SNOWSHOE HARE
WINTER RANGE

HABITAT SUITABILITY INDEX MODEL
VERSION 4

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1. INTRODUCTION

Habitat Suitability Index models (HSI) predict the suitability of habitat for a species based on an assessment of habitat attributes such as habitat structure, habitat type and spatial arrangements between habitat features. This HSI model for the snowshoe hare (*Lepus americanus*) applies to habitats of the Foothills Model Forest (FMF) in west-central Alberta. The intended use is to predict habitat suitability at landscape scales and over long-time periods. The model will be used to determine potential changes in snowshoe hare habitat area and carrying capacity throughout an entire forest management cycle (200 years). The model was primarily developed using literature review.

2. SPECIES DESCRIPTION AND DISTRIBUTION

Snowshoe hares occur only in North America and are found throughout most of the boreal forest (Dolbeer and Clark 1975). Snowshoe hares occur as far south as North Carolina and New Mexico in coniferous forests along the Appalachian Mountains in the east, and the Rocky Mountains in the west (Dolbeer and Clark 1975). The northern limits are at the Arctic Ocean along the Mackenzie River Delta (Banfield 1974). Snowshoe hares are found throughout Alberta and the FMF (Banfield 1974).

Snowshoe hares are one of the most common forest mammals in Canada and occur in pure coniferous, pure deciduous or mixedwood forests (Banfield 1974, Wolff 1980). Snowshoe hares change colour from grayish-brown in the summer to grayish-white in the winter (Banfield 1974) and because of this colour change are sometimes called varying hares. In areas where it rarely snows, snowshoe hares remain grayish-brown throughout the year (Banfield 1974). The snowshoe hare was named for its extremely large hind feet which act as snowshoes in the winter. These hares average 1.5 kg (Gadd 1995). Snowshoe hares are most active when they feed heavily just after sundown and just before dawn (Banfield 1974). During the day they rest quietly in sheltered areas (Banfield 1974). The most important habitat attribute for their survival is dense understory cover (Wolff 1980, Litvaitis et al. 1985).

Snowshoe hares are a major prey item for carnivores. Predators that depend heavily on snowshoe hares include coyotes (*Canis latrans*), marten (*Martes americana*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), great-horned owls (*Bubo virginianus*), and northern goshawks (*Accipiter gentilis*) (Wolfe et al. 1982, Bateman 1986, Halpin and Bissonette 1988, MacCracken et al. 1988).

In Canada’s boreal forests, snowshoe hares exhibit a 9-10 year population cycle (Boutin 1995). While the cause of these population fluctuations is not fully understood, predation and a limited food supply resulting in decreased reproductive rates and increased mortality are thought to be involved (Keith 1974b, Keith and Windberg 1978).

3. FOOD

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Snowshoe hares utilize different areas of their home range at different times of the year in relation to food availability (Litvaitis et al. 1985). Hares switch from a diet of mainly woody browse during the winter (de Vos 1964, Litvaitis et al. 1985) to a diet of forbs, grasses, and leaves during the summer (Wolff 1980). They are adapted to feed within a small vertical band of vegetation 0-1.5 m high (Bider 1974, Keith et al. 1984). During the winter, as snow accumulates, snowshoe hares utilize higher branches of trees and shrubs (de Vos 1964, Bider 1974, Keith et al. 1984). After many years of heavy and consistent browsing, a browse line becomes established below which edible twigs no longer grow (Bider 1974). Snowshoe hares seldom, if ever, dig in the snow for food (Bider 1974).

The range of foods consumed is dependent on availability and includes a large variety of different plant species. During the spring and summer, snowshoe hares forage in more open areas due to the availability of forbs and grasses (Wolff 1980). During the spring, when snow is melting and sap begins to flow, snowshoe hares strip bark off young trees (de Vos 1964, Bider 1974). Common forbs eaten include grass, dandelion (*Taraxacum* spp.) vetch (*Vicia americana*), other legumes, strawberry (*Fragaria* spp.), dewberry (*Rubus* spp.), fireweed (*Epilobium angustifolium*) and clover (*Trifolium* spp.; Dodds 1960, Keith 1974a). When these forbs and grasses dry up or are covered with snow, hares feed on the new growth of woody plants (Bider 1974).

During the winter, snowshoe hares feed on buds, small twigs, and the bark of a variety of woody shrubs and trees (Telfer 1972**,** MacCracken et al. 1988, Smith et al. 1988). Conifers consumed by snowshoe hares include pines, spruces, tamarack, hemlock (*Tsuga* spp.), cedars (*Thuja* spp.) and fir (Walski and Maritz 1977, Parker 1986). In addition to woody vegetation, snowshoe hares browse the needles and bark of many conifers (Wolff 1980) and may do considerable damage to coniferous seedlings (Parker 1984, Sullivan and Moses 1986). Pines tend to be preferred over spruces (de Vos 1964). Deciduous species consumed by snowshoe hares include alder, willow, labrador tea, dogwood, elderberry, blueberry, raspberry, birch, aspen, balsam poplar, buffaloberry, and rose (Walski and Maritz 1977, Parker 1986, MacCracken et al. 1988, Smith et al. 1988). Snowshoe hares prefer to eat deciduous over coniferous species but consume coniferous browse when deciduous species are lacking.

In spruce stands and jack pine (*Pinus banksiana*) stands in New Brunswick, sugar maple (*Acer saccharum*), alder, and beech were heavily browsed while red osier dogwood, hazelnut, and elderberry were moderately browsed (Parker 1986). Deciduous twigs were the preferred winter food of hares, however, spruce twigs comprised a considerable portion of their winter diet when deciduous twigs were scarce (Parker 1986). The winter diet of snowshoe hares in Kluane was dominated by bog birch, grey-leafed willow (*Salix glauca*), white spruce, and buffalo berry (Smith et al. 1988). Birch exhibits good terminal regrowth after being browsed and was most preferred by hares (63% of browse). Willow (26%) was eaten in mid-winter when birch was under snow. Spruce (14%) was not preferred and was eaten only when birch and willow were absent, and buffalo berry (20%) was consumed at low levels. A similar finding was also found in Kluane (Sinclair et al. 1982). In Maine, Canadian rhododendron, beaked filbert, witherod viburnum and grey birch composed 78% of browse species utilized by snowshoe hares in deciduous forests, and red spruce, paper birch, and red and striped maple composed 83% of the consumed browse in a coniferous forest (Litvaitis et al. 1985). Plant species generally unpalatable to snowshoe hares include cranberry (*Viburnum edule*), black spruce, Labrador tea (*Ledum groenlandicum*), snowberry (*Symphoricarpos occidentalis*), and honeysuckle (*Lonicera* spp.) (Keith et al. 1984).

Most hare browsing occurs within 0.5 m of the ground in Kluane during winter (Smith et al.1988). Twigs consumed are usually < 5 mm in diameter (Smith et al. 1988) but hares will occasionally consume twigs up to 15 mm in diameter (Keith et al. 1984).

4. COVER

In any forest cover type, understorey cover is the most important factor determining habitat suitability (Meslow and Keith 1968), especially during the winter (Wolff 1980, Buehler and Keith 1982**,** Wolfe et al. 1982, Pietz and Tester 1983, Litvaitis et al. 1985). The low critical temperature for hares during the winter is -8 °C, therefore, sufficient thermal cover is essential for their survival in areas which drop below -8 °C (Irving et al. 1957). Winter has been suggested as the critical season influencing hare populations (Keith and Windberg 1978**,** Pease et al. 1979). Hares increase their use of areas with dense understories during the winter in an attempt to reduce metabolic expenditures (Litvaitis et al. 1985). Low brushy coniferous and deciduous vegetation serve as protection from predators and as shelter from inclement weather in addition to supplying sufficient winter browse (Buehler and Keith 1982). Conifers provide superior thermal cover and reduce wind-chill (Litvaitis et al. 1985). Deciduous trees and shrubs, while providing sufficient cover during the summer, may not provide suitable cover during the winter after leaves are shed (Dolbeer and Clark 1975). During the summer, snowshoe hares move into areas that do not necessarily provide suitable winter habitat cover to feed on herbaceous forage (Wolff 1980, Litvaitis et al. 1985).

Many studies suggest that habitat dominated by conifers is preferred by snowshoe hares. In New Brunswick, snowshoe hare pellet densities were highest in 11-16 year old spruce plantations (Parker 1984). In Utah and Colorado, highest densities of snowshoe hares were in spruce-fir forests with a very dense understory (Dolbeer and Clark 1975). Few hares were in aspen forests with little understory cover (Dolbeer and Clark 1975). In Washington, snowshoe hares were more often in young lodgepole pine stands (< 25 years old) compared with mature lodgepole pine stands (46 or 80 years old) or old growth Englemann spruce/subalpine fir stands (100 years plus; Koehler 1990). Coniferous lowlands and plantations were classified as optimal habitat in Wisconsin (Buehler and Keith 1982). The distribution of snowshoe hare populations in the south is dependent on the availability of dense conifers for thermal cover and for protection from predators (Buehler and Keith 1982). Coniferous forests contained relatively high densities of snowshoe hares in New York (Brocke 1975), and Alaska (Wolff 1980).

Deciduous cover is important to snowshoe hares in some areas. Dense stands of immature hardwoods were the preferred habitat of snowshoe hares in Alberta (Meslow and Keith 1968), and parts of New York (Tompkins and Woehr 1979). In Alberta, the highest densities of hares during a low period were in thickets of small black spruce and alder at the edges of bogs, in patches of beaked hazel and in areas of dense trembling aspen and willow in all seasons (Keith 1966). In mixedwood forests in Alberta, snowshoe hares were in young deciduous dominated stands consisting of trees less than 20 cm diameter at breast height (dbh at 1.3 m), with high grass cover (during summer only) and high shrub/sapling and willow densities throughout the year (Roy et al. 1995). In the Prairies, snowshoe hares were abundant in heavy brush of parklands where combinations of thick rose, alder, hazelnut, saskatoon, snowberry, willow and young aspen occurred (Bider 1974).

Snowshoe hares utilizes a wide variety of forest types provided that adequate understory cover is available. The pattern of habitat use by snowshoe hares is based primarily on understory density not on species composition, however, species composition may influence population density (Litvaitis et al. 1985). Dense softwood understories support higher hare densities than hardwood understories because the former provide superior thermal and hiding cover (Litvaitis et al. 1985).

The relationship between understorey cover and snowshoe hare abundance has been studied extensively. Hares in the boreal-tundra transition zone were associated with closed forest cover located near a shrub edge (St-Georges et al. 1995). Areas with > 16 000 tree and shrub stems/ha were associated with a high abundance of snowshoe hares (Koehler 1990). A positive correlation was found between intensity of habitat use and percent cover of shrubs over 1 m tall (Pietz and Tester 1983). Open areas are considered poor quality habitat due to increased exposure to predation and less forage availability (Wolff 1980, Pietz and Tester 1983). Cover is critical in determining the abundance of hares in an area; the more cover in an area, the more hares/ha the area will sustain (Litvaitis et al. 1985). Predation rates of snowshoe hares were lower in dense understory patches than in patches with sparse understory (Wolff 1980).

Snowshoe hares utilize different types of cover for feeding and resting (Ferron and Ouellet 1992). Feeding sites had dense herbaceous plants, and less litter and moss than resting sites (Ferron and Ouellet 1992). In addition, feeding sites had higher densities of deciduous trees and shrubs, whereas, resting sites had higher densities of conifers (Ferron and Ouellet 1992). Utilization of an area as a feeding or resting site depends on the microhabitat structure and not on species composition (Ferron and Ouellet 1992). A trail or runway is frequently used by several snowshoe hares as a travel lane between feeding and resting sites (Ferron and Ouellet 1992).

Logging and forest fires in the boreal forest create early successional stages ideal for snowshoe hares (Radvanyi 1987). Following fire, regeneration of a stand provides dense shrub and sapling growth which provides optimal cover and abundant food (Keith and Surrendi 1971, Keith 1974a). Fifteen months after a fire burned an area near Rochester, Alberta, snowshoe hare density increased with increasing shrub and seedling densities (Keith and Surrendi 1971). Hares recolonized a burn three years later in another study (Meslow and Keith 1968). Spruce plantations in New Brunswick were extensively used by snowshoe hares once trees reached a sufficient height to provide the critical foliage cover < 2 m above ground (Parker 1984). Highest densities of snowshoe hares in both summer and winter were in 11-16 year old regenerating stands (Parker 1984). In areas with spruce-fir regeneration, hares began colonizing clearcuts 6-7 years after harvest and increased to peak levels after 20-25 years (Burgason 1977). In clearcut areas, snowshoe hare activity was concentrated along the edge of the clearcut rather than in the centre, however, slash piles can provide refugia for hares foraging near the middle (Radvanyi 1987).

5. REPRODUCTION

The breeding season occurs in mid March and lasts till September. Females are polyoestrous and may mate with several males during a cycle (Banfield 1974). Gestation is 36 days and an average litter of 4 leverets are born in May (Banfield 1974). Up to 4 litters are produced in a summer (Banfield 1974). Hares are precocious and are out on their own eating forbs within a week (Banfield 1974). Weaning occurs in two to three weeks (Banfield 1974).

6. HABITAT AREA

Snowshoe hares are not considered territorial but do have well defined home ranges. In spruce-fir forests of Colorado and Utah, where snowshoe hare populations remain relatively stable over time, 0.59 hares per hectare were found (Dolbeer and Clark 1975). In Maine, spring hare densities were 1.2 hares/ha in conifer dominated forests and 0.2 and 0.4 hares/ha in deciduous dominated forests (Litvaitis et al. 1985). The cyclic phenomenon which occurs in northern snowshoe hare populations results in a wide range of densities. In Alberta, hare densities were 2.4 hares/ha during a high period and 0.1 hares/ha during a low period (Keith 1966, Meslow and Keith 1968). In Alaska, 6 hares/ha were reported during a high period and less than 1 hare/ha during a low period (Wolff 1980).

There are conflicting reports on the size of male and female home ranges. Some studies found males had larger home ranges than females (Adams 1959, Bider 1974) and was explained by polyandrism (males obtain 2-3 females during the breeding season, so a male's home range covers the combined home range of the females; Bider 1974). One study found females had a 2-3 ha home range and males had a 7-8 ha home range (Bider 1974) and another study found female home ranges averaged 8 ha and males averaged 10 ha (Adams 1959). Other authors found no difference in size of male and female home ranges (Dolbeer and Clark 1975, Wolff 1980). The average home range of snowshoe hares in spruce/fir forests of the central Rocky Mountains was 8 ha (Dolbeer and Clark 1975). In Alaska, the home range over a 10 day period was 8.85 ha but approximately 80% of activity was concentrated in a 3 ha area (Wolff 1980).

7. HSI MODEL

7.1 MODEL APPLICABILITY

Species: Snowshoe hare (*Lepus americanus*).

Habitat Evaluated: Foraging, Thermal, and Protective Cover.

Geographic area: This model is applicable to the Foothills Model Forest in west-central Alberta.

Seasonal Applicability: This model produces HSI values for critical winter habitat.

Cover types: This model applies to all forest and non-forest habitat areas of the Lower and Upper Foothills, Montane and Subalpine Natural Subregions (Beckingham et al. 1996) since suitability is determined from structural characteristics within stands rather than classified forest stands directly. The model should also be broadly applicable to other habitat areas dominated by vegetation similar to that in this region, including pure deciduous, mixedwood and pure coniferous forest types, as well as wetland and riparian forests, meadows, shrublands, and areas regenerating after forest harvesting.

Minimum habitat area: Minimum habitat area is the minimum amount of contiguous habitat that is required before a species will live and reproduce in an area. Snowshoe hares use a wide variety of habitats around dense cover. It is assumed that snowshoe hares can use any habitat area which has suitable cover.

Model output: The model will produce Habitat Units (HU) of food and cover for each habitat area based on HSI value and stand or type area. HU are calculated by multiplying the HSI score with the area in hectares. The performance measure for the model is potential carrying capacity (snowshoe hares per hectare). Model output should be correlated to estimates of carrying capacity to verify model performance.

Carrying Capacity (Breeding Males per ha where HSI = 1.0): This value is applicable to the low population cycle in the FMF. Based on the literature (Keith 1966, Meslow and Keith 1968, Wolff 1980) this value is 0.5 snowshoe hares per hectare.

Verification level: The reliability of this model has not been evaluated against local data. The verification level is 1: model is based on literature and has not been tested.

Application: This HSI model is designed to assess habitat suitability for relatively large forest landscapes using generalized species-habitat relationships and stand-level vegetation inventory. Its purpose is to predict relative changes in snowshoe hare habitat supply at the landscape level over long time periods (200 years), for integration with forest management planning. The model is not designed to provide accurate prediction of suitability or use at the stand level. Approximate population size can be calculated by assuming linear habitat-population relationships, but the model is not designed to provide accurate population density estimates. Any attempt to use the model in a different geographic area or for other than the intended purpose should be accompanied by model testing procedures, verification analysis, and other modifications to meet specific objectives.

7.2 MODEL DESCRIPTION

The snowshoe hare habitat model assumes that winter cover and foraging habitat is limiting. In addition, the same habitat structures that provide cover are assumed to provide winter food.

7.2.1 Habitat Variables and HSI Components

Snowshoe hares require horizontal and vertical cover for protection from predators and inclement weather. Cover is determined from a combination of vegetation height, tree stem density, and sapling/shrub cover (Table 1). To support a population of snowshoe hares, an area must also have winter browse.

To provide security from avian predation and shelter during periods of deep snow, cover for snowshoe hares must extend to some height above the ground. The height at which visual obstruction of lateral foliage is useful depends upon the average snow depth in an area. This model assumes that in the FMF, visual obstruction above 3 m will be sufficient to provide protection for snowshoe hares for all snow depths. The model uses the maximum height of coniferous trees, deciduous trees, or shrubs to determine the first HSI component (S_1).

The second component, S_2, is determined from total tree stem density per hectare. In very dense stands, the density of tree stems in itself can provide suitable cover for snowshoe hares. Very dense stands would impede most avian and mammalian predators from successfully capturing snowshoe hares.

The final component is predicted from sapling cover ≤ 2 m in height and shrub cover. This component determines both cover and food supply for snowshoe hares. The combination of S_2 and S_3 will ensure that suitable cover and food will be present for snowshoe hares during the winter.

Table 1. Relationship between habitat variables and life requisites for the snowshoe hare winter range HSI model.

HSI Component	Life Requisite	Habitat Variable	Habitat Variable Definition
S_1	Winter Habitat	Maximum Layer Height (m)	Maximum coniferous or deciduous canopy height, sapling height or shrub layer height.
S_2	Winter Habitat	Tree Stem Density (stems/ha)	Sum of all tree stems ≥ 8 cm dbh.
S_3	Winter Habitat	Sapling cover ≤ 2 m in height and shrub cover (%)	Percent of ground covered by a vertical projection of sapling and shrub crown areas onto the ground. Includes only saplings ≤ 2 m in height and all shrubs.

7.2.2 Graphical HSI Component Relationships

S_1 Maximum height of tree or shrub layers in the stand is used to determine if vertical cover necessary for protection from predators is adequate. Heights of 0-1 m is unsuitable ($S_1 = 0$). Suitability increases from 1-3 m and all heights ≥ 3 m are optimal (Figure 1a).

S_2 Cover and food availability is assumed optimal ($S_2 = 1$) when total tree stem density is ≥ 8 000 stems per hectare. Stands with average stem densities between 3000 and 8000 stems/ha are assumed to have marginal value. Unsuitable cover habitat occurs when stands have total stem densities ≤ 3000 stems/ha (Figure 1b).

S_3 The snowshoe hare model will only give positive values for stands which have some sapling cover ≤ 2 m in height or shrub cover. The range at which the canopy closure gives optimum suitability is 80-100%.

Stands with less than 30% cover are unsuitable and stands between 30-80% have increasing suitability (Figure 1c).

7.3 MODEL ASSUMPTIONS

1. Areas that provide adequate food and cover during winter will also provide adequate summer food, cover, and reproductive habitat.
2. Winter cover habitat is equal to or more limiting than summer cover habitat.
3. In habitats dominated by conifers, an adequate amount of deciduous and/or herbaceous vegetation will be present to support snowshoe hares during the winter.
4. All shrub species provide the same quality of cover regardless of differences in growth form.
5. Habitats which provide abundant cover provide adequate winter food.
6. When trees are > 3 m tall, regardless of the presence of a shrub understorey, there will be appropriate vertical cover and winter food.
7. Snowshoe hare habitat is not affected by human disturbances, settlements, or roads.

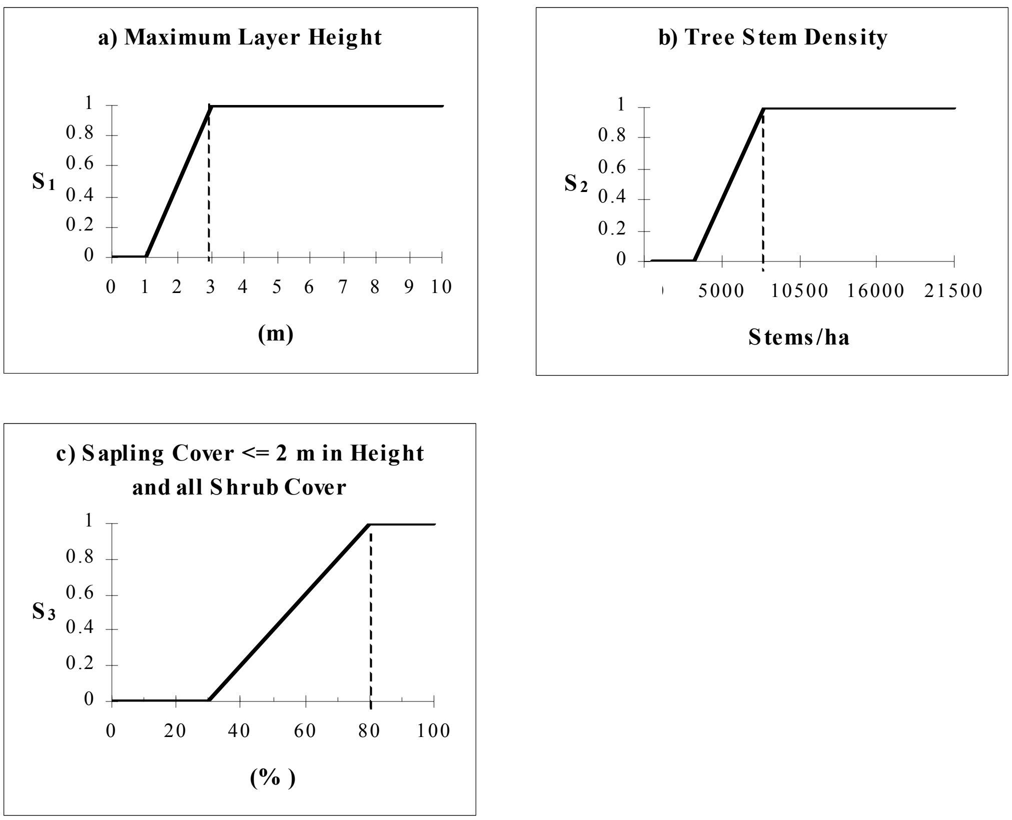

Figure 1. Graphical relationships between habitat variables and HSI components in the snowshoe hare model.

7.4 EQUATION

In this equation, S_2 and S_3 are compensatory so cover can be provided by a dense tree stem density or by a high shrub/sapling cover. The result is then multiplied by S_1, which ensures that an optimal cover height is present.

$$HSI = S_1 \times \text{Minimum}(1, S_2 + S_3)$$

8. SOURCES OF OTHER MODELS

The U.S. Fish and Wildlife Service developed an HSI model for snowshoe hares (Carreker 1985) and the Saskatchewan Forest Habitat Project released a model in their 1991 annual report.

Version 1 of this model was developed by Jody Watson. The model was modified by the senior author in a habitat modelling course at the University of Alberta (Version 2). Editing and formatting were performed by Wayne Bessie in 1996 (Version 3). New information from the literature was incorporated into the text during the fall of 1998 and modifications to the curves were made to better fit the new information (Version 4). This model was formulated from data and information obtained from a literature search and has not been tested in relation to local habitat and population data.

Model History

All of the HSI models for the Weldwood Forest Management Area have undergone several revisions, and they will be revised again as new information becomes available. Contact Rick Bonar for information about the most current version.

- Version 1 (1995) was written by Andrea Hoover and Jody Watson in cooperation with Melissa Todd and James Beck as part of a habitat modelling course at the University of Alberta.
- Version 2 (1996) was edited and reformatted by Wayne Bessie.
- Version 3 (1999) was revised by Karen Graham, Rick Bonar, Barb Beck, and Jim Beck to incorporate information from recent literature.

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