# **SNOWSHOE HARE**

(Lepus americanus)



Source: Savage and Savage (1981)

# Prepared for Millar Western Forest Products' Biodiversity Assessment Project

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#### 1.0 CONSERVATION AND THE EFFECT OF ACTIVITIES

# **1.1 Introduction**

Snowshoe Hares (*Lepus americanus*) are found only in North America and are distributed throughout much of the boreal forest (Hoover *et al.* 1995, Figure 1). Active yearround, the hare performs most of its activities in the late evening and early morning. For the rest of the day, the hare tends to remain within its 'form', the shallow depression it has scraped out in the forest floor. Optimal form creation sites are located in stands with dense shelter of ground vegetation or downed woody debris (Bider 1974; Keith 1974; Hik pers. comm. 1999; Hodges pers. comm. 1999).

The population size of the Snowshoe Hare is known to be cyclic in nature (Keith 1974; Wolff 1980; Keith 1983; Smith 1983; Keith *et al.* 1984; Fuller and Heisey 1986). The relationship between Snowshoe Hare population size

and the availability of suitable vegetation for forage is a habitat factor closely monitored by biologists. It has been found that as the population size of the Snowshoe Hare increases, the amount of nutritious and palatable vegetation remaining to support it decreases. In particular, it is thought that the critical point occurs when the existing food supply is insufficient to support the population over winter (Keith 1974; Wolff 1980). This process is thought to initiate Snowshoe Hare decline as the lack of suitable forage may cause lower reproduction and juvenile survival rates (Keith 1983). The population sizes of obligate predator species such as Canada Lynx, Coyotes, and Northern Goshawks do not begin to decline at exactly the same time as the hare. Instead, they remain abundant for a period of time while Snowshoe Hares







become increasingly scarce (O'Donoghue et al. 1997; Hik pers. comm. 1999). Predator populations are large relative to hare populations and the number of remaining hares declines further in response to the significant predation pressure (Wolff 1980) that accounts for 75 to 90% of hare mortality (Keith et al. 1984; Sievert and Keith 1985; Keith and Bloomer 1993; Hodges pers. comm. 1999). Once the hare population density becomes sufficiently low, preferred vegetation is able to recover. Obligate predator population sizes respond to the scarcity of the principal prev species, and this decrease correspondingly reduces predation pressure. With a reduction in mortality from starvation and predation, the hares again successfully reproduce and recruit new members to the population, thus beginning the next population high (Wolff 1980; Smith et al. 1988).

# 1.2 Effects of Forest Management Activities

Although forest fires have traditionally created the early successional habitat required by Snowshoe Hares, clearcutting can also stimulate dense growth of shrubs and saplings that will provide ample cover and foraging opportunities (Keith and Surrendi 1971; Radvanyi 1987; Monthey 1986). Nevertheless, timber management activities have the potential to negatively impact Snowshoe Hare populations. As the juxtaposition of foraging and cover habitats is vital to these animals (Keith 1974; Keith et al. 1984; Radvanyi 1987), large-scale harvesting that alters their balance within the landscape can be detrimental. In addition, once logging has occurred, it may take up to 15 years for hares to again colonise the area since time must pass before sufficient understorey cover is able to be established (Todd 1983; Ferron et al. 1998). In particular, hares appear to prefer stands of age 20 to 30 years (Thompson et al. 1989).

Ferron *et al.* (1998) found that in the boreal forest, the hare reacts immediately to logging. It increased the magnitude of its daily movements and expanded its home range to avoid parts or all of the logged areas. It is important to point out, however, that no change in hare survival rate was identified as a consequence of logging (Ferron *et al.* 1998).



### 2.0 HABITAT USE INFORMATION

### 2.1 Food Requirements

#### Seasonal Food Requirements

Studies by Whittaker and Thomas (1983) and Thomas (1987) have found that a Snowshoe Hare's protein and lipid reserves are sufficient to support metabolism for four to six days, depending on the season. When food is not immediately available, the hares must begin to metabolise these reserves. For this reason, a constant supply of food is vital to their survival.

In winter, the hare uses the leaves or needles, buds, small twigs, and bark of woody shrubs and trees that exist above the snow-line (Bookhout 1965; Meslow and Keith 1971; Telfer 1972; Bider 1974; Keith 1974a; Wolff 1978; Ranvanyi 1987). The preferred winter foods in western Canada are willow, aspen, poplar, birch, lodgepole pine, and white spruce (Meslow and Keith 1968; Bider 1974; Keith 1974b; Walski and Maritz 1977; Sinclair et al. 1982; Sullivan and Sullivan 1982; Litvaitis et al. 1985; Parker 1986; Smith et al. 1988; Ferron and Ouellet 1992). In Alaska and boreal Canada, willow, birch, rose, and aspen leaves may comprise up to 76% of summer food (Wolff 1978; Smith et al. 1988). White spruce needles may make up more than 45% of the winter diet (Wolff 1978; Smith et al. 1988). In fact, Wolff (1980) noted that hares tend to move into dense spruce thickets during winter.

During summer, when herbaceous vegetation is abundant, Snowshoe Hares may take advantage of this nutritious resource (Parker 1984). Hares have also been known to dig feeding craters in the snow to access these plants, as long as the energetic cost of doing so does not outweigh the benefit of obtaining it as forage. Since energy expenditure increases with snow depth and density, hares generally do not create craters in snow deeper than 40 cm (Gilbert 1990). It is likely, however, that the animals will use this food resource most often during periods of population highs. During population lows, Snowshoe Hares are significantly influenced by predation and must remain within or close to thick shrubby vegetation, consuming shrubs and small trees. In fact, Wolff (1980) pointed out the habitats with abundant food resources but poor hiding cover conditions were not able to sustain the hare population into the winter.

#### Food Availability and Accessibility

The hare will consume virtually any plant material (Hodges pers. comm. 1999) and tends to browse based on availability and accessibility. During winter, a hare will most often consume the branches of shrubs and small trees within 50 cm of the ground. It will be able to reach higher as the snow pack develops, which makes the range of accessibility between 0 and 1.5 m above the ground (Bider 1974; Keith *et al.* 1984; Radvanyi 1987). The Snowshoe Hare prefers to feed on small twigs less than 3 mm in diameter (Pease *et al.* 1979; Wolff 1980) but may ingest stems up to 1.5 cm in diameter if thinner branches are not available (Keith *et al.* 1984).

#### Foraging Habitat Requirements

In summary, a Snowshoe Hare population requires the following characteristics for suitable foraging habitat:

- Habitat with plentiful herbaceous and shrubby vegetation;
- Preferable species composition, especially willow, aspen, birch, rose, and white spruce; and
- Shrub and young tree height of 0 to 1.5 m.



### 2.2 Cover Requirements

There are two types of cover habitats that may be required by Snowshoe Hares: thermal cover and hiding cover. These two cover habitats are discussed below.

#### Thermal Cover

Several authors have presented data displaying the Snowshoe Hare's capacity to tolerate low temperatures (Hart *et al.* 1965; Whittaker and Thomas 1983; Thomas 1987). Physiological adaptations include such factors as changes to the insulative properties of the fur and metabolic efficiency as well as a variety of other dietary and physiological responses. In fact, these mechanisms allow Snowshoe Hares to survive in the Yukon Territory and in Alaska where they are often exposed to temperatures  $< -40^{\circ}$ C (Hodges pers. comm. 1999).

Since thermal cover is not thought to influence hare habitat selection in Alberta (Hik pers. comm. 1999; Hodges pers. comm. 1999), it will not be considered further in the development of this HSM.

#### **Hiding Cover**

The Snowshoe Hare is a major prey item for many carnivores including Canada Lynx, Coyote, Marten, Red Fox, Northern Goshawk, and Great Horned Owl (Zielinski 1983; Parker 1984; Bateman 1986; Parker 1986; Halpin and Bissonette 1988; Ferron and Ouellet 1992; Small and Keith 1992; Murray *et al.* 1994). Therefore, it requires significant hiding cover to shelter itself from both avian and terrestrial predators. For this reason, the condition of the understorey represents the most important component of cover habitat (Meslow and Keith 1968; Wolff 1980; Buehler and Keith 1982; Litvaitis *et al.* 1985; Radvanyi 1987).

Optimal hiding cover conditions are provided by stands with dense, low-growing coniferous understoreys (Fuller and Heisey 1986) or dense shrub thickets (Wolff 1980; Rogowitz 1988; Wolff 1988; Todd pers. comm. 1999). In particular, as the population size begins to decline at the beginning of the population low, hares are found predominantly in stands with stem density greater than 22,000 stems per ha (Wolff 1980). Those with stem density > 40,000 stems per ha are most suitable, however (Ferron and Ouellet 1992). Ground cover of shrubby vegetation, trees with low height to crown, or downed woody debris can provide suitable hiding cover (Meslow and Keith 1968; Wolff 1980; Wolfe et al. 1982; Litvaitis et al. 1985; Sievert and Keith 1985; Parker 1986; MacCracken et al. 1988; Koehler and Brittell 1990; Koehler 1991). In particular, vegetation of height 1 to 3 m provides suitable hiding cover as it offers both vertical and horizontal visual interference, protecting the hare from its avian and terrestrial predators. The coniferous component of the understorey is significant since hares are active year-round and require foliage as shelter from predators both in summer and in winter. Therefore, although hares are able to use deciduous stands with dense understorey as cover in summer, the optimal condition is provided by coniferous, particularly spruce-dominated, stands with suitable understorey (Adams 1959; Brocke 1975; Dolbeer and Clark 1975; Wolff 1980; Lloyd-Smith and Piene 1981; Buehler and Keith 1982; Parker 1984; Litvaitis et al. 1985; Fuller and Heisey 1986; Parker 1986; Halpin and Bissonette 1988; MacCracken et al. 1988; Barta et al. 1989; Koehler 1990). Observations in Alaska by Wolff (1980) and in Minnesota by Fuller and Heisey (1986) have revealed that hares tend to use different types of cover habitat at different times during their ten-year population cycle. During population lows, they are found in stands that provide excellent hiding cover. This is due to the fact that, at this time, as many as 75 to 90% of hares may be killed by predators (Keith et al. 1984; Sievert and Keith 1985; Keith and Bloomer 1993; Hodges pers. comm. 1999). In contrast, during population highs, hares will use virtually all cover habitats and only stands that have little or no understorey will support fewer hares.

#### Snowshoe Hare HSM



Winter hare activity is highest where browse is available and where juxtaposition of browse and cover is high. Activity is the lowest in clearcuts where little sapling cover reaches above the snow (Monthey 1986). Hares are often found in ecotones between two habitat types (Ferron and Ouellet 1992). Depending on the point of time within the ten-year cycle, deciduous-dominated understories may not provide suitable hiding cover during winter. To accommodate the needs of the hares during population lows, it is essential that foraging areas are positioned in close proximity (within 200 to 400 m) to coniferous stands with dense understorey (Keith 1974; Conroy et al. 1979; Keith et al. 1984; Radvanyi 1987). This factor makes edge habitat valuable for Snowshoe Hares.

#### **Cover Habitat Requirements**

Hare populations require access to cover with the following features:

- At least 50 to 60% coniferous representation and
- Dense shrub understorey < 3 m high or the presence of abundant downed woody debris.

#### 2.3 Reproduction Requirements

Female Snowshoe Hares may have two to four litters per summer with the first litter born in May. An average litter size is three to five young and though the gestation period ranges from 35 to 40 days, a female may conceive again after 35 days gestation, even if the first litter has not yet been born (USDA 1998). Females scrape a natal form into the soil under the ground vegetation in which to give birth to the young. Although hares are not thought to seek a particular habitat type for breeding, they tend to have their young in well-sheltered areas within their home range (USDA 1998).

Hare litters remain at the natal site for about 2.7 days then separate into individual hiding spaces, continuing to disperse for approximately 20 days (O'Donoghue and Bergman 1992). Predation rates by Red and Ground

Squirrels on young are very high. In fact, 51% of litters have no known survivors 14 days after birth and 70% of this early juvenile mortality occurs during the first five days (O'Donoghue 1994).

# 2.4 Habitat Area Requirements

An average home range is estimated at 8 to 12 ha (Dolbeer and Clark 1975; Wolff 1980). It is thought that though the hares may use the entire home range occasionally, more than 80% of activity occurs within 3 ha of the total area (Wolff 1980). While a Snowshoe Hare tends to remain within its chosen home range, it is not considered a territorial animal and the home range of one may overlap significantly with that of another of either sex (Bider 1974; Ferron and Ouellet 1992).

There is controversy over the relative home range size of male and female Snowshoe Hares. Due to the polygonous nature of a male hare's lifestyle, its home range may be larger than that of a female and may actually encompass the ranges of several females (Bider 1974; Ferron and Ouellet 1992).

# 2.5 Landscape Configuration Requirements

The Snowshoe Hare generally selects habitat containing a mosaic of different foraging and resting sites. Most stands it frequents possess significant shrub cover of < 3 m in height. The habitat must contain sections suitable for foraging within 200 to 400 m of well-sheltered resting sites. Though it is best if these two habitat requirements could be fulfilled at the same location, edge habitat may be valuable since from there, the hares may be able to use adjacent habitat types (Radvanyi 1987). In fact, it has been noted by Sievert and Keith (1985) that Snowshoe Hares may elect to remain within dense coniferous hiding cover at the expense of optimal foraging conditions.



# 2.6 Sensitivity to Human Disturbance

While Snowshoe Hares commonly create difficulty for forest managers as they are destructive to young plantations (Corson and Cheyney 1928), our literature review did not reveal any evidence that humans negatively affect the Snowshoe Hare populations except through habitat alteration as previously discussed.

# 3.0 MODEL

# 3.1 Envirogram

A Snowshoe Hare requires plentiful food and suitable shelter within its home range (Figure 2). Forage consists of bark, buds, leaves, and thin branches of trees and shrubs. Hiding cover is provided by dense shrubby vegetation or downed woody debris.

# 3.2 Application Boundaries

Season:

This model produces SI values for use in winter. In particular, the variables used indicate the value of the forest as habitat during population lows. Since the requirements of the Snowshoe Hares are more stringent during population lows, one can assume that habitat supporting hares at this sensitive time will also provide suitable habitat during population highs.



Figure 2. Envirogram of the Snowshoe Hare based on available habitat information for HSM development.





- **Habitat Area:** Home range size used in home range smoothing is 12.6 ha for a Snowshoe Hare.
- **Model Output:** The model assigns a SI value for foraging and hiding cover habitat suitability to each 25 m pixel of forested habitat.

# 3.3 Model Description

The HSM for Snowshoe Hare habitat follows the structure of the envirogram (Figure 3). Foraging and shelter requirements must be fulfilled at all times. It is possible that the same stand will provide the hares with both of these habitat elements. In locations where this occurs, the value of both foraging and hiding cover is enhanced.

The  $SI_{food}$  considers the presence of white spruce, aspen, and birch trees and thick shrub cover, particularly willow and rose. As any of these materials can be consumed as forage, they are fully compensatory, though shrub species other than willow and rose are less

desirable and are, therefore, weighted slightly lower. Although hares may also consume herbaceous vegetation, during population lows, they select habitat based on provision of hiding cover instead of foraging habitat suitability. Herbaceous vegetation is generally lacking in hiding cover habitat. Therefore, it is no longer considered. Since tree branches must be within reach of the Snowshoe Hare to be valuable as forage, the tree species composition rating is modified by the height to live crown suitability. Tree species composition and height to live crown is approximated by habitat type for the purposes of this HSM.

The SI<sub>hiding</sub> consists of shrub coverage weighted by height, downed woody debris coverage, and habitat type (since young dense coniferous stands are preferred). Either shrubby vegetation, coniferous trees with low height to crown, or downed woody debris may be used as hiding cover. Since shrubs and small trees are considered more valuable for the purpose, downed woody debris cover is included as a bonus function, slightly improving the quality of the habitat.



Figure 3. HSM structure for the Snowshoe Hare within Millar Western's FMA area.



#### 3.4 Habitat Variable SIs

#### Food

The variables associated with food supply are the percentage of desirable tree species with low height to crown, shown by habitat type in Table 1 ( $S_{f1}$ ), willow and rose cover ( $S_{f2}$ ), and shrub cover ( $S_{f3}$ ). Suitability increases with willow and rose cover as shown in Figure 4 and with shrub cover as shown in Figure 5.

#### Cover

Optimal cover habitat is found in stands of habitat types shown in Table 2 ( $S_{h1}$ ). In addition, hiding cover habitat suitability is enhanced with density of the shrubby understorey ( $S_{h2}$ ) and coverage of downed woody debris ( $S_{h3}$ ). Suitability increases with shrub cover of height less than 3 m to a maximum at 50% coverage (Figure 6). The value of habitat increases with downed woody debris cover to a high point at 15% cover (Figure 7).

#### Table 1.Habitat type suitability as foraging habitat for Snowshoe Hare.

	Specific	Opening Clearcut	Developing		Forest		Old	
Broad			Regenerating	Young	Immature	Mature	Old	
Hardwoods	Aspen		1					
	Poplar							
	White birch		1					
Hardwood Mixed	Aspen-Pine		1					
	Aspen-White spruce		1					
	Aspen-Black spruce		0.75					
	Poplar-Pine		0.5					
	Poplar-White spruce		0.5					
	Poplar-Black spruce							
Softwood Mixed	Pine-Poplar		0.75					
	Pine-Aspen		1					
	White spruce-Poplar		0.75					
	White spruce-Aspen		1					
	Black spruce-Poplar							
	Black spruce-Aspen		0.5					
Conifers	Pine		1					
	White spruce		1	1				
	Black spruce							
	Larch							

#### Table 2. Habitat type suitability as hiding cover habitat for Snowshoe Hare.

	Specific	Opening Clearcut	Developing		Forest		Old	
Broad			Regenerating	Young	Immature	Mature	Old	
Hardwoods	Aspen							
	Poplar							
	White birch							
Hardwood Mixed	Aspen-Pine		0.5	0.5				
	Aspen-White spruce		0.5	0.5				
	Aspen-Black spruce		0.5	0.5				
	Poplar-Pine		0.5	0.5				
	Poplar-White spruce		0.5	0.5				
	Poplar-Black spruce		0.5	0.5				
Softwood Mixed	Pine-Poplar		1	1				
	Pine-Aspen		1	1				
	White spruce-Poplar		1	1				
	White spruce-Aspen		1	1				
	Black spruce-Poplar		1	1				
	Black spruce-Aspen		1	1				
Conifers	Pine		1	1				
	White spruce		1	1				
	Black spruce		1	1				
	Larch							







Figure 4. Snowshoe Hare foraging habitat suitability in relation to willow and rose cover within Millar Western's FMA area.



Figure 5. Snowshoe Hare foraging habitat suitability in relation to shrub cover within Millar Western's FMA area. Weighting: 0 - 25 cm = 0, 26 cm - 1 m = 1, 1.1 - 2 m = 0.5, > 2 m = 0.









Figure 7. Snowshoe Hare cover habitat suitability in relation to downed woody debris cover within Millar Western's FMA area.



# 3.5 Computation

It is our goal to create HSMs that allow the user to identify the potential impacts of proposed forest management strategies on foraging and cover habitats. Therefore, the outputs of the  $SI_{food}$  and  $SI_{hiding}$  calculations are considered individually to display trends in habitat availability.

#### Foraging Habitat Index

The  $\mathrm{SI}_{\mathrm{food}}$  is calculated for every pixel of forested habitat by the equation:

 $SI_{food} = S_{f1} + Max (S_{f2'} 0.8S_{f3});$ where  $SI_{food} \leq 1$ .

### Cover Habitat Index

The  $SI_{cover}$  is calculated for each pixel of forested habitat within Millar Western's FMA using the following equation:

$$\begin{split} \mathbf{SI}_{\text{cover}} &= \mathbf{S}_{\text{c1}} + \mathbf{S}_{\text{c2}} + \mathbf{0.2S}_{\text{c3}};\\ \text{where } \mathbf{SI}_{\text{cover}} &\leq \mathbf{1}. \end{split}$$

#### Adjustment of SIs Based on Proximity of Foraging and Cover Habitats

Cover and foraging habitats should be proximate to each other to be valuable. The suitability ratings of both foraging and cover habitats are, therefore, enhanced if coincident or proximate to each other. The literature review suggested that foraging and cover habitats should be no more than 200 to 400 m apart. Within a roving window or radius 300 m, the following adjustments are made to the SI<sub>food</sub> and SI<sub>hiding</sub> values:



### 4.0 EXTERNAL REVISION

Arlen Todd, wildlife biologist with Alberta Environment, Fisheries and Wildlife Management Division in Whitecourt, AB, provided comments on the Snowshoe Hare HSM on April 26, 1999. We made the following changes from the original document based on his advice:

- Timber harvesting activities may influence the Snowshoe Hare population more than we had indicated. The juxtaposition of different habitat types left following harvest is important to Snowshoe Hare habitat suitability. As well, the animals may not be able to use a stand until 15 years following harvest since sufficient understorey must again develop.
- The fact that hares use different cover types at different times in their ten-year population cycle was included in the literature review.
- Terminology used in the original document referring to 'open spaces' suitable for foraging was changed so that the importance of shrub and herb cover, instead of tree cover was stressed.
- Todd's own observations show that hares will use thick alder patches as hiding cover during peak population sizes. This fact was supported by literature and incorporated into the model.
- 5) The idea that the importance of thermal cover was over-emphasised was accounted for by removing the exponent that had appeared after  $SI_{cover}$  in the HSM equation.
- 6) Within the text, some references had been left out and these were added.
- 7) Todd believes that the food and hiding cover SIs may be able to compensate for each other during periods of population highs. Therefore, these two SIs were made partially compensatory.

Both David Hik (University of Alberta) and Dr. Karen Hodges (University of Memphis) have extensive experience with Snowshoe Hares and their habitat requirements in boreal Canada. They provided comments on the Snowshoe Hare HSM, which were received on June 15, 1999 and June 18, 1999, respectively. The following alterations were made from the original document:

- Both Hik and Hodges recommended that the SI for thermal cover be removed as they do not believe that it is required for the hare. They provided references on the hare's adaptations that allow it to tolerate low temperatures.
- 2) The reviewers provided additional references to help explain the relationship between browse availability, predator population size, and hare population cycling.
- Hodges mentioned that hares are able to use downed woody debris as hiding cover, under which forms may be created. This was included in the literature review.



# 5.0 LITERATURE CITED

- Adams, L. 1959. An analysis of population of Snowshoe Hare in northwestern Montana. Ecol. Monogr. 29: 141-170.
- Barta, R.M., L.B. Keith and S.M. Fitzgerald. 1989. Demography of sympatric arctic and Snowshoe Hare populations: an experimental assessment of interspecific competition. Can. J. Zool. 67: 2762-2775.
- Bateman, M.C. 1986. Winter habitat use, food habits and home range size of the marten, *Martes americana*, in western Newfoundland. Can. Field Nat 100(1): 58-62.
- Bider, J.R. 1974. Snowshoe Hare in the North Woods. Nature Canada 3: 21-24.
- Bookhout, T.A. 1965. The Snowshoe Hare in Upper Michigan: its biology and feeding coactions with white-tailed deer. Michigan Department of Conservation, Lansing, MI. Rep. No. 38.
- Brocke, R.H. 1975. Preliminary guidelines for managing Snowshoe Hare habitat in the Adirondacks. Trans. Northeast Fish and Wildl. Conf. 32:46-66.
- Buehler, D.A. and L.B. Keith. 1982. Snowshoe Hare distribution and habitat use in Wisconsin. Can. Field Nat. 96:19-29.
- Conroy, M.J., L.W. Gysel and G.R. Dudderan. 1979. Habitat components of clearcut areas for Snowshoe Hares in Michigan. J. Wildl. Manage. 43(3): 680-690.
- Corson, C.W. and E.G. Cheyney. 1928. Injury by rabbits to coniferous reproduction. J. For. 26: 539-543.
- Dolbeer, R.A. and W.R. Clark. 1975. Population ecology of Snowshoe Hares in the central Rocky Mountains. J. Wildl. Manage. 39: 535-539.
- Ferron, J. and J.P. Ouellet. 1992. Daily partitioning of summer habitat and use of space by the Snowshoe Hare in southern boreal forest. Can. J. Zool. 70: 2178-1283.

- Ferron, J., F. Potvin and C. Dussault. 1998. Short-term effects of logging on Snowshoe Hares in the boreal forest. Can. J. For. Res. 28: 1335-1343.
- Fuller, T.K. and D.M. Heisey. 1986. Densityrelated changes in winter distribution of Snowshoe Hares in northcentral Minnesota.J. Wildl. Manage. 50(2): 261-264.
- Gilbert, B.S. 1990. Use of winter feeding craters by Snowshoe Hares. Can. J. Zool. 68: 1600-1602.
- Halpin, M.A. and J.A. Bissonette. 1988. Influence of snow depth on prey availability and habitat use by the red fox. Can. J. Zool. 66:587-592.
- Hart, J.S., H. Pohl and J.S. Tener. 1965. Seasonal acclimation in varying hare (*Lepus americanus*). Can. J. Zool. 43: 731-744.
- Hik, D. University of Alberta. 1999. Personal communication.
- Hodges, K.E. University of Memphis. 1999. Personal communication.
- Hoover, A., J. Watson, J. Beck, B. Beck, M. Todd and R. Bonar. 1995. Draft Habitat Suitability Index Model: Snowshoe Hare. Foothills Model Forest, Hinton, AB.
- Keith, L.B. 1974a. Some features of population dynamics in mammals. Proc. Int. Congr. Game Biol. 11:17-58. Cited in Sinclair, A.R.E., C.J. Krebs and J.N.M Smith. 1982. Diet quality and food limitation in herbivores: the case of the Snowshoe Hare. Can. J. Zool. 60:889-897.
- Keith, L.B. 1974b. Hinterland who's who: Snowshoe Hare. Canadian Wildlife Service Catalogue No. CW 69-4/44.
- Keith, L.B. 1983. Role of food in hare population cycles. Oikos 40: 385-395.

#### Snowshoe Hare HSM



- Keith, L.B. and S.E.M. Bloomer. 1993. Differential mortality of sympatric Snowshoe Hares and cottontail rabbits in central Wisconsin. Can. J. Zool. 71: 1694-1697.
- Keith, L.B., J.R. Cary, O. J. Rongstad and M.C. Brittingham. 1984. Demography and ecology of a declining Snowshoe Hare population. Wildl. Monogr. 90. 43pp.
- Keith, L.B. and P.C. Surrendi. 1971. Effects of fire on a Snowshoe Hare population. J. Wildl. Manage. 35: 16-26.
- Koehler, G.M. 1990. Population and habitat characteristics of lynx and Snowshoe Hares in north central Washington. Can. J. Zool. 68(5):845-851.
- Koehler, G.M. 1991. Snowshoe Hare, *Lepus americanus*, use of forest successional stages and population changes during 1985-1989 in north central Washington. Can. Field Nat. 105:291-293.
- Koehler, G.M. and J.D. Brittell. 1990. Managing spruce-fir habitat for lynx and Snowshoe Hares. J. For. (Oct): 10-15.
- Litvaitis, J.A., J.A. Sherburne and J.A. Bissonette. 1985. Influence of understory characteristics on Snowshoe Hare management and conservation in North America. J. Wildl. Manage. 49(4): 866-873.
- Lloyd-Smith, J. and H. Piene. 1981. Snowshoe Hare girdling of balsam fir on the Cape Breton Highlands. Canadian Forest Resource Centre. Information Report. M-X-124. 8p.
- MacCracken, J.G., W.D. Steigers Jr. and P.V. Mayer. 1988. Winter and early spring habitat use by Snowshoe Hare (*Lepus americanus*) in south central Alaska. Can. Field Nat. 102(1): 25-30.
- Meslow, E.C. and L.B. Keith. 1968. Demographic parameters of a Snowshoe Hare population. J. Wildl. Manage. 32: 812-834.

- Meslow, E.C. and L.B. Keith. 1971. A correlation analysis of weather versus Snowshoe Hare population parameters. J. Wildl. Manage. 35: 1-15.
- Monthey, R.W. 1986. Responses of Snowshoe Hares, *Lepus americanus*, to timber harvesting in northern Maine. Can. Field Nat. 110(4): 568-570.
- Murray, D.L., S. Boutin and M. O'Donoghue. 1994. Winter habitat selection by lynx and coyotes in relation to Snowshoe Hare abundance. Can. J. Zool. 72: 1444-1451.
- O'Donoghue, M. 1994. Early survival of juvenile Snowshoe Hares. Ecology 75: 1582-1592.
- O'Donoghue, M. and C.M. Bergman. 1992. Early movement and dispersal of juvenile Snowshoe Hares. Can. J. Zool. V. 70: 1787-91.
- O'Donoghue, M., S. Boutin, C.J. Krebs and E.J. Hofer. 1997. Numerical responses of coyotes and lynx to the Snowshoe Hare cycle. Oikos 80: 150-162.
- Parker, G.R. 1984. Use of spruce plantations by Snowshoe Hare in New Brunswick. For. Chron. 60:162-166.
- Parker, G.R. 1986. The importance of cover on use of conifer plantations by Snowshoe Hare in northern New Brunswick. Can. Field Nat. 100(1): 74-77.
- Pease, J.L, R.H. Vowles and L.B. Keith. 1979. Interaction of Snowshoe Hares and woody vegetation. J. Wildl. Manage. 43(1): 43-60.
- Radvanyi, A. 1987. Snowshoe Hares and forest plantations: A literature review and problem analysis. Northern Forestry Service, Canadian Forestry Service. Information Report NOR-X-290.
- Rogowitz, G.L. 1988. Forage quality and use of reforested habitats by Snowshoe Hares. Can. J. Zool. 66: 2080-2083.



- Savage, A. and C. Savage. 1981. Wild mammals of western Canada. Western Producer Prairie Books, Saskatoon, SK. 209 p.
- Sievert, P.R. and L.B. Keith. 1985. Survival of Snowshoe Hares at a geographic range boundary. J. Wildl. Manage. 49(4): 854-866.
- Sinclair, A.R.E., C.J. Krebs and J.N.M Smith. 1982. Diet quality and food limitation in herbivores: the case of the Snowshoe Hare. Can. J. Zool. 60:889-897.
- Small, R.J. and L.B. Keith. 1992. An experimental study of red fox predation on arctic and Snowshoe Hares. Can. J. Zool. 70: 1614-1621.
- Smith, C.H. 1983. Spatial trends in Canadian Snowshoe Hare, *Lepus americanus*, population cycles. Can. Field Nat. 97: 151-160.
- Smith, J.N.M., C.J. Krebs, A.R.E. Sinclair and R. Boonstra. 1988. Population biology of Snowshoe Hares. II. Interactions with winter food plants. J. Anim. Ecol. 57: 269-286.
- Sullivan, T.P. and D.S. Sullivan. 1982. Barking damage by Snowshoe Hares and Red Squirrels in lodgepole pine stands in central British Columbia. Can. J. For. Res. 12: 443-448.
- Telfer, E.S. 1972. Browse selection by deer and hare. J. Wildl. Manage. 36: 1344-1349.
- Thomas, V.G. 1987. Similar winter energy strategies of grouse, hares and rabbits in northern biomes. Oikos 50: 206-212.
- Thompson, I.D., I.J. Davidson, S. O'Donnell, and F. Brazeau. 1989. Use of track transects to measure the relative occurrence of some boreal mammals in uncut forest and regeneration stands. Can. J. Zool. 67: 1816-1823.
- Todd, A.W. 1983. A review of furbearer production and trends in the hunting/trapping territory of the Lubicon Lake band. Alberta Fish and Wildlife Division, Edmonton, AB.

- Todd, A.W. Alberta Environment, Fisheries and Wildlife Management Division. 1999. Personal communication.
- USDA. 1998. Biological data and habitat requirements: Snowshoe Hare. Accessed from website: http://www.fs.fed.us/database/feis/
- Walski, T.W. and W.W. Maritz. 1977. Nutritional evaluation of three winter browse species of Snowshoe Hare. J. Wildl. Manage. 41(1): 144-147.
- Whittaker, M.E. and V.G. Thomas. 1983. Seasonal levels of fat and protein reserves of Snowshoe Hares in Ontario. Can. J. Zool. 61: 1339-1345.
- Wolfe, M.L., N.V. Debyle, C.S. Winchell and T.R. McCabe. 1982. Snowshoe Hare cover relationships in northern Utah. J. Wildl. Manage. 46(3): 662-670.
- Wolff, J.O. 1978. Food habits of Snowshoe Hares in interior Alaska. J. Wildl. Manage. 42(1): 148-153.
- Wolff, J.O. 1980. The role of habitat patchiness in the population dynamics of Snowshoe Hares. Ecol. Monogr. 50(1): 111-130.
- Zielinski, W.J., W.D. Spencer, and R.H. Barrett. 1983. Relationship between food habits and activity patterns of pine martens. J. Mamm. 64: 387-396.