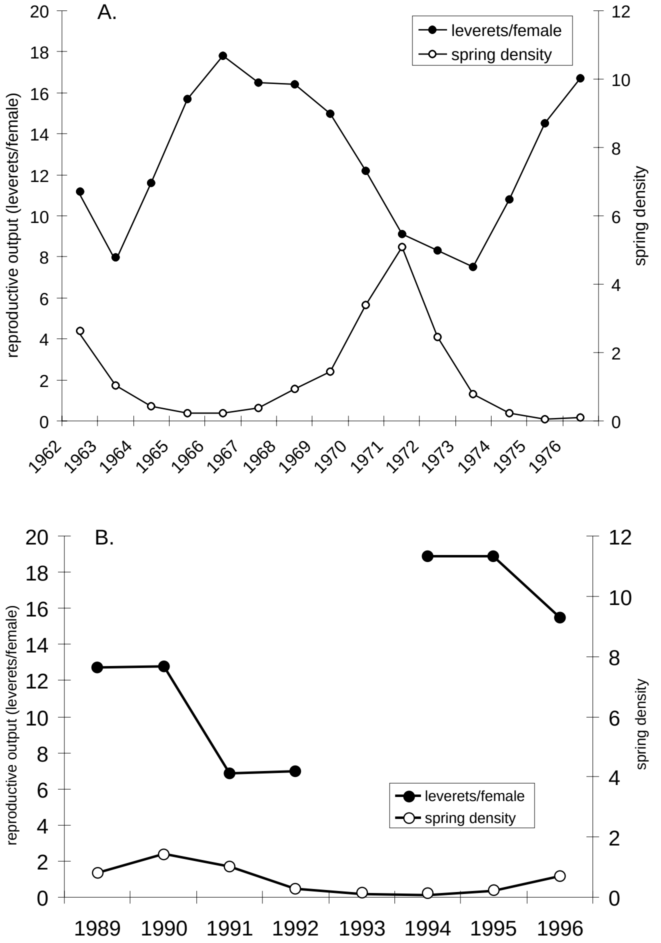

Figure 6.1—Reproductive output in two cyclic populations of hares: Alberta (1A) (Keith & Windberg 1978; Cary & Keith 1979) and Yukon (1B) (Stefan 1998). Total annual natalities were calculated by summing pregnancy rates x mean litter sizes for each litter.

this difference cannot account for the cyclic changes because the lowest reproduction occurs in the decline phase of the cycle when the proportion of adults is highest and average body mass is also high (Hodges et al. 1999; Hodges et al., in press).

Hares regularly lose mass overwinter (Newson and de Vos 1964). Keith (1981, 1990; Keith et al. 1984; Vaughan and Keith 1981) has argued that food shortage leads to the overwinter mass loss and negatively affects total natality in the subsequent summer. However, there is no clear link between

Table 6.2—Reproductive attributes of snowshoe hares from two cyclic populations.

Alberta[a]	Low 1964-1966 1975-1976	Increase 1967-1969	Peak 1961 1970-1971	Decline 1962-1963 1972-1974
Number of litters	4	4	3 to 4[b]	3 to 4[b]
Litter 1				
Range of parturition dates	30 April-15 May	29 April-15 May	4 May-20 May	15 May-20 May
Pregnancy rate	87.2	96.2	92.1	82.3
Mean litter size	3.0	2.8	2.6	2.7
Litter 2				
Range of parturition dates	4 June-19 June	3 June-19 June	8 June-24 June	19 June-24 June
Pregnancy rate	95.7	94.0	85.6	89.8
Mean litter size	5.7	5.3	4.8	4.4
Litter 3				
Range of parturition dates	9 July-24 July	8 July-24 July	13 July-29 July	24 July-29 July
Pregnancy rate	88.0	91.9	72.2	71.0
Litter size	5.1	5.6	4.6	3.7
Litter 4				
Range of parturition dates	13 Aug- 28 Aug	12 Aug-28 Aug	17 Aug-2 Sept	28 Aug-2 Sept
Pregnancy rate	77.3	63.9	14.5	5.7
Litter size	3.7	4.8	4.2	4.0

Yukon[c]	Low 1993-1994[d]	Increase 1995-1996	Peak 1989-1990	Decline 1991-1992
Number of litters	3 to 4[d]	3 to 4[d]	3	2
Litter 1				
Range of parturition dates	9 May-17 May	16 May-2 June	20 May-29 May	27 May-11 June
Pregnancy rate	100	100	89.9	87.5
Mean litter size	3.2	3.4	3.8	3.3
Litter 2				
Range of parturition dates	14 June-24 June	13 June-4 July	21 June-7 July	26 June-11 July
Pregnancy rate	100	100	96.4	90.1
Mean litter size	5.9	6.2	5.9	4.2
Litter 3				
Range of parturition dates	20 July-2 Aug	28 July-5 Aug	28 July-13 Aug	–
Pregnancy rate	100	100	84.5	0
Mean litter size	6.4	5.9	4.3	–

[a] Data are from Cary & Keith (1979) and Keith & Windberg (1978). Parturition dates are the range of mean dates for the years given and were calculated by adding 35 days per litter to the conception dates presented in Keith & Windberg (1978). Pregnancy rates were calculated from necropsies and palpation of live hares; litter sizes from necropsies.

[b] In 1971, 1972, and 1974, hares had only three litters. Average fourth litter pregnancy rates are calculated including these years.

[c] Data are from O'Donoghue & Krebs (1992) and Stefan (1998). Parturition dates are the range of dates from individual hares held in captivity for each litter. Pregnancy rates were calculated by palpation and litter sizes from hares held in captivity until birthing.

[d] Although there were four litters in Yukon during some years, no data were collected on the fourth litter or in 1993.

mass loss and total annual natality. Changes in total annual natality come from changes in pregnancy rates and litter sizes for later litters, whereas the effects of overwinter mass loss might be expected to be most pronounced for the first litter of the season. Hares do not store fat readily and are most nutritionally stressed when food is limited rather than showing delayed effects (Whittaker and Thomas 1983; Thomas 1987). Additionally, studies in the Yukon have not been able to demonstrate a relationship between either mass or mass loss and total annual reproductive output (O'Donoghue and Krebs 1992; Stefan 1998; C. I. Stefan and K. E. Hodges, unpublished). Neither the Yukon studies nor an Alberta study (Vaughan and Keith 1981) found an effect of mass loss on the size of the first litter.

Across both the cycle and the continent, the consistent patterns in reproductive output are: (1) The percentage of females pregnant declines with each successive litter group. Most females have at least two litters, but pregnancy rates for the third and fourth litters are highly variable. (2) Litter two is usually the largest and litter one the smallest. (3) Total annual natality is highest in the low phase, followed by increase, peak, and decline phases. The magnitude of variation is around 2.5 fold. (4) Reproductive output does not appear to be affected by the mother's skeletal size, mass, or parasite load. Age of the mother may affect ovulation rates. Stress levels are correlated temporally with and may contribute to reproductive changes. Overwinter mass loss and limited winter food supplies may reduce reproductive output through reductions in pregnancy rates and litter sizes, but the data are contradictory.

Survival and Causes of Death

Almost all hares die of predation. During the 1990 cycle in Yukon, 95% of the hares for whom cause of death could be positively identified were killed by predators, with approximately half of all deaths due to mammalian predators (Table 6.3) (Hodges et al., in press). Slightly lower estimates of predation were derived from previous cycles in Yukon (Table 6.4) (Boutin et al. 1986) and Alberta (Keith et al. 1977), but these analyses incorporated hares for whom cause of death could not be determined, which would lower the predation estimate. The 1980 and 1990 Yukon cycles showed that starvation and other non-predation deaths occurred during the late increase and peak and into the decline phases, counter to observations in Alberta that most starvation deaths occurred during the decline phase (Keith et al. 1984; Keith 1990). Most leverets that die are killed by predators (81% through a cycle) (O'Donoghue 1994; Stefan 1998), with deaths from exposure or maternal abandonment (starvation) occurring mainly during the decline phase.

The main predators of adult hares are coyotes, lynx, goshawks, and great horned owls (Table 6.3) (Keith et al. 1977; O'Donoghue et al. 1997; Gillis 1997, 1998; Hodges et al., in press). In contrast, leverets are predominantly preyed upon by small raptors (boreal owls, Harlan's hawks, kestrels, hawk owls) and small mammals (red squirrels, ground squirrels, weasels). No leveret kills by lynx or coyotes were observed during a cycle in Yukon (O'Donoghue 1994; Stefan 1998).

Table 6.3—Causes of death for hares near Kluane Lake, Yukon, 1988 through 1996. Years are counted from 1 April through 31 March. Values are percentages of the deaths of radiocollared juvenile and adult hares for which the cause was identifiable (and non-human caused) attributable to each mortality source. The mammalian, avian, and predation categories include kills by marten, weasels, wolves, eagles, hawk-owls, Harlan's hawks, and kills for which predation was certain but the predator species could not be identified. Non-predation deaths are hares that died of starvation, injury, or some other non-predation cause. Data are from C. J. Krebs, unpublished, and Hodges et al., in press.

	1988-89 increase	1989-90 peak	1990-91 decline	1991-92 decline	1992-93 decline	1993-94 low	1994-95 low	1995-96 increase
	Percent							
Coyote	20	27	6	51	18	57	48	26
Lynx	0	14	13	17	25	21	7	17
Goshawk	13	14	19	5	14	7	10	14
Great horned owl	0	5	15	12	11	0	2	6
Mammalian	7	0	2	0	11	0	10	14
Avian	20	5	22	4	4	7	5	6
Predation	13	23	9	11	18	7	19	14
Non-predation	27	14	15	0	0	0	0	3
% predation	73	86	85	100	100	100	100	97
n dead	15	22	54	107	28	14	42	35

Table 6.4—Snowshoe hare mortality data from 1978-1988, Kluane Lake, Yukon. Predator species were not identified for hare kills. Winter (November-April) 1986-1987 and summer (May-October) 1987-1988 data are from Krebs et al. 1992. The remaining data are from Trostel et al. 1987 (winter, December-May; summer, June-November). Data were recalculated to exclude hares for which the cause of death was unidentifiable. Values are the percentage of hares dead of each cause.

Summer	1978 increase	1979 increase	1980 peak	1981 peak	1984 low	1985 low	1987 increase	1988 increase
	Percent							
Mammalian	14	0	23	20	13	0	50	19
Avian	29	33	11	12	38	50	13	16
Predation	57	50	54	64	25	50	13	53
Non-predation	0	17	11	4	25	0	25	13
% predation	100	83	89	96	75	100	75	87
n dead	7	6	35	25	8	6	8	32

Winter	1978 increase	1979 increase	1980 peak	1981 peak	1984 low	1985 low	1986 increase	1987 increase
	Percent							
Mammalian	8	7	26	17	47	45	60	47
Avian	15	20	9	10	0	18	40	27
Predation	62	40	55	40	33	27	0	13
Non-predation	15	33	9	33	20	9	0	13
% predation	85	67	91	67	80	91	100	87
n dead	13	30	53	30	15	11	5	15

Hare survival rates have been measured from either trapping or radiotelemetry data. The trapping data yields less reliable estimates (Boutin and Krebs 1986). This method typically underestimates survival rates because hares are hard to trap (Trapp 1962; Boulanger 1993; Sullivan 1994) and have variable and sometimes high dispersal rates (Boutin et al. 1985; O'Donoghue and Bergman 1992; Gillis 1997; Hodges 1998). Survival estimates from trapping may also be biased by different amounts through the cycle, especially when comparing adult to juvenile survival or when estimating seasonal survival. These biases occur because dispersal and trapability vary seasonally, cyclically, and with age (Boutin et al. 1985, 1986; Krebs et al. 1986b; Boulanger 1993; Hodges 1998).

Snowshoe hare survival estimates from trapping suggest that survival is higher in the increase and peak phases than in the decline and low phases (Fig. 6.2a,b) (Krebs et al. 1986b; see also Keith and Windberg 1978). These data indicate that juvenile hares have lower survival than adults, and that whereas adult hares have lower overwinter survival than summer survival, juveniles may have lower survival during the summer. Snowshoe hare survival data from radiotelemetry only partially confirm these patterns (Fig. 6.3) (Krebs et al. 1995; Hodges et al., in press). Adult survival is indeed lower in the decline phase than at other times, but survival in the low phase is not noticeably different than survival in the increase and peak phases (Hodges et al. 1999). The survival estimates from radiotelemetry are much higher and more biologically reasonable; positive growth rates essentially cannot occur when 30-day survival is lower than 0.90 (corresponding to 25% survival through the year) (Hodges et al., in press), and the estimates from trapping therefore do not come close to an accurate estimation. Furthermore, even radiotelemetry estimates may be biased low (Haydon et al. 1999; C. J. Krebs and W. Hochachka, unpublished).

Survival of leverets to weaning is higher in the increase phase than in the decline phase (Stefan 1998). Post-weaning juvenile survival seems to depend on the litter group: in one year of an increase phase, juveniles in litters one and two survived as well as adults, whereas juveniles from litters three and four fared much worse (Gillis 1997, 1998). In this instance, most of the deaths occurred in the fall, when hares from later litters were simultaneously growing, changing coat color, and switching from forbs to woody browse. Snowshoe hare survival rates and causes of death are typically seasonal (Tables 6.3 and 6.4; Fig. 6.2) (Gillis 1998; Hodges et al., in press). Of the adult hares killed by lynx during a cycle in Yukon, 80% were killed between November and March (Hodges et al., in press). Most coyote predation occurred in October and November, and non-predation deaths occurred most often in late winter.

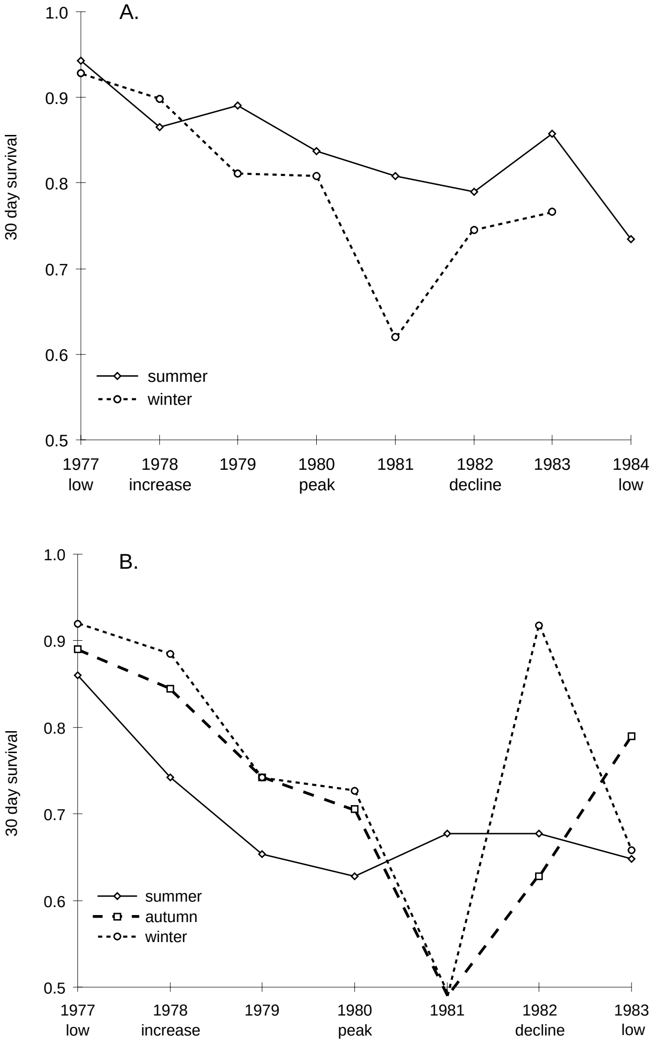

Figure 6.2—Snowshoe hare survival in Yukon, indexed by trapping. These data are mean survival values (2A) from four control areas, calculated from Jolly-Seber estimates using data in Krebs et al. 1986b. For adults, summer is April-September and winter is October-March; juvenile survival (2B) is broken into May-September (summer), October-December (autumn), and January-March (winter).

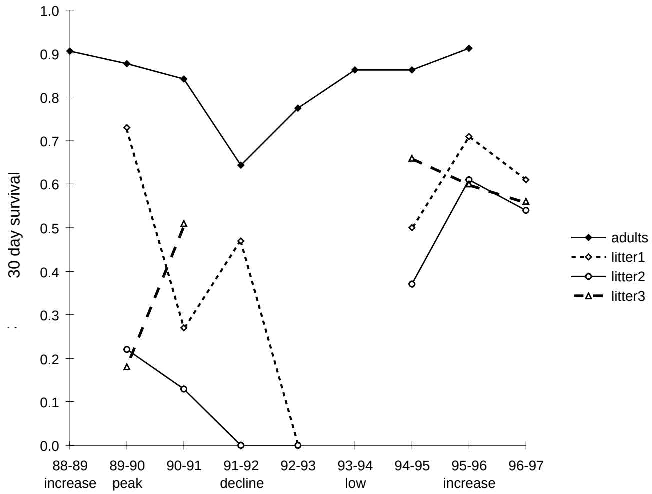

Figure 6.3—Radiotelemetry estimates of snowshoe hare survival in Yukon. Adult 30-day survival is based on the full year, whereas leveret survival is from birth to 30 days. The data are from Stefan 1998 and Hodges et al., in press.

There are anecdotal reports of massive overwinter die-offs, typically during the winter following peak fall densities (Severaid 1942; Keith 1963; C. Silver, unpublished; E. Hofer, personal communication; D. Henry, personal communication). Unfortunately, these reports are non-numeric, but they suggest that starvation or deaths due to disease are prevalent during that initial winter of decline. In some cases, dying hares had infections, some of which were due to *Staphylococcus aureus* (MacLulich 1937). There are hints that these die-offs occur following particularly high cyclic peaks. If such a pattern does exist, these cyclic declines may not be initiated by predation.

In addition to the cyclic patterns of survival, which are largely due to the numerical and functional responses of predators (Keith et al. 1977; Royama 1992; O'Donoghue et al. 1997, 1998), several other factors have been considered for their effects on the survival of hares (Table 6.5). The data on the effect of habitat type on hare survival are equivocal. In several studies, no effect of habitat on hare survival has been detected (Keith and Bloomer 1993; Cox et al. 1997), but other studies have observed lower survival in more open habitat types (Dolbeer and Clark 1975; Sievert and Keith 1985). Small patch size is associated with reduced survival in Wisconsin (Keith et al. 1993).

Avian predators kill hares in open areas more often than expected from the distribution of habitat types (Table 6.5) (Rohner and Krebs 1996; Cox et al.

Table 6.5—Correlates of snowshoe hare mortality. The following studies examined snowshoe hare survival or causes of death with respect to an individual factor to test whether the factor affected hare survival.

Factor and test	Effect of factor	Location	Reference
Habitat			
Deciduous vs. coniferous forest	No statistical effect on survival; potentially lower survival in deciduous habitat in Nov.-Dec.	Wisconsin	Keith & Bloomer 1993
Percent of hares killed by lynx in 4 densities of spruce, deciduous, and shrub habitats	No effect relative to habitat use by lynx	Yukon	Murray et al. 1994
Percent of hares killed by coyotes in 4 densities of spruce, deciduous, and shrub habitats	No effect relative to habitat use by coyotes in 2 yr; in 1 yr, more kills than expected in dense spruce	Yukon	Murray et al. 1994
Percent of hare kills in closed spruce, open spruce, and shrub habitats	More kills in shrub habitats with low canopy cover relative to availability	Yukon	Hik 1994, 1995
Percent hares killed by owls in 5 densities of spruce	More owl kills in open habitats relative to availability	Yukon	Rohner & Krebs 1996
Lynx hunting success in 4 densities of spruce, deciduous, and shrub habitats (kills/chase)	No effect	Yukon	Murray et al. 1995 (see also Murray et al. 1994)
Coyote hunting success in 4 densities of spruce, deciduous, and shrub habitats (kills/chase)	More successful in dense spruce than in open spruce	Yukon	Murray et al. 1995 (see also Murray et al. 1994)
Dense vs. sparse understory cover	Lower survival in areas with low understory cover	Wisconsin	Sievert & Keith 1985
Patch size (7 areas, 5-28 ha)	Lower survival in smaller patches	Wisconsin	Keith et al. 1993
Microhabitat: ≥2 brush piles/ha added to sites	No effect on hare survival rates	Wisconsin	Cox et al. 1997
Vertical foliage density	Coyote kill sites similar to habitat availability; raptor kill sites had lower foliage density	Wisconsin	Cox et al. 1997
Food addition			
Ad lib. Rabbit Chow added year-round to 36 ha areas	No effect on post-weaning juvenile survival	Yukon	Gillis 1997
Ad lib. Rabbit Chow added year-round to 36 ha areas	No effect on leveret or adult survival	Yukon	O'Donoghue 1994; Hodges et al., in press
Ad lib. Rabbit Chow added year-round to 9 ha areas	Survival higher in increase & peak, but lower in decline	Yukon	Krebs et al. 1986b
Downed spruce trees added to a 9 ha area	No effect on survival	Yukon	Krebs et al. 1986a
Ad lib. Rabbit Chow added to 25 ha areas over winter	No effect in 3 time periods; higher survival of fed hares in 1 time period	Manitoba	Murray et al. 1997
2.9-5.8 ha pens stocked with hares; 4/8 had food added; avian predators had access	Higher overwinter survival in pens with food added	Alberta	Vaughan & Keith 1981
Reproductive synchrony			
Days away from mean parturition date	Leverets near mean survived better	Yukon	O'Donoghue & Boutin 1995
Parasite load			
Hares given Ivermectin (anti-nematode) vs. control hares	No effect on survival in 3 time periods; higher survival of parasite-reduced hares in 1 time period	Manitoba	Murray et al. 1997

(con.)

Table 6.5—Con.

Factor and test	Effect of factor	Location	Reference
Hares given Ivermectin & Droncit (anti-cestode) vs. control hares	No effect on survival	Wisconsin	Bloomer et al. 1995
Hares given Ivermectin vs. control hares	No effect on survival	Yukon	Sovell 1993
Other hares			
2.9-5.8 ha pens stocked with hares; 4/8 had food added; avian predators had access	Survival lower at higher densities	Alberta	Vaughan & Keith 1981
Adults and 1st litter juveniles removed from 9 ha grids	Removal of adults improved juvenile survival in summer & fall	Yukon	Boutin 1984a
Body condition			
Condition and foot size smaller than mean for population	Lower survival of poor condition and smaller hares	Wisconsin	Sievert & Keith 1985
Bone marrow of hares killed by owls vs. shot hares	Owl killed hares were in better condition	Yukon	Rohner & Krebs 1996
Age			
2.9-5.8 ha pens stocked with hares; 4/8 had food added; avian predators had access	Juveniles survived less well than adults	Alberta	Vaughan & Keith 1981
% of the hares killed by owls in each age class	Owls preferred juvenile hares over adults relative to age structure in population	Yukon	Rohner & Krebs 1996
Season			
May-August, Sept-Dec, Jan-April	No effect of season on survival in low phase	Yukon	Hodges 1998
April-September, October-March	Adult survival higher in summer than in winter	Yukon	Krebs et al. 1986b

1997; Hodges 1998). Coyotes and lynx have kill rates comparable to the amount of time they spend in each habitat (Murray et al. 1994; O'Donoghue 1997), and their hunting success rates may vary with cover type (Murray et al. 1995). These predators select habitats, but it is unclear whether they select habitats that have the highest prey densities (Ward and Krebs 1985; Theberge and Wedeles 1989; Koehler 1990a; Murray et al. 1994; Poole et al. 1996) or habitats that are easier for them to traverse or hunt in (Murray and Boutin 1991; Murray et al. 1995; O'Donoghue 1997). Although these analyses suggest that hare survival may vary among habitat types, the definitive test for hares is per capita survival in each habitat. Hare survival in each habitat depends on hare density, predator presence, and the hunting success of predators within each habitat. Evaluating these parameters simultaneously will address the question of per capita hare survival as a function of habitat type.

The effect of food supply on hare survival has been studied by adding supplemental food to areas and comparing hare survival on these areas to survival of hares on non-supplemented areas (Table 6.5). Relative to control populations, hare populations on food-supplemented sites have shown reduced survival (Krebs et al. 1986b; Hodges et al., in press), similar survival (Krebs et al. 1986a; O'Donoghue 1994; Gillis 1998; Hodges et al., in press), and increased survival (Vaughan and Keith 1981; Krebs et al. 1986b; Murray et al. 1997). The potential effects of food supply on survival are two-fold: the distribution of food affects feeding locations and hare availability to predators, while the quality and abundance of the food affect physiology and starvation. The effects of food supply on hare survival may therefore depend upon the predation pressure. Starvation deaths mainly occur during and just after peak densities (Boutin et al. 1986; Keith 1990; Hodges et al., in press), which corresponds to the time when there is the least browse available (Smith et al. 1988; Keith 1990), but it is unclear whether starvation deaths are compensatory or additive to predation deaths. If the distribution of food forces hares into habitats that are riskier (as argued by Wolff 1980, 1981; Hik 1994, 1995), survival rates could be reduced, but there is a lack of consensus on the safety of various habitats for hares.

Snowshoe hare mortality patterns are: (1) Most hares of all ages are killed by predators, predominantly coyotes, goshawks, lynx, and great horned owls. (2) Starvation is most prevalent during high densities and into the decline phase. Anecdotal evidence of die-offs indicate that some declines involve more non-predation deaths than others; these die-offs may be linked to especially high cyclic peaks. (3) Survival is lowest during the decline phase and is typically lower in winter than in summer. Mortality rates are highest for leverets, intermediate for juveniles, and lowest for adults. Post-weaning juveniles from early litters may survive as well as adults. (4) Predators' hunting patterns and hunting success vary with habitat type, but few if any studies have shown clearly that per capita survival of hares varies among habitat types.

Dispersal

Snowshoe hares are known to disperse for distances up to 20 km (O'Farrell 1965; Keith et al. 1993; Gillis 1997; Hodges 1998). Assuming a home range size of 10 ha, a hare that relocated to an adjacent area would have to travel only 350 to 400 m from the center of the original range. This definition is probably inadequate because both juvenile and adult hares have been observed traveling >500 m a night but later returning to their home ranges. These forays away from home ranges last anywhere from overnight up to four to five weeks. It is unknown whether these trips are for mating, are precursors to dispersal, or are for some other purpose (O'Donoghue and Bergman 1992; Chu 1996; Gillis 1997; Hodges 1998). Given this range of types of long-distance movements, defining dispersal for hares is problematic.

Estimates of hare dispersal rates (movement greater than a given distance, or movement into trapping and/or removal grids) suggest that there may not be much difference in dispersal rate through the cycle (Table 6.6). Although immigration indices are biased because they may sample animals that were present but previously untrapped and because removal grids may attract animals (Dobson 1981; Boutin et al. 1985; Koenig et al. 1996), neither capture-recapture data nor the more reliable radiotelemetry data show a clear cyclic pattern in dispersal. Snowshoe hares have no clear season nor age of dispersal. The youngest recorded dispersers were 31 and 32 days old (respectively, Gillis 1997; O'Donoghue and Bergman 1992), and adults as old as three and four years have also dispersed (K. E. Hodges, unpublished). Both juveniles and adults disperse throughout the year, and there does not appear to be a sex bias in dispersal (Windberg and Keith 1976; Boutin 1979; Boutin et al. 1985; Keith et al. 1984, 1993; Hodges 1998). Hares that disperse appear to survive as well as hares that remain resident (Boutin 1984a; Keith 1990; Gillis 1997), but in an experiment transplanting hares to simulate dispersal, survival was lower for the first week following transplantation (Sievert and Keith 1985).

Table 6.6—Indices of dispersal rates of snowshoe hares. The trapping data may include animals that were resident but previously untrapped. The radiotelemetry data include animals that moved more than two home-range diameters and animals that died outside their observed home ranges.

Location	Method	Low	Increase	Peak	Decline	Reference
Alberta	Net ingress[a] (% of hares trapped new at time t & present at t + 1)	0-21	0-37	0-35	0-41	Keith & Windberg 1978
Yukon	% of hares new in spring population	52	40	42	40	Hodges et al., in press
Yukon	% of radiocollared hares dispersing	—[b]	4.0	2.8	2.7	Boutin et al. 1985
Yukon	% of radiocollared hares dispersing	4.7 (m); 8.4 (f)				Hodges 1998
Yukon	% of radiocollared post-weaning juveniles dispersing	—[b]	50	—[b]	—[b]	Gillis 1997

[a] Ranges are for multiple years within each phase.
[b] No data.

The proximate causes of hare dispersal are unknown, but several potential correlates have been examined. Keith et al. (1993) found little effect of habitat patch size on dispersal rates. Food addition treatments tend to attract immigrants, but there is no indication that hares on control areas disperse at a greater rate than do hares on food addition areas (Boutin 1984b; Hodges et al., in press). Hares that disperse may be lighter than hares that do not disperse (Windberg and Keith 1976; Boutin et al. 1985). That pattern could arise due to sampling (i.e., if juveniles and adults are not readily distinguished morphologically and more juveniles disperse), or it could indicate that lighter hares move to find better food resources or to avoid aggressive encounters (see also Graf 1985; Sinclair 1986; Ferron 1993). Settling rates of dispersing hares are higher when residents are few or have been removed, which could be due to aggression or through hares' assessment of resource availability (Keith and Surrendi 1971; Windberg and Keith 1976; Boutin 1984a).

Snowshoe Hare Behavior

Habitat Use Patterns

Because snowshoe hares eat conifers, they have been studied by foresters to minimize hare damage to naturally regenerating stands or plantations (Aldous and Aldous 1944; Cook and Robeson 1945; Borrecco 1976, unpublished; Radvanyi 1987, unpublished). Other studies have considered how to manage for snowshoe hares as a game species or as food for forest carnivores (Brocke 1975; Carreker 1985, unpublished; Thompson 1988; Koehler and Brittell 1990). These studies often have not considered the availability of different habitat types, thus making it impossible to determine hare habitat selection.

Most studies of hare habitat use have used fecal pellet plots, but some have used numbers per plot and others have used presence/absence per plot; the bias in the latter method may depend on the phase of the cycle. Additionally, hares excrete their pellets while they are active (Hodges 1998), so fecal pellet plots do not sample the resting habitats of hares, even though hares may spend approximately one-third of their time resting (Keith 1964; Hodges 1998). Other studies have used track transects and live trapping as indices of hares' habitat use patterns. Track transects assume that distance traveled is correlated with time spent, which may not be true if hares are traveling through certain habitats and spending time eating (and not creating tracks) in other habitats. Trapping may create a bias by attracting hares to baits. The three methods describe similar patterns of habitat use by hares (Litvaitis et al. 1985a), but the numeric estimates vary with the technique used.

Radiotelemetry may allow a more accurate estimation of hares' habitat use patterns, because it samples locations of active and inactive hares. However, triangulation does not allow fine-scale analysis of habitat use and walking to find hares visually may be slightly biased by startling hares into particular types of habitat (but see Hodges 1998).

Nonetheless, a fairly consistent picture of hare habitat use emerges from the various techniques (Table 6.7). Snowshoe hares typically use coniferous forests and often use areas with dense understory cover (Wolff 1980; Orr and Dodds 1982; Parker 1984, 1986; Thompson et al. 1989; Hik 1994; St-Georges et al. 1995). Hares' use of different stand types appears to be based primarily on the cover afforded by the stand, which varies with species composition and age, and secondarily on the palatability of the species present in the stand (Wolff 1980; Hik 1994). Hares essentially avoid clear-cuts, young stands of regrowth, and open areas. Hares also are more likely to use

Table 6.7—Snowshoe hares' use of regenerating forests. < and > indicate significance of $p < 0.05$.

Location	Measure	Species	Results	Reference
Stand age				
Ontario	Track transects	Picea spp. Betula papyrifera Populus tremuloides Abies balsamea	Use of 20 and 30 yr old stands >10 yr old & uncut stands > clearcuts and stands younger than 5 yr	Thompson et al. 1989; Thompson 1988
New Brunswick	Pellet plots Browsed twigs	Picea mariana Pinus banksiana Pinus resinosa	Jack pine: use in 8 yr old stands > 13 yr old Black spruce: use in 13 yr old stands > 8 yr old	Parker 1986
New Brunswick	Live-trapping Pellet plots	Picea spp.	Use of 10-17 yr old stands >uncut stands and stands younger than 10 yr	Parker 1984
Newfoundland	Track transects	Abies balsamea	Use of 40 yr stands >60 yr stands and uncut	Thompson & Curran 1995
Species				
New Brunswick	Pellet plots Browsed twigs	Picea mariana Pinus banksiana Pinus resinosa	Use of jack pine >black spruce >red pine (8 yr-old stands) Use of black spruce >jack pine (13 yr-old stands)	Parker 1986
Stand density				
Nova Scotia	Damage to trees	Abies balsamea	Use of dense stand (~32,000 stems/ha) >use of open stand (7,000 stems/ha)	Lloyd-Smith & Piene 1981, unpublished
British Columbia	Live-trapping Damage to trees	Pinus contorta	More hares caught & more trees damaged in heavily stocked stands (regressions, $p < 0.05$ for both)	Sullivan & Sullivan 1983; Sullivan & Sullivan 1988
British Columbia	% of trees damaged Number of wounds	Pinus contorta	Higher % damaged and more wounds/tree with increasing stocking density (regressions $p < 0.05$ for both)	Sullivan & Sullivan 1982a,b

regrowing stands with dense understory cover than uncut or even-aged stands with little understory cover (Monthey 1986; Thompson 1988; Thompson et al. 1989; Koehler 1990a,b). Conroy et al. (1979) suggested that habitat interspersion increased hares use of areas. Studies that have compared the distribution of hares to the availability of the various habitat types have found that hares actively select habitats with dense cover and avoid open habitats (O'Donoghue 1983; Litvaitis et al. 1985b; Hik 1994; St-Georges et al. 1995; Hodges 1998).

Several other factors may influence habitat use by hares. Hares may be more likely to use deciduous cover in summer than in winter because the presence of leaves helps to protect them from detection (Wolff 1980; O'Donoghue 1983; Litvaitis et al. 1985b). Similarly, hares are more likely to use areas of sparse cover when it is dark and moonless (Gilbert and Boutin 1991). Hares appear to use roughly the same habitats when active as when resting, although resting hares often use denser microhabitats (e.g., brushpiles, deadfall) (Ferron and Ouellet 1992; Cox et al. 1997; Hodges 1998). A few studies have found limited differences in habitat use between the sexes (Litvaitis 1990; Hik 1994). Several authors have suggested that juveniles use more open habitats than adults do (Dolbeer and Clark 1975; Boutin 1984a). This pattern could result from social interactions because juveniles are subordinate to adults (Graf 1985; Graf and Sinclair 1987).

Several authors have suggested that the densest habitats provide hares with refuges that protect them from predators during the low phase (leading to relatively dense pockets of hares) and that hares then disperse into more open habitats as their densities increase (Keith 1966; Wolff 1980, 1981; Hik 1994, 1995). The spatial scale of this phenomenon has not been well articulated, and studies of multi-annual patterns of habitat use have typically focused on small scale habitat shifts (i.e., m^2 rather than ha or km^2). That approach could be problematic if refugia are at a larger scale such as the patchiness that results from fires (Fox 1978; Finerty 1980).

The current evidence about refugia is equivocal. Several studies over three to five years have shown shifts in hare habitat use, typically with hares using more dense habitats as the population moves from the peak into decline years (Keith 1966; Wolff 1980; Hik 1994; Mowat et al. 1996). Two longer studies, however, although showing interannual variation, did not show regular cyclic patterns in hare habitat use (Fuller and Heisey 1986; Koonz 1988, unpublished). In Manitoba, very different proportions of hares were caught in each of four habitats through 16 years (Fig. 6.4) (Koonz 1988, unpublished), but neither the two low phases nor the two decline phases showed the same pattern of hare habitat use. Furthermore, the refugium hypothesis predicts that open habitats will not be used when hare densities

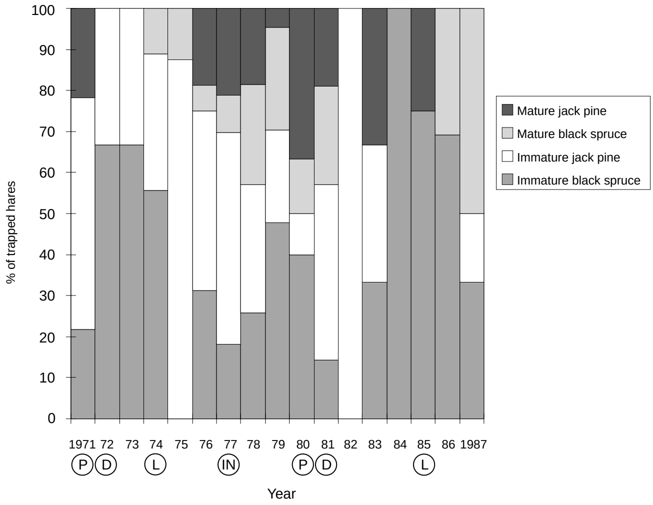

Figure 6.4—Snowshoe hare habitat use through the cycle. Koonz (1988 unpublished) trapped four grids in Manitoba, one in each habitat type; each grid was four ha. The y-axis gives the percentage of hares trapped in each habitat in each year, P = peak, D = decline, L = low, IN = increase.

are low, but several studies have shown that hares do use open habitats during population lows (Fuller and Heisey 1986; Hodges 1998). The refugium hypothesis also suggests that hare habitat shifts arise either through predation on hares in open habitats (Keith 1966) or through behavioral shifts by the hares (Wolff 1980). Yet experimental reduction of predation (and consequently predation risk) did not lead to differential habitat use or selection by hares during the low phase (Hodges 1998).

Only a few studies have explicitly considered hare demography within different habitat types or fragments of habitat. Hare survival may be higher in coniferous than in deciduous cover, especially in winter when deciduous trees lose their leaves (Keith and Bloomer 1993). Similarly, hares may have lower survival in habitats with little understory cover (Sievert and Keith 1985; Sullivan and Moses 1986), but spraying herbicides to reduce the cover of shrubs and ground vegetation and to encourage coniferous growth does not appear to affect hare densities, survival, or reproduction (Sullivan 1994, 1996). In Alberta, hares in fragmented woodlots displayed a numeric decline of reduced amplitude and had slightly higher total annual natalities than hares in nearby contiguous forest in two of four years, but both adult and juvenile survival showed no consistent differences between the fragmented and non-fragmented areas (Windberg and Keith 1978). In another study, Keith et al. (1993) examined demography in fragments of different sizes (5 to 28 ha); hare density and reproduction were unrelated to patch size, whereas survival was lower on small fragments. In all of these studies, predation was the main cause of death.

In summary: (1) Hares' habitat use is linked to dense understory cover rather than to canopy closure. (2) Hares appear to select habitats for cover rather than for food, but cover and food often covary. (3) Predator abundance does not appear to affect the habitat selection patterns of hares. (4) There is no clear shift of habitat use or selection through the cycle, counter to the suggestion that hares may concentrate in refugia during the low phase. Determining the appropriate scale for measuring refugia would help to substantiate this conclusion. (5) There is limited evidence to suggest that hares' survival and reproduction vary among different habitats, but the evidence is so patchy that this idea needs corroboration and further testing.

Diets and Food Limitation

Snowshoe hares eat a variety of coniferous and deciduous woody plants through the winter (Table 6.8) (see also Chapter 7). Regional studies have determined preferences of hares for certain plant species (Bryant and Kuropat 1980; Parker 1984; Bergeron and Tardif 1988; Smith et al. 1988; Hodges 1998), but because hares are distributed across the continent, their preferences vary with the local plant community. Studies on the diet selection of snowshoe hares indicate that hares choose species and twig sizes by responding to some combination of the nutritive and defensive chemistry of the twigs. Protein, fibre, secondary compounds, digestibility, and specific nutrients have all been suggested as arbiters of choice, and hares may be able to balance negative and positive attributes of the various food plants (Bryant and Kuropat 1980; Bryant 1981a,b; Belovsky 1984; Fox and Bryant 1984; Sinclair and Smith 1984b; Reichardt et al. 1984; Schmitz et al. 1992; Rodgers and Sinclair 1997; Hodges 1998).

Snowshoe hares survive on low-protein browse by eating a lot of it, passing it through the digestive system quickly, excreting fibrous pellets, and reingesting soft pellets to extract additional protein and other nutrients (Cheeke 1983, 1987; Sinclair and Smith 1984a). A corollary to this strategy is that hares tend to eat the same amount of food daily (Holter et al. 1974; Pease et al. 1979; Sinclair et al. 1982), and reductions in dietary energy or digestibility therefore lead to mass loss (Rodgers and Sinclair 1997). Additionally, hares have small fat reserves that are capable of maintaining them for only four to six days without eating (Whittaker and Thomas 1983), so mass loss occurs soon after hares start eating inadequate diets. Hares appear to need

Table 6.8—Diet of snowshoe hares and diameters of browsed twigs through the population cycle.

Index	Location	Species	Low	Increase	Peak	Decline	Reference
Mean diameter (mm) of browsed twigs[a]	Yukon	Salix glauca	2.4	2.0-2.7	3.3-3.6	1.5-2.8	Smith et al. 1988
		Betula glandulosa	1.7-2.4	1.8-2.1	2.3-2.5	1.7	
		Picea glauca	2.1	2.2	1.8-2.9	2.1	
Mean diameter (mm) of browsed twigs[a]	Yukon	Salix glauca	2.0-3.5				Hodges 1998
		Betula glandulosa	2.0-2.2				
		Picea glauca	2.6-3.7				
Mean diameter (mm) of browsed twigs[b]	Alaska	Shrubs, mainly Alnus crispa, Salix spp., Betula spp.	yr 1: 2.7-4.8 yr 2: 2.7-3.3	yr 1: 2.7-3.2	—	yr 1: 8.6-13.6 yr 2: 6.2-11.9 yr 3: 2.6-7.5	Wolff 1980
% surveyed twigs that were browsed overwinter on 11 sites[b]	Alaska	Shrubs, mainly Alnus crispa, Salix spp., Betula spp.	yr 1: 0-99; 7/11 sites 0-4 yr 2: 0-50; 7/11 sites 0-3	—	—	yr 1: 100 yr 2: 91-100 yr 3: 3-99	Wolff 1980
% of tagged twigs eaten by hares overwinter[a]	Yukon	Betula glandulosa	—	7-36	71-82	4	Smith et al. 1988
		Salix glauca		10-24	27	2	
		Picea glauca		4-21	8-13	3	
		Shepherdia canadensis		5-17	23-26	1	
% of trees with damage[a]	British Columbia	Pinus contorta		35	57-69	25-54	Sullivan & Sullivan 1988

[a] Ranges are for years within each phase.

[b] Ranges are for sites within each year; yr 1, yr 2, yr 3 refer to the first, second, and third year within each phase.

about 300 g of browse daily, and are better able to maintain their mass on 300 g of small rather than large twigs (Pease et al. 1979). Diets in which the mean twig diameter is >3 mm lead to mass loss, while diets composed of twigs with a mean diameter ≤ 3 mm are thought to be sufficient for hares to maintain their mass (Pease et al. 1979).

Despite this apparent threshold for identifying adequate food for hares, determining food availability is next to impossible (Sinclair et al. 1982, 1988). Hares' dietary composition fluctuates through the cycle (Table 6.8) and classifying food availability is difficult because twigs that a hare would not eat in the low phase are readily consumed during the peak phase. Snowshoe hares can maintain themselves for extended periods of time on sub-optimal foods (Sinclair et al. 1982) and overwinter mass loss is common (Newson and de Vos 1964; Keith 1990), so dietary stress is difficult to measure. Another problem is that hares may not use foods in habitats with high predation risk (Hik 1994), and many food plants show cyclic changes in secondary compound content, with high levels deterring hares from eating those twigs (Bryant 1981a; Fox and Bryant 1984; Sinclair et al. 1988). It is therefore difficult to define food for hares, let alone measure it.

When consistent food indices are applied across a cycle at any one site, most studies show cyclic fluctuations with food least abundant during the peak and early decline phases and becoming abundant during the low phase (Pease et al. 1979; Wolff 1980; Smith et al. 1988; Keith 1990). Some researchers have used such data coupled with estimates of hares' dietary needs to infer absolute food shortage at peak densities (Pease et al. 1979; Keith 1990), while other researchers have not found absolute food shortage (Smith et al. 1988; Sinclair et al. 1988). It is difficult to interpret the results of such studies because of the large error associated with browse estimation and the underlying problem of what food requirements are for hares. A similar difficulty applies to the question of whether hares might be relatively food limited during particular phases of the cycle.

An alternative to the food estimation problems has been to examine hares' dietary intake, physiology, or starvation rates as measures that might indicate nutritional stress. Hare diets do show cyclic fluctuations, with hares eating more large twigs during cyclic peaks (Table 6.8). Hares seldom eat bark at low densities, but will eat it when densities are high; most girdling of trees in conifer plantations occurs when hare densities are high (Radvanyi 1987, unpublished; Hodges 1998). There are also cyclic changes in hare mass losses overwinter (Keith and Windberg 1978; Keith 1990), but it is unclear whether overwinter mass loss is a regular facet of snowshoe hare biology or a sensitive reflection of food shortage. Neither the dietary shifts nor the mass loss patterns necessarily indicate food shortage of a magnitude that would affect demography. The strongest indication of potential food shortage is that starvation rates are higher at high hare densities and into the decline phase, but starvation deaths typically are a small proportion of total mortality and it is unknown if they are additive to or compensatory with predation deaths (Tables 6.3 and 6.4) (Keith et al. 1984; Trostel et al. 1987; Keith 1990; Krebs et al. 1992; Hodges et al., in press).

Food addition experiments circumvent some of these interpretation problems by artificially creating areas of abundant food. These studies have shown little to no effect of food addition on hare survival, reproduction, or cyclic dynamics, leading to the conclusion that food shortage is not a necessary component of cyclic declines (O'Donoghue and Krebs 1992; Stefan 1998; Krebs et al. 1986a,b, 1995; Hodges et al., in press; but see Vaughan and Keith 1981). It is possible that food addition treatments may attract hares (Boutin 1984b; Hodges et al., in press), thus leading to higher hare densities; it is therefore possible that the per capita food supply is still limiting.

Assessing per capita food supply and the effects of food limitation are difficult for snowshoe hares but overall the following patterns seem to hold: (1) Hares eat most woody species, selecting smaller twigs and twigs with fewer chemical defenses. There is a clear cycle in the size of twigs in hare diets, with the largest twigs eaten during high hare densities. (2) Hares at peak densities are capable of consuming a large proportion of the available browse, and hares may girdle trees when densities are high. (3) Food supplementation experiments have been unable to stop cyclic declines, and hare survival and reproduction are similar between food-supplemented and control sites. (4) Absolute food shortage does not appear to occur during hare cycles, but relative food shortage and changes in food quality may occur. (5) Starvation deaths do not seem to occur during the low and increase phases of the cycle, but starvation deaths may reflect either relative or absolute food shortage.

Movements, Home Ranges, and Activity

Snowshoe hares' home range sizes cannot be compared directly among studies because data have been collected differently. Locations have been obtained from trapping records (O'Farrell 1965; Tompkins and Woehr 1979; Wolff 1980), flushing hares repeatedly (Keith et al. 1993), triangulating on radiocollared animals (Boutin 1979, 1984c; Boulanger 1993; Hik 1994), and walking in to observe radiocollared hares (Ferron and Ouellet 1992; Allcock 1994; Chu 1996; Jekielek 1996; Hodges 1998). Additionally, researchers have used varying numbers of locations and time periods for estimating home ranges, the statistical methods of calculating home ranges are not comparable (Worton 1987; Harris et al. 1990), and different software packages may have different algorithms for the "same" statistical method (Lawson and Rodgers 1997). The following generalizations are therefore based on conclusions derived in each paper rather than on a reappraisal of numeric estimates.

Most home range estimates for snowshoe hares indicate that they use areas that are five to 10 ha, and often hares are located within a small subset of their total range (O'Farrell 1965; Wolff 1980; Hodges 1998). Males, but not females, appear to choose resting spots within a smaller area than the area in which they feed, but for both sexes there is a high degree of overlap between areas used for these different activities (Ferron and Ouellet 1992). Hares do not have territories and overlapping home ranges are common, but they may try to avoid encountering each other (Adams 1959; Boutin 1980, 1984c).

Female hares have smaller home ranges than males (Bider 1961; Ferron and Ouellet 1992; Hik 1994; Hodges 1998). Some authors have concluded that the sexes have similar home range sizes, but typically this conclusion is based on trapping data (O'Farrell 1965; Tompkins and Woehr 1979; Wolff 1980; see also Keith et al. 1993; Boulanger 1993). However, males appear to use much more area (assessed by radiotelemetry) than their trapping records indicate, whereas females are more likely to be trapped throughout their observed radiotelemetry ranges (Hodges, in press). The equal home range sizes in the trapping studies are therefore probably the result of a methodological bias that reduces the observed home range size of males.

Snowshoe hares may modify their home range sizes in response to breeding, food supply, population density, and predators. Females constrict the areas they use when they have very young litters (Bider 1961; Graf and Sinclair 1987; O'Donoghue and Bergman 1992; Allcock 1994; Jekielek 1996). Because mating is usually within 24 hours post-partum and females are synchronous breeders (O'Donoghue and Boutin 1995), males increase their movements and the area covered (about 5 fold) around the time when females are oestrous (Bider 1961; Chu 1996). Hares may have smaller home ranges at higher densities (Boutin 1984c; Hik 1994), but hares on sites with supplemental food do not appear to have smaller home ranges than hares on unsupplemented sites, despite higher densities (Boutin 1984b; Hodges 1998) and contrary to the typical pattern for other small mammals (Boutin 1990). Hares in predator exclosures may have smaller home ranges than unprotected hares (Hodges 1998), but Small and Keith (1992) found no differences in hares' home range sizes before and after red foxes were introduced to islands.

Hares are mostly active in twilight, although during summer in high latitudes they are active in daylight (Keith 1964; Boulanger 1993; Boulanger and Krebs 1996; Hodges 1998). Movement rates are high in summer, which may be related to breeding. Winter movement rates are low, possibly to minimize exposure to the cold (Hodges 1998). In both winter and summer, foraging movements do not appear to be related to hare density, and males have higher movement rates than females (Boulanger 1993; Hik 1994; Hodges 1998). Hares on food addition sites have movement patterns similar to hares on control sites, whereas hares protected from predators may respond by decreasing movements (Hodges 1998).

In summary: (1) Home ranges for hares are not well defined; hares often make extra-range movements, especially during the breeding season, and home-range overlap is high among hares. (2) Male hares move more and use larger areas than do females. (3) Neither food supply nor predator abundance have clear effects on hares' movement patterns and home ranges. (4) Hare density does not appear to have a strong effect on hares' movements.

Physiological Changes Through the Cycle

Several authors have argued that cyclic changes in hares' physiology (parasitic infestation, mass or mass loss, hematology, immunochemistry, fat reserves) might be partially causal of cyclic reproductive or survival changes (Keith et al. 1985; Boonstra et al. 1998a). For any of these factors to be causal, it must demonstrate the appropriate cyclicity and its impact on reproduction or survival should be of a magnitude comparable to the observed changes in these parameters.

Hares exhibit cycles in mass, overwinter mass loss, and mass-based condition indices (Newson and de Vos 1964; Keith and Windberg 1978; Hodges et al. 2000, in press). Mean spring mass of hares varied by approximately 200 g through the 1990 cycle in Yukon (K. E. Hodges and C. J. Krebs, unpublished). The lowest average mass was during the low phase and highest average mass was during the peak and early decline phases (see also Keith and Windberg 1978; Cary and Keith 1979). Keith and Windberg (1978) suggested that survival was lower for lower-mass individuals, but their use of trapping data for this point does not allow them to distinguish among dispersal, death, and low trapability. Elsewhere, lower-mass individuals were thought to have higher dispersal rates (Windberg and Keith 1976). Keith (1990) has suggested that hares with high overwinter mass loss have reduced reproductive output, but studies in Yukon have failed to find an impact of mass (or mass corrected for skeletal size) on reproductive output (Hodges et al. 2000, in press; C. I. Stefan and K. E. Hodges, unpublished).

Bone marrow fat content may be a more sensitive indicator of body condition, but it can only be ascertained after death. Hares dying of starvation have low marrow fat relative to hares in the rest of the population (Keith et al. 1984; Murray et al. 1997), and hares killed by predators may have lower marrow fat than hares in the population at large (Keith et al. 1984), but in some cases their marrow fat content is similar (Murray et al. 1997). Hares killed by great horned owls in Yukon had a slightly higher marrow fat content than did hares in the rest of the population (Rohner and Krebs 1996). Furthermore, food addition does not necessarily lead to higher marrow fat, despite the presumably better nutrition of hares on food-added sites (Murray et al. 1998). Other fat indices, such as kidney fat, may be better indicators of body condition than bone marrow fat content if they respond continuously to hare body condition rather than having some maximum value as bone marrow appears to.

Hares that are stressed might have reduced reproduction or survival rates. Chronic exposure to predators, nutritional limitation, or aggressive interactions potentially may lead to deleterious feedbacks in the hypothalamic-pituitary-adrenal system (Feist 1980; Boonstra and Singleton 1993; Boonstra et al. 1998a). Adrenal hypertrophy could index such stress, but the mass of adrenals show neither a cyclic pattern nor a clear relationship with hare density (Windberg and Keith 1976; Höhn and Stelfox 1977; Cary and Keith 1979), although food shortage can lead to lighter adrenals (Vaughan and Keith 1981). More sensitive examinations of the biochemistry (e.g., free cortisol levels, leucocyte counts, testosterone levels) indicate that hares are more stressed during the peak and decline phases than during the low phase (Dieterich and Feist 1980; Boonstra and Singleton 1993; Boonstra et al. 1998a). These biochemical responses have yet to be shown to be causally linked to changes in reproductive output or survival rates of hares.

Snowshoe hares are parasitized by many nematode and cestode species. *Trichuris leporis*, *Obeliscoides cuniculi*, *Dirofilaria scapiceps*, *Trichostrongylus* spp., *Nematodirus triangularis*, *Passalurus nonanulatus*, *Taenia pisiformis*, and *Eimeria* spp. can have relatively high infestation rates and/or show cyclic fluctuations (Erickson 1944; Bookhout 1971; Cary and Keith 1979; Keith et al. 1985; Sovell 1993). Juvenile hares often have heavier parasite infestations than adults (Maltais and Ouellette 1983; Keith et al. 1985; Keith et al. 1986; but see Erickson 1944). Theoretically, the presence of a cycle in parasite abundance can enhance the hare population cycle through sublethal effects (Ives and Murray 1997). Empirically, however, both correlative analyses and experimental manipulations of parasite load have failed to link parasite infestation levels and reproductive output (Cary and Keith 1979; Sovell 1993; Bloomer et al. 1995; Murray et al. 1998) or survival (Sovell 1993; Bloomer et al. 1995; but see Murray et al. 1997).

Explanations for the Cycle

Given the variety of physiological and demographic cycles that occur during the numeric hare cycle, not to mention the plant and predator cycles, it is no surprise that many explanations exist to explain the hare cycle. There are two basic tiers of explanation: (1) Describing the regular changes in reproduction, survival, and dispersal that contribute to the numeric cycle. (2) Explaining the factors that lead to changes in each of these demographic parameters. This second class of explanation is broadly divided into trophic interactions and behavioral and physiological effects.

Most of the numeric change is driven by changes in juvenile survival, followed by changes in adult survival and leveret survival (Keith 1990; Krebs 1996; Haydon et al. 1999). Adult survival is more important than juvenile survival during the decline phase, when juvenile survival is so low that small changes in it have little impact on the dynamics (Haydon et al. 1999). Changes in reproductive output and dispersal do not have a very large effect on numeric changes because hares are short-lived and have high fecundity. The breeding population is therefore determined more by recruitment than by adult survival (see also Lebreton and Clobert 1991). Because the young hares have to survive for six to nine months before breeding, their survival rates have more impact on the population than do their starting numbers.

Explaining the changes in each of the demographic parameters is the next step of explaining the numeric hare cycle, and it is here that many different stories are told (for reviews, see Finerty 1980; Keith 1990; Krebs et al. 1992; Boonstra et al. 1998b). Although hypotheses invoking intrinsic regulation, hare-plant interactions, or hare-predator interactions have been proposed (Chitty 1967; Krebs 1978; Finerty 1980; Bryant 1981a; Fox and Bryant 1984; Trostel et al. 1987), available evidence suggests that hares' interactions with both food plants and predators are integral to demographic changes (Keith 1963; Krebs et al. 1992, 1995, 1996; Hodges et al., in press). Keith (1974, 1981, 1990) has proposed that food shortage at peak densities initiates the decline through an increase in starvation rates, and that the high mortality that characterizes the decline phase is then largely imposed by predators. Recent experimental work in the Yukon does not substantiate the argument that food shortage initiates the decline, but shows instead that the cycle is most likely due to interactions of food plants, hares, and predators throughout the cycle (Smith et al. 1988; Sinclair et al. 1988; Krebs et al. 1986b, 1995; Hodges et al., in press). In Yukon, single factor manipulations of food and predators increased hare densities but failed to alter either the numeric cycle or the cyclic changes in survival and natality. However, the simultaneous addition of food and reduction of predators resulted in a hare population with higher survival, higher annual natality, and higher densities than control populations (Krebs et al. 1995; Hodges et al., in press).

Recent models have attempted to unify behavior, physiology, trophic interactions, and demographic changes. Hik (1994, 1995) proposed that hares change habitat types when faced with high predation risk, with safer habitats also being poorer in food. Under this scenario, the combination of high predation risk and voluntary dietary restriction cause low survival and poor reproduction during the decline phase. When risk is reduced and hares again use better habitats, survival and reproduction rebound (see also Keith 1966; Wolff 1980). Boonstra et al. (1998a) have expanded this model to suggest that hares also experience physiological stress (that may or may not be food linked) as a result of high predation risk, and that the stress can impact reproduction directly and through maternal effects. These models putatively explain the prolonged low phase of the cycle: hare densities stay low for several years, even after food plants have regrown and predator numbers have declined (Smith et al. 1988; Boonstra et al. 1998b; Hodges et al. 1999). If hares affect their nutrition and stress by behavioral changes, or if they experience maternal effects from mothers who were stressed during the decline phase, both reproduction and survival could be depressed (Hik 1994; Boonstra et al. 1998b). Another scenario invokes the sub-lethal impacts of parasites, suggesting that cyclic changes in parasite infestation rates and loads impact hare survival and reproduction (Ives and Murray 1997; Murray et al. 1997). These scenarios are worth testing; at present they are based mostly on chains of correlation and linking population level analyses together. To substantiate these arguments, it is critical to examine individual hares to determine the impacts of predation risk, nutrition, stress, and parasite load on hare survival and reproduction.

Conclusion

In the north, snowshoe hares undergo regular population cycles of five to 25 fold amplitude. Survival and reproductive changes are responsible for the numeric changes, but there is uncertainty about the relative impacts of the factors (food supply, stress, habitats, parasites) affecting these survival and reproductive changes. Differences in amplitude and duration of the cycle could possibly be due to variation in hare behavior or habitat characteristics, if these do affect demography. It would be valuable to develop models that show how much and what kinds of demographic variation are necessary to create cycles of different amplitudes and durations. Field studies that can explain patterns of demographic variation would also be useful.

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