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HABITAT SUITABILITY INDEX MODELS: SNOWSHOE HARE

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by

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PREFACE

This document is part of the Habitat Suitability Index (HSI) Model Series [Biological Report 82(10)] which provides habitat information useful for impact assessment and habitat management. Several types of habitat information are provided. The Habitat Use Information Section is largely constrained to those data that can be used to derive quantitative relationships between key environmental variables and habitat suitability. This information provides the foundation for the HSI model and may be useful in the development of other models more appropriate to specific assessment or evaluation needs.

The HSI Model Section documents the habitat model and includes information pertinent to its application. The model synthesizes the habitat use information into a framework appropriate for field application and is scaled to produce an index value between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). The HSI Model Section includes information about the geographic range and seasonal application of the model, its current verification status, and a list of the model variables with recommended measurement techniques for each variable.

The model is a formalized synthesis of biological and habitat information published in the scientific literature and may include unpublished information reflecting the opinions of identified experts. Habitat information about wildlife species frequently is represented by scattered data sets collected during different seasons and years and from different sites throughout the range of a species. The model presents this broad data base in a formal, logical, and simplified manner. The assumptions necessary for organizing and synthesizing the species-habitat information into the model are discussed. The model should be regarded as a hypothesis of species-habitat relationships and not as a statement of proven cause and effect relationships. The model may have merit in planning wildlife habitat research studies about a species, as well as in providing an estimate of the relative suitability of habitat for that species. User feedback concerning model improvements and other suggestions that may increase the utility and effectiveness of this habitat-based approach to fish and wildlife planning are encouraged. Please send suggestions to:

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ACKNOWLEDGMENTS

Mr. John R. Cary and Dr. Lloyd B. Keith, University of Wisconsin; Dr. Michael R. Vaughan, Virginia Cooperative Fish and Wildlife Research Unit; Mr. Lamar A. Windberg, U.S. Fish and Wildlife Service; and Dr. Michael L. Wolfe, Utah State University, have provided critiques of an earlier draft of the snowshoe hare HSI model. The comments and suggestions of these individuals have added to the quality of this model, and their time and contributions are gratefully acknowledged.

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SNOWSHOE HARE (*Lepus americanus*)

HABITAT USE INFORMATION

General

The snowshoe hare (*Lepus americanus*) is indigenous to boreal forests throughout North America (Dolbeer and Clark 1975). Snowshoe hares consume herbaceous vegetation during the growing season and change to a woody diet in the fall and winter (Baker et al. 1921; Dodds 1960). Young forests with abundant understory that provide food and cover are preferred habitat (Grange 1932). Snowshoe hares exhibit approximate 10-year cycles of abundance and scarcity throughout much of their range, which have been attributed to hare-food interactions (Vowles 1972; Bryant 1981a) and hare-food-predator interactions (Keith 1974; Wolff 1980, 1981).

Food

During spring and summer, snowshoe hares feed on a wide variety of herbaceous vegetation, including grasses (Gramineae), legumes (Leguminosae) (Brooks 1955), sedges (*Carex* spp.), ferns (Polypodiaceae) (Dodds 1960), and the leaves of deciduous trees (Wolff 1978). Fall and winter foods consist of dead grass, small twigs, buds, bark, conifer needles, lichens, and mosses (Lycopodiaceae) (Severaid 1942).

Important factors determining diet composition include the density and frequency of occurrence, nutritive value, and palatability of plant species (Wolff 1978). Snowshoe hares can show a high degree of adaptation to the browse available and can feed on almost all species present (Telfer 1972). Foraging hares also can exhibit decided preferences (Criddle 1938) and the foods eaten in an area can be largely a function of availability (Pease et al. 1979). In Eastern Canada, deVos (1964) observed that whenever conifers were available in smaller quantities than deciduous species, the former were browsed more heavily, whereas Telfer (1972) found that deciduous species were more heavily browsed than the more abundant evergreen species. Preferential feeding by snowshoe hares can change plant composition and affect the future availability of plants (Cook and Robeson 1945; deVos 1964).

Snowshoe hares selectively browse on certain parts of a plant. Vowles (1972) noted that small twigs were the preferred food of hares in Alberta and referred to rough bark and stem wood as "starvation foods". There is a direct correlation between woody stem diameter and nutritional quality (Grigal and Moody 1980; Wolff 1980). Pease et al. (1979) found that captive hares in

Alberta primarily ate terminal twigs that were up to 3 to 4 mm in diameter when supplied with adequate quantities of browse. Keith (1974) believed browse ≤ 3 mm was essential for snowshoe hare survival. Wolff (1980) stated that snowshoe hares normally consume browse ≤ 3 mm in diameter and that 3 mm diameter twigs contained more nutrients than larger diameter twigs. The author suggested that the consumption of twigs with diameters > 3 mm was a sign of hares exceeding the habitat carrying capacity, resulting in their feeding on low quality forage. Grigal and Moody (1980) found the maximum stem diameter at point of browsing (dpb) to be 1 cm in Minnesota. Wolff (1980) found that hares at high density in Alaska ate browse that exceeded 1 cm dpb. A dpb of 1.5 cm was the maximum considered to be clipped by hares in Alberta (Vowles 1972; Pease et al. 1979).

The supply of high quality winter browse is one of the most crucial factors affecting snowshoe hare survival in northern areas (Walski and Mautz 1977). Vowles (1972) and Pease et al. (1979) determined that only part of the total standing biomass of woody browse is sufficiently digestible or nutritious to sustain snowshoe hares in Alberta. They estimated that 3,000 g (wet weight) of browse ≤ 1.5 cm in diameter must be available to a hare each day. A hare then can select 300 g of essential food in the form of choice terminal twigs, buds, and bark.

The nutritive quality of browse has been shown to be directly proportional to its palatability (Bryant 1981b). Bryant (1981a) suggested that high populations of snowshoe hares that deplete the supply of preferred foods are forced to feed on low preference browse species, which initiates a crash in the population even though the total supply of small diameter twigs has not yet been exhausted. Snowshoe hares in Alaska moved when they increased beyond the carrying capacity and temporarily depleted their food supply (Wolff 1980). Vowles (1972) noted an inverse relationship between the abundance of browse and snowshoe hares in Alberta. Browse abundance declined after several years of browsing by high populations of hares. When hare populations declined, browse abundance increased correspondingly.

Various species of, and different parts of, plants can produce resins that are unpalatable to hares (Bryant 1981a). Some plant species found to be unpalatable to snowshoe hares are listed in Table 1. Stephenson (1985) found that black spruce (<u>Picea mariana</u>) became more palatable to snowshoe hares in the Northwest Territories after the amount of unpalatable compounds in this species was decreased by fire.

<u>Water</u>

Snowshoe hares are believed to satisfy their water needs from dew and succulent plants in the summer and by eating snow in the winter (Hansen and Flinders 1969).

Table 1. Plant species found to be unpalatable to snowshoe hares.

Species	Location	Source
Balsam fir (*Abies balsamea*)	Michigan	Bookhout (1965a)
American linden (*Tilia americana*)		
Black cherry (*Prunus serotina*)		
Red-osier dogwood (*Cornus stolonifera*)		
Viburnum (*Viburnum cassinoides*)		
Winterberry holly (*Ilex verticillata*)		
Black ash (*Fraxinus nigra*)		
European red elder (*Sambucus pubens*)		
Black spruce (*Picea mariana*)	Alberta	Keith et al. (1984)
Labrador tea (*Ledum groenlandicum*)		
Viburnum (*V. edule*)		
Honeysuckle (*Lonicera glaucescens*, *L. involucrata*)		
Snowberry (*Symphoricarpos occidentalis*)		
Green alder (*Alnus crispa*)	Alberta	Cary (Department of Wildlife Ecology, University of Wisconsin, Madison; pers. comm.)

Cover

The presence of adequate understory cover is the primary determinant of snowshoe hare habitat quality (Buehler and Keith 1982; Wolfe et al. 1982). Several authors (Bookhout 1965a,b; Buehler and Keith 1982) suggested that cover availability is a more significant habitat factor than food availability. In addition to supplying winter browse, low brushy coniferous and deciduous vegetation serves as protection from predators and as shelter from inclement weather (Buehler and Keith 1982).

Many authors suggest that habitat dominated by coniferous vegetation is preferred. In Nova Scotia, Orr and Dodds (1982) found that snowshoe hare pellet densities in coniferous habitats were twice as high as those recorded in deciduous dominated cover. Coniferous lowland forests and conifer plantations were classified as optimum habitat in Wisconsin (Buehler and Keith 1982), swamp conifer was the most favorable habitat in northern Michigan (Bookhout 1965a,b), and young softwood swamp and fir thickets were preferred in Maine (Severaid 1942). Snowshoe hares in southern Ontario were mainly found in poorly drained or swampy areas in which there was heavy coniferous cover (deVos 1962).

Deciduous cover also can be an important component of snowshoe hare habitat. Although hares are mainly restricted to areas of red spruce (Picea rubens) in the Virginias, second growth forests of birch-beech-maple (Betula-Fagus-Acer) were found to harbor "fair" populations according to Brooks (1955), particularly when they had a rhododendron (Rhododendron maximum) or heavy evergreen heath understory. Alder (Alnus spp.) and willow (Salix spp.) thickets have been described as good winter cover in Wisconsin (Bailey 1946) and Alaska (Wolff 1980). Tompkins and Woehr (1979) reported that immature hardwood habitat, which provided abundant winter browse and cover, was preferred in New York. They concluded that snowshoe hares may be best adapted to such habitat, and use small conifer stands only out of necessity, due to the scarcity of hardwood stands since fire suppression and the prohibition of logging. Aspen (Populus tremuloides) stands with dense understories were believed to constitute marginal to good snowshoe hare habitat in Utah (Wolfe et al. 1982).

Apparently, a wide variety of forest types can be utilized if adequate cover is available. Pietz and Tester (1983) believed that cover quality is the crucial factor defining habitat preference regardless of the species composition of the stand. Grange (1932) stated that snowshoe hares can occupy fairly mature woodlands if beaver (Castor canadensis) were present, since hares make use of cuttings left from beaver foraging activities. Brushpiles were heavily used in New York and may have been important to hare survival where conifers were sparse or absent (Richmond and Chien 1976). Old burns containing dense brush and fallen logs and limbs can also be used extensively as cover (Grange 1932). Snowshoe hares are often most abundant in sapling and pole stage forest stands (Brooks 1955; Bookhout 1965a; Richmond and Chien 1976).

The relationship between the amount of cover and snowshoe hare abundance has been investigated by several workers. Adams (1959) subjectively evaluated cover conditions in Montana. On the basis of mean pellet density, he found that snowshoe hares preferred "heavy" cover [dense stands of early pole-size Douglas-fir (Pseudotsuga menziesii) with abundant ground litter of dead saplings and tree limbs] to "light" cover (open stands with no shrub understory), such as Ponderosa pine (Pinus ponderosa) stands. Using a density board to measure obstruction to lateral visibility in New York, Brocke (1975) found that "base cover" (used primarily for shelter) visibility ranged from 2% (98% obstruction) at 5 m to 0% (100% obstruction) at 20 m whereas "travel cover" (used for travel from base cover to foraging areas) visibility ranged from 14.7% (85.3% obstruction) at 5 m to 2.6% (97.4% obstruction) at 20 m. He suggested that lateral visibility is the single most important stimulus in selecting cover to avoid predation. Wolfe et al. (1982) determined that areas with horizontal vegetation densities of 40% (60% visibility) to 100% (0% visibility), as read from a profile board at a distance of 15 m, can be adequate snowshoe hare winter habitat in Utah.

Vertical foliage density also is considered an important factor in habitat preference (Wolff 1980). Brocke (1975) concluded that tree height was the most important factor determining base cover because it integrates the characteristics of stand density and obstruction to visibility. Heavy cover 3 m above the surface provides concealment from avian predators, whereas heavy cover < 1 m provides concealment from terrestrial predators (Wolff 1980). Pietz and Tester (1983) noted an increase in the number of snowshoe hare pellets with an increase in shrub cover > 1 m in height in Minnesota.

The abundance of forage can vary inversely with the density of tree cover due to shading, which inhibits the growth of food species (i.e., herbaceous vegetation and shrubs) (Adams 1959). In Nova Scotia, Orr and Dodds (1982) found a trend for reduced snowshoe hare densities in areas dominated by taller trees with dense canopies. They recorded lower hare use where trees were taller than 12 m and canopy closure exceeded 60% because adequate cover and food were not as available. Similarly, Richmond and Chien (1976) noted that snowshoe hares did not significantly use Red pine (P. resinosa) plantations in New York where most of the lower limbs were either dead or missing and the thick canopy inhibited the growth of understory vegetation. In Utah, however, the removal of aspen overstory in areas of dense understory resulted in a marked decrease in hare use, suggesting that overstory also is an important habitat component (Wolfe et al. 1982). In Michigan, cover provided by the understory was found to be more important in defining snowshoe hare use than the cover provided by the overstory (Bookhout 1965a).

Reproduction

Criddle (1938) described a snowshoe hare nest as a shallow depression in dead leaves beneath a leaning tree or among scrub, while Cory (1912) described the nest as being composed of a mass of grass covered with fur and concealed under a bush or weeds. However, other workers contend that no nest is constructed (Adams 1959; Keith, Department of Wildlife Ecology, University of Wisconsin, Madison; letter dated January 1985). Adams (1959) found a small pile of evergreen saplings that was used as a "nursery".

Young snowshoe hares leave the location of birth within a few days and scatter into the surrounding undergrowth (Criddle 1938; Rongstad and Tester 1971). Young snowshoe hares in Minnesota spent days in separate hiding places and came together once a night to nurse (Rongstad and Tester 1971). Severaid (1942) found that captive snowshoe hares began to feed on vegetation at 10 to 12 days of age and suggested that wild hares become independent at 2 weeks.

A shortage of winter browse can affect the reproductive performance of females throughout the summer despite adequate spring herbaceous growth, which in turn affects the survival of juveniles in the summer (Vowles 1972, Vaughan and Keith 1981). Vowles (1972) also suggested that light-weight juvenile hares suffer high mortality during the transition period between a summer herbaceous diet and a fall diet of browse.

Interspersion and Composition

Snowshoe hares travel via runways that are used and maintained year-round (Grange 1932; Criddle 1938). Runways are used when crossing open areas from one stand of dense vegetation to another (O'Farrell 1965) and allow quick escape from predators through thick underbrush (Criddle 1938). Snowshoe hares also are known to swim back and forth across rivers (Criddle 1938; Hunt 1950). Travel through more open areas is usually done only at night (Aldous 1937; Bider 1961; Brocke 1975).

Snowshoe hares occupy fairly well-defined home ranges that can overlap considerably. Most authorities believe snowshoe hares have an active core area of 2 to 3 ha, and that 8 to 10 ha are the limits of home range (Wolff 1980). However, home ranges probably vary with the cover type (Severaid 1942). Criddle (1938) believed that the radius of the home range measures only a few hundred yards in dense woods but a mile or more in areas dominated by sparse underbrush.

Habitat interspersion is an important factor determining snowshoe hare density and activity. Tompkins and Woehr (1979) reported that hare density in an area of numerous cover types was nearly twice that of an adjacent area of less numerous cover types in New York. In a patchy environment, which provides dense cover in winter and more open foraging areas in summer, snowshoe hares are able to shift seasonally to a change in diet and to take advantage of changing environmental conditions (Wolff 1980). In Montana, however, Adams (1959) found that as food growing in areas of dense cover was used up, hares were attracted away from cover to feed and became more vulnerable to predation. He concluded that snowshoe hare distribution was a result of adjustments among the spatial relationships of food, cover, and predators.

Habitat selection can be influenced by the season of the year. Although forage was plentiful in summer, Bider (1961) found that snowshoe hare movements and ranges during the rest of the year were influenced by the availability of certain plant species in Quebec. However, in Alaska, Wolff (1980) found that snowshoe hares moved to more open areas in the summer, due to the scarcity of summer foods in dense winter refuge areas. He also suggested that seasonal movements were in response to forage preferences. Pietz and Tester (1983) noted that snowshoe hares in Minnesota used areas of deciduous vegetation more often during snow-free periods, probably due to a dietary shift.

Snowshoe hares occasionally leave areas of cover to forage. Vowles (1972) noted that hares of high population density crossed large fields to feed at grainaries and entered farmyards to feed on hay bales and shelterbelts in Alberta. However, open areas are apparently used most often when they are associated with cover. Wolff (1980) in Alaska and Wolfe et al. (1982) in Utah found that snowshoe hares moved to more open areas to forage during the summer growing season when adequate cover was available. Snowshoe hares in Newfoundland entered open areas by traversing alder beds or broken stands of conifers in winter (Dodds 1960). Feeding is often concentrated in vegetative community edges that supply both food and nearby escape cover (Cook and Robeson 1945; Richmond and Chien 1976; Conroy et al. 1979).

Cover continuity is an important habitat factor. Brocke (1975) found that small, discontinuous patches of forest were used as travel cover but not as base cover in New York. Wolfe et al. (1982) noted that snowshoe hares in Utah were concentrated in small islands of forested habitat due to a clumped distribution of young fir trees. The use of a mature forest is often dependent primarily upon the interspersion of openings (i.e., cutover areas and areas of young growth caused by fire) (Dodds 1960; Grange 1965). Brocke (1975) suggested that the maximum width of continuous base and travel cover tracts should not exceed 200 m unless interspersed with openings of browse. Conroy et al. (1979) recommended that cover should not exceed a distance of 200 to 400 m from cutover areas.

Adequate interspersion of cover is often most critical during the winter. Conroy et al. (1979) determined that cedar-fir (Thuja occidentalis-A. balsamea) cover in Michigan acted as "reservoirs" where snowshoe hare populations persisted during the winter. Baker et al. (1921) in Utah and Criddle (1938) in Manitoba noted that snowshoe hares scattered in the spring and summer but congregated in thickets after heavy winter snows. Snowshoe hares in Alaska distributed themselves evenly throughout all suitable habitats during summer (Wolff 1980). In winter, hares moved to an area that provided 75% vertical foliage density (25% visibility) at all levels up to 4 m, as measured from a distance of 3 m using a checkerboard placard. Grange (1965) noted that snowshoe hares were forced to move when deep snows covered pine trees that were 1.1 m high in Minnesota. Snowshoe hares in Quebec were more active in summer due to the cover provided by an increase in canopy density at that time (Bider 1961). Snowshoe hare tracks were found crossing a large plain in Manitoba when hares were leaving outlying bushes and the less dense parts of large woods for more dense areas in the fall (Criddle 1938).

Population pressures also can affect the availability of adequate cover. Dispersal movements have been observed when young snowshoe hares augment populations in large numbers (Adams 1959; Dolbeer 1972). Due to the discontinuous nature of snowshoe hare habitat in the Western United States, juvenile hares can be forced to disperse into less favorable (more open) habitat, resulting in high mortality (Dolbeer 1972; Dolbeer and Clark 1975). In Alaska, the boreal forest consists of a mosaic of spruce, deciduous, mixed coniferous-deciduous, and willow-shrub communities. This heterogeneity allows snowshoe hares to disperse and become established in less favorable habitat during a population increase (Wolff 1981). During population declines, snowshoe hares avoid local extinction by seeking refuge in dense cover (Keith 1966; Wolff 1980). Wolff (1980) believed that the magnitude and frequency of cycles can be controlled in part by the size and number of such areas of cover.

Snowshoe hares can be affected by barriers to normal movement. Conroy et al. (1979) noted that areas of sparse woody cover appeared to inhibit the movements of hares in Michigan. Brocke (1975) found that hares in New York crossed a clearing 70 m in width only in a narrow neck dominated by sparse conifer cover. He also found a two-lane paved highway to be a major barrier to movements.

Special Considerations

Snowshoe hare populations exhibit 8 to 11-year cycles in Alaska (Wolff 1980) and all Canadian provinces except the Maritimes (Keith 1963). Populations in the northeastern (Cook and Robeson 1945) and western (Howell 1923) United States do not exhibit extreme fluctuations in numbers. The magnitude of cycles generally appears to be greater northward over the snowshoe hare's range (Adams 1959).

Predators exhibit a well-defined functional and numerical response to changes in snowshoe hare abundance (Keith et al. 1977). Predators can move to areas of high hare abundance and depress local hare populations. Major predators in the North include the lynx (*Lynx canadensis*), goshawk (*Accipiter gentilis*), great horned owl (*Bubo virginianus*), red fox (*Vulpes fulva*), red-tailed hawk (*Buteo jamaicensis*), and pine marten (*Martes americana*). The red fox, coyote (*Canis latrans*), bobcat (*Lynx rufus*), and several hawk and owl species are important southern predators (Wolff 1980). Dogs (O'Farrell 1965) and house cats (Severaid 1942) can be important predators in settled areas.

Several major factors can limit snowshoe hare population size. These include lack of adequate cover (Cook and Robeson 1945; Bookhout 1965a, Brocke 1975), winter food (deVos 1964; Vowles 1972; Walski and Mautz 1977), and severe winter weather (Meslow and Keith 1971; Vowles 1972). Conroy et al. (1979) believed that winter represented the critical season for snowshoe hares in Michigan.

Snowshoe hares can experience competition from other animals. Dodds (1960) believed that overgrazing by domestic sheep in Newfoundland caused summer food scarcity, thereby limiting snowshoe hare populations. Moose (*Alces alces*) (Dodds 1960) and whitetail deer (*Odocoileus virginianus*) (Bookhout 1965a,b) browsing can reduce the amount of food and cover available to snowshoe hares. Cottontail rabbits (*Sylvilagus* spp.) and snowshoe hares can exclude one another in areas of suitable habitat (Buehler and Keith 1982).

Modifications of habitat, such as drainage and deforestation, can eliminate snowshoe hares from an area (deVos 1962; Windberg and Keith 1978).

Large numbers of snowshoe hares can be a serious decimating factor to natural regeneration in forest stands and in tree plantations (Baker et al. 1921). Barking and browsing damage can kill, deform, and reduce the vigor of trees and shrubs (deVos 1964). Snowshoe hares prefer the increased food and cover associated with overstocked stands (Sullivan and Sullivan 1982, 1983). These authors found maximum hare damage with a stocking rate of about 35,000 stems/ha and a minimum with 5,000 to 10,000 stems/ha on a stand of young sapling and pole-size lodgepole pine (P. contorta) in British Columbia. To minimize snowshoe hare damage, Cox (1938) recommended against heavy plantings that would provide good cover while trees are still small and low enough to be browsed. Bailey (1946) and Sullivan and Sullivan (1982) recommended planting during periods of low snowshoe hare abundance. Sullivan and Sullivan (1982) also suggested thinning the stands during the predicted damage period and providing fallen pine foliage and slash as an alternate food source.

Browsing by snowshoe hares also can be useful by accelerating tree growth (Cox 1938; Cook and Robeson 1945) and by thinning stands (Roe and Stoeckeler 1950), thereby reducing fire and insect damage (Cox 1938). Snowshoe hare habitat can be enhanced by clearcutting (Conroy et al. 1979; Tompkins and Woehr 1979; Wolfe et al. 1982) and prescribed burning (Tompkins and Woehr 1979; Wolff 1980). Grange (1965) stated that fire and other disturbances allow hares to survive in small numbers in mature forests. Buehler and Keith (1982) believed that unsuitable snowshoe hare habitat increases in the absence of extensive fires and logging. Adams (1959) recommended lightly thinning extremely dense forested areas to allow the growth of forage plants and planting clumps of coniferous cover in areas with inadequate cover. Conroy et al. (1979) believed that cutover can be enhanced for snowshoe hares by leaving slash on the site.

HABITAT SUITABILITY INDEX (HSI) MODEL

Model Applicability

Geographic area. This model was developed for application throughout the range of the snowshoe hare (Fig. 1).

Season. This model was developed to evaluate the winter habitat of the snowshoe hare.

Cover types. This model was developed to evaluate habitat in the following cover types (terminology follows that of U.S. Fish and Wildlife Service 1981): Evergreen Forest (EF); Deciduous Forest (DF); Evergreen Tree Savanna (ETS); Deciduous Tree Savanna (DTS); Evergreen Shrubland (ES); Deciduous Shrubland (DS); Evergreen Shrub Savanna (ESS); Deciduous Shrub Savanna (DSS); Evergreen Forested Wetland (EFW); Deciduous Forested Wetland (DFW); Evergreen Scrub-Shrub Wetland (ESW); and Deciduous Scrub-Shrub Wetland (DSW).

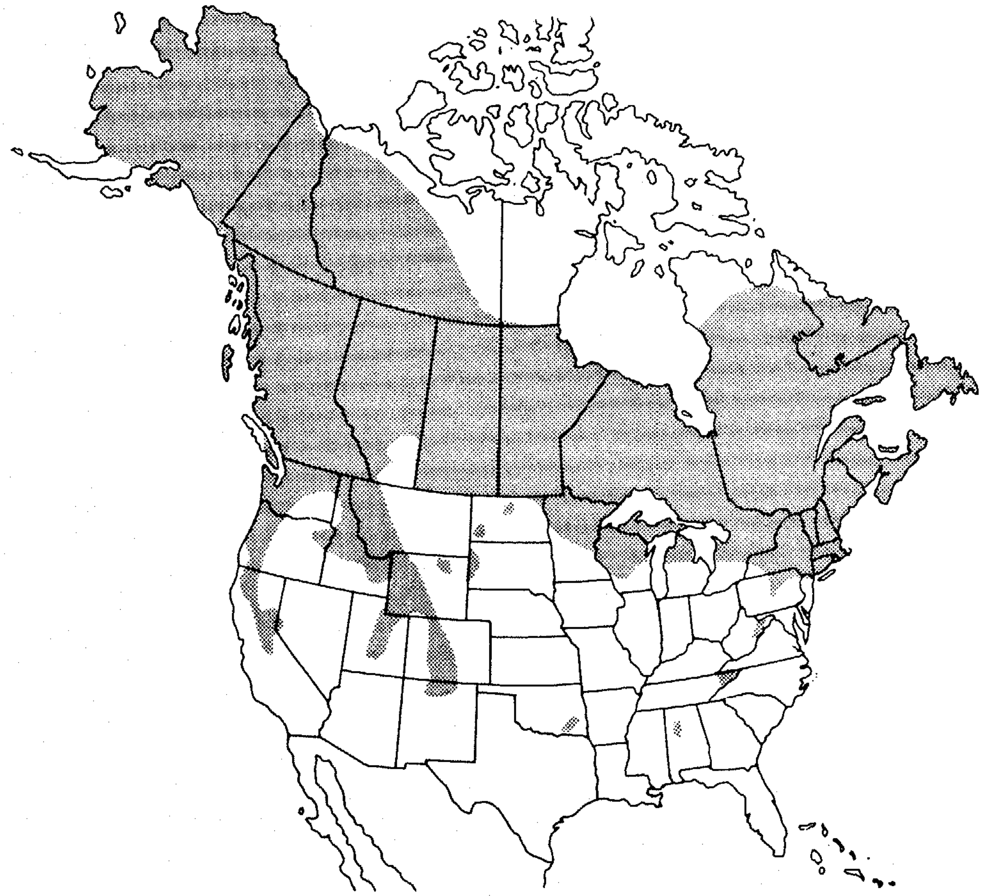

Figure 1. Approximate range of the snowshoe hare (modified from Bittner and Rongstad 1982).

Minimum habitat area. Minimum habitat area is defined as the minimum amount of contiguous habitat that is required before a species will live and reproduce in an area. Buehler and Keith (1982) determined that sites with > 160 ha of suitable habitat in Wisconsin were most often occupied by snowshoe hares. However, snowshoe hares are known to inhabit woodlot habitat blocks of 1 to 5 ha when within 1.6 to 8 km of larger areas of contiguous habitat (Keith, unpubl.).

Verification level. The first draft of this model was critiqued by John R. Cary and Lloyd B. Keith, University of Wisconsin, Madison; Michael R. Vaughan, Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, VA; Lamar A. Windberg, U.S. Fish and Wildlife Service, Laredo, TX; and Michael L. Wolfe, Utah State University, Logan. Comments from these reviewers have been incorporated into the current model.

Model Description

Overview. The snowshoe hare habitat model considers the ability of winter habitat to meet the food and cover needs of the species as an indication of year-round habitat suitability. It is believed that snowshoe hares inhabit areas during the summer that do not provide suitable winter habitat. The ability of summer habitat to continually support populations of snowshoe hares is determined by its interspersion with winter habitat. A major assumption of this model is that areas that provide adequate food and cover during the winter also will provide adequate summer food and cover. This assumption is based on the belief that deciduous species that provide adequate winter food also will provide adequate foliage for the summer diets of snowshoe hares. In habitats dominated by coniferous species, it is assumed that an adequate amount of deciduous forage and/or herbaceous vegetation will occur to support snowshoe hares during the growing season. It also is assumed that summer cover will never be more limiting than winter cover. Reproductive habitat requirements of the snowshoe hare are assumed to be met by the same habitat characteristics that define the species' winter habitat.

The following sections provide a written documentation of the logic and assumptions used to interpret the habitat information for the snowshoe hare and to explain and justify the variables and equations used in the HSI model. Specifically, these sections cover identification of variables that will be used in the model, definition and justification of the suitability levels of each variable, and a description of the assumed relationship between variables.

Food component. Snowshoe hares require enough forage in the form of woody browse and coniferous foliage to sustain them over the winter months. Information on the amount of coniferous foliage snowshoe hares consume was not found in the literature. The following discussion pertains only to the woody portion of the snowshoe hares' diet.

Snowshoe hares clip stems up to 1.5 cm in diameter during the winter, although stems < 1 cm are clipped far more commonly (Keith et al. 1984). Snowshoe hares reach browse within 60 cm of the ground or snowcover. Keith et al. (1984) emphasized the difference between available browse and available food. They defined available food as that portion of the available browse that was ≤ 4 mm in diameter, excluding unpalatable species. This definition was based on evidence that snowshoe hares lose weight and die rapidly when forced to subsist on browse with a diameter > 4 mm. In addition to diameter, other factors including palatability, digestibility, species diversity (Keith et al. 1984), nutritive value, and hare behavior (Sinclair et al. 1982) determine what portion of available browse is actually food. An attempt to define and quantify these variables is beyond the scope of this model. It is assumed that an estimate of available browse, as defined by this model, will give a reasonable indication of food availability for snowshoe hares. Available browse is thereby defined as woody stems and branches that are: (1) within the height from ground level to 60 cm above the average local snow depth; (2) ≤ 1.5 cm in diameter; and (3) live [i.e., contain live buds and bark, and which bend rather than break easily (Grigal and Moody 1980)]. Browse species known to be unpalatable to snowshoe hares are not considered as available browse (Table 1).

In order to support a population of snowshoe hares, a habitat must provide a sufficient quantity of browse throughout the non-growing season. In this model, a standard food requirement (SFR) is used to define the optimum browse condition. The SFR can be calculated as follows:

$$SFR = \frac{(KHD) \times (NFD)}{SD} \quad (1)$$

where KHD = the total number of kilograms (wet weight) of available browse required per hare per day [e.g., 3 kg reported by Vowles (1972) and Pease et al. (1979)].

NFD = the average number of frost days per year (from local records).

SD = the standard density of hares used to define optimum food conditions [e.g., 4 hares/ha based on data from Wolff (1980)].

The value of the standard density (SD) for Equation 1 was arbitrarily chosen as a means of defining optimum browse conditions. An optimum foraging habitat would provide enough browse to support the metabolic requirements of the chosen density of hares. For example, the data of Wolff (1980), whose study area consisted of diverse, highly productive hare habitats, can be used to define the optimum browse condition for interior Alaska. Wolff used a dpb of > 3 mm as an indication of browse consumption in excess of carrying capacity. He noted that a population of 1.4 hares/ha could be maintained by twigs < 3 mm in diameter, whereas larger, less nutritious twigs ($\bar{x}$ dpb = 9.4 mm) were consumed when populations were approximately 6 hares/ha. Assuming that the low density was below carrying capacity and the high density was above carrying capacity, a midrange figure of 3.7 hares/ha might be a good estimate for the SD in interior Alaska. When the field estimate of available browse (EAB) is obtained and compared with the SFR, the resulting ratio equals the SI for food (Equation 2). If the ratio > 1, then SIV1 = 1.0

$$\frac{EAB}{SFR} = SIV1 \quad (2)$$

The above method of browse estimation requires intensive sampling which may be beyond the resources or requirements of some users of this model. Therefore, an alternate method of browse estimation is provided in the following discussion.

The literature indicates that snowshoe hares prefer stem and twig sizes that commonly occur in young-growth forests. It is assumed that habitats that provide abundant coniferous foliage and deciduous browse in the form of shrubs and young trees will provide adequate winter food for snowshoe hares. Forage class vegetation is thereby defined as palatable, live vegetation in the form of coniferous and deciduous shrubs, seedlings (< 2.5 cm dbh), and saplings (2.5 - 12.4 cm dbh) (U.S. Forest Service 1982). It is assumed that cover types have no suitability as foraging habitat where live coniferous foliage and the live woody portions of deciduous shrubs and young trees provide 0% visual obstruction. Cover types in which these vegetation classes provide ≥ 50% visual obstruction provide optimum foraging habitat suitability (Fig. 2). Snowshoe hares are known to clip down vegetation that would otherwise be out of reach (Keith et al. 1984). It is assumed that a measurement of forage class vegetation up to 3 m above the ground will adequately represent vegetation available to snowshoe hares when clipped, as well as vegetation available during periods of deep snow.

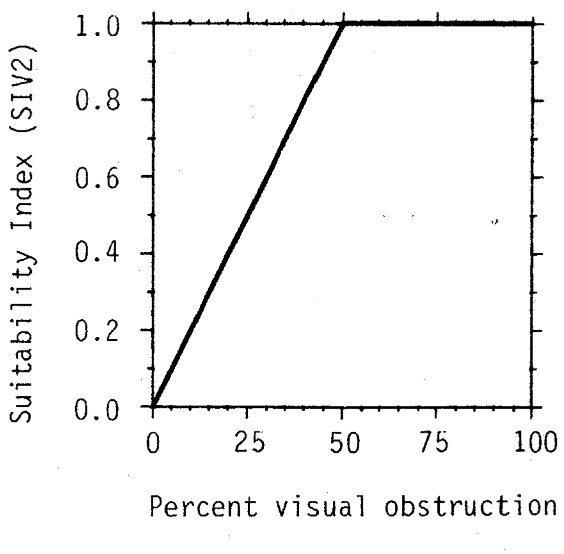

Figure 2. The relationship between the average visual obstruction of live forage class vegetation and the suitability index value for snowshoe hare winter food.

Cover component. Snowshoe hares require sufficient cover for protection from predators and inclement weather. Cover for snowshoe hares can consist of both living and dead vegetation. Measurements of lateral visibility are assumed to be the most accurate method of assessing cover for snowshoe hares. Cover height is also an important consideration. In order to provide security from avian predation and shelter during periods of deep snowpack, adequate cover for snowshoe hares must extend from the ground to some height above ground level. It is assumed that cover types that provide < 40% visual obstruction up to a height of 3 m above the ground have no suitability as cover (Fig. 3). Cover types that provide ≥ 90% visual obstruction up to 3 m have optimum suitability (Fig. 3). As a standard, visual obstruction should be measured from a distance of 15 m. Because this model is intended to evaluate the winter habitat of snowshoe hares, it is essential that measurements of cover be conducted during the period after leaf-fall or before new growth. If measurements must be done during the growing season, a best guess of winter conditions, based on prevailing conditions, must be made in order to obtain a reasonably accurate estimate of winter habitat parameters.

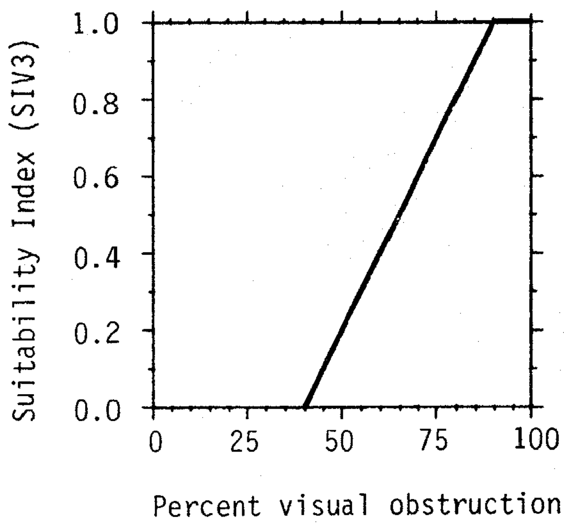

Figure 3. The relationship between the average visual obstruction of all living and dead vegetation and the suitability index value for snowshoe hare winter cover.

HSI determination. The Habitat Suitability Index for the snowshoe hare is determined by the quality of foraging habitat (SIV1 or SIV2) and cover habitat (SIV3). The relationship between cover and foraging habitat quality is illustrated in the following equations:

$$HSI = (SIV1 \times SIV3) \qquad (3)$$

$$HSI = (SIV2 \times SIV3) \qquad (4)$$

Application of the model

Application procedure. When using SIV2 as an index of food suitability, measurements of winter food can be taken at the same time and by the same method as measurements of winter cover. In essence, SIV2 will be represented as a fraction of SIV3. Using this combined method, it would be possible to simultaneously evaluate food and cover characteristics of the habitat and to determine which component is limiting. For example, an old growth forest habitat with abundant deadfall can provide adequate cover but be deficient in size classes of plants foraged by snowshoe hares. Relatively open areas with inadequate cover also can provide either inadequate quantities of forage or reduced opportunities for snowshoe hares to exploit available food resources. Optimum habitat would provide adequate cover in the form of vegetation which also constitutes winter forage for snowshoe hares.

In habitats that display a high degree of cover type diversity (e.g., a mature forest interspersed with islands of early successional stage vegetation), the potential value of a cover type is influenced by the mix of cover types. The literature indicates that snowshoe hares commonly move among different cover types to secure life requisites (i.e., food and cover). In order to accurately assess the true potential of the total habitat, the contribution of the various cover types must be determined. The following procedure is recommended:

1. Stratify the evaluation area into characteristic cover types. The cover types should be defined to delineate areas that differ significantly with respect to SIV1 or SIV2 and SIV3.

2. Determine the HSI values for each characteristic cover type.

3. Calculate the overall HSI using the following equation:

$$HSIo = \frac{\sum_{i=1}^{n} (HSIi) \times (Ai)}{\sum_{i=1}^{n} Ai} \qquad (5)$$

where HSIo = the overall HSI value for the study area.

HSIi = the HSI for cover type "i".

Ai = the area of cover type "i".

Summary of model variables. The relationship between habitat variables, life requisites, cover types, and the HSI value are summarized in Figure 4. Figure 5 provides variable definitions and suggested measurement techniques (Hays et al. 1981).

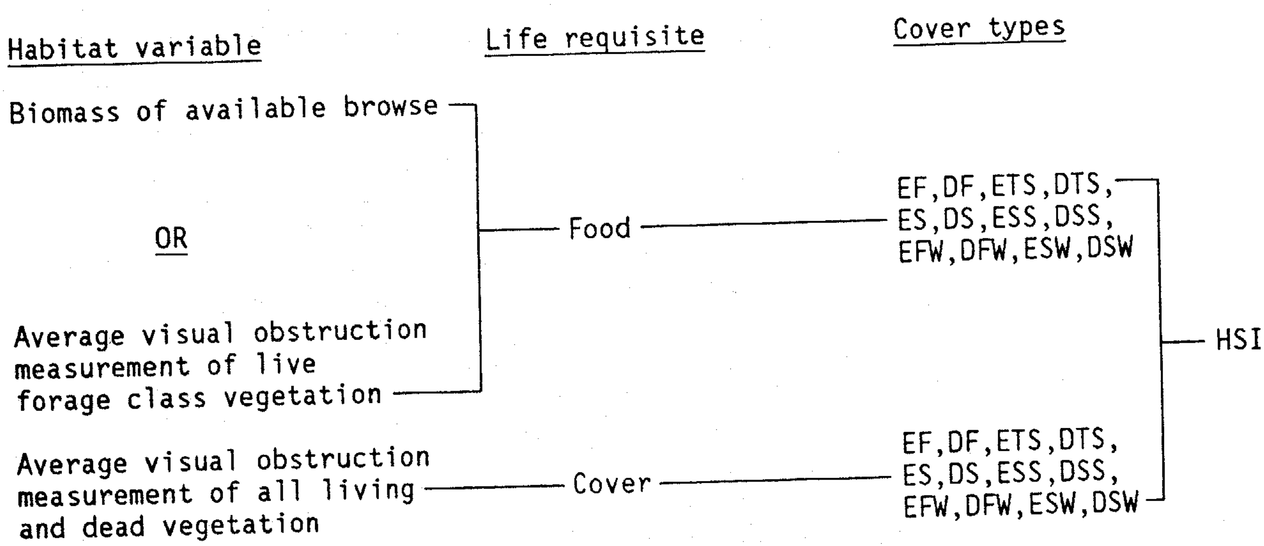

Figure 4. Relationships of habitat variables, life requisites, and cover types to the HSI for snowshoe hare winter habitat.

Variable (definition)	Cover types	Suggested technique
Biomass of available browse [the quantity of live, palatable woody stems and branches ≤ 1.5 cm (0.6 inches) in diameter and between ground level and 60 cm (23.6 inches) above the average snow depth].	EF,DF,ETS,DTS, ES,DS,ESS,DSS, EFW,DFW,ESW,DSW	Quadrat, clip-and-weigh (Keith et al. 1984)
Average visual obstruction measurement of live forage class vegetation [to a height of 3 m (9.8 ft) above the ground].	EF,DF,ETS,DTS, ES,DS,ESS,DSS EFW,DFW,ESW,DSW	Profile board
Average visual obstruction measurement of all living and dead vegetation [to a height of 3 m (9.8 ft) above the ground].	EF,DF,ETS,DTS, ES,DS,ESS,DSS, EFW,DFW,ESW,DSW	Profile board

Figure 5. Definitions of variables and suggested measurement techniques.

Model assumptions. This model was developed with information obtained from the publications of and communications with professional biologists familiar with the species and its habitat requirements. It attempts to identify those physical parameters assumed most important in explaining habitat potential, and then attempts to combine those parameters into simple algorithms that yield an index value between 0.0 and 1.0. Major assumptions include:

1. An assessment of winter habitat quality will give a reasonable indication of year-round habitat suitability, assuming that winter is the most critical season for snowshoe hare survival.

2. This model evaluates the long-term average suitability of habitat and does not attempt to predict or explain the cyclic behavior of some snowshoe hare populations.

3. If browse cannot be clipped and weighed (i.e., SIV1), an ocular estimate of food biomass (i.e., SIV2) is a reasonable method of indexing food suitability.

Modifications of the model can be made if the user believes that such modifications will better approximate conditions in the intended area of application. Users should be aware that the assumptions inherent to modified models can be different than those listed above.

SOURCES OF OTHER MODELS

No habitat models for the snowshoe hare were located.

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16. Abstract (Limit: 200 words)

A review and synthesis of existing information were used to develop a Habitat Suitability Index (HSI) model for the Snowshoe hare (Lepus americanus). The model consolidates habitat use information into a framework appropriate for field application, and is scaled to produce an index between 0.0 (unsuitable habitat) and 1.0 (optimum habitat). HSI models are designed to be used with Habitat Evaluation Procedures previously developed by the U.S. Fish and Wildlife Service.

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