

APPLICATION OF A MOOSE HABITAT SUITABILITY INDEX MODEL TO VERMONT WILDLIFE MANAGEMENT UNITS

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ABSTRACT: Habitat Suitability Index (HSI) models translate existing knowledge of a species' habitat requirements into quantitative measures of habitat quality. The HSI is a numerical index that represents the ability of a given habitat to provide life requisites for a species on a scale from 0 (unsuitable habitat) to 1 (optimal habitat). Habitat Suitability Index models are useful in natural resource planning for predicting the impacts of resource management practices on wildlife habitat. Many moose (*Alces alces*) HSI models require the labor-intensive collection of ground-level browse density data, which limits their applications for analyzing large landscapes required by moose. Some, however, have been developed utilizing remotely sensed data to analyze large study areas. I tested the usefulness of one of these models, created for the Lake Superior region, to 2 Wildlife Management Units (WMUs) in Vermont. Areas of study WMUs, "E1" and "I", were 680 km² and 729 km², respectively. The model quantified 4 landscape-scale habitat variables representing annual cover types required by moose: percent area of regenerating forest, non-forested wetland, spruce/fir forest, and deciduous/mixed forest. Model analyses were performed using a Geographic Information System (GIS). The model was useful in estimating relative habitat suitability of both WMUs, identifying within-WMU habitat variation, quantifying change in habitat suitability following a natural habitat-altering event, and predicting temporal change in moose habitat due to changes in forest management practices. The model revealed significant differences in habitat suitability of 0.64 for WMU E1 and 0.34 for WMU I. To determine within-WMU habitat variation, both WMUs were divided into 25-km² evaluation units, which approximated the annual home range of moose in New England, and a HSI was calculated for each unit. Habitat suitability of 81 km² of WMU I increased from 0.30 to 0.53 due to an increase in regenerating forest following heavy canopy damage from an ice storm in January 1998. A reduction in habitat suitability from 0.81 to 0.35 of Silvio O. Conte National Fish and Wildlife Refuge lands within WMU E1 was observed following a simulation in which all timber harvesting as a forest management practice was eliminated. Initial validation of this model for analyzing moose habitat at the WMU-scale is supported by correlation of HSI output to moose harvest data for WMU E1 25-km² evaluation units and by comparison of HSI to estimated moose densities for both WMUs.

ALCES VOL. 38: 89-107 (2002)

Key words: *Alces alces*, Geographic Information System (GIS), Habitat Suitability Index (HSI) model, moose, Vermont, Wildlife Management Unit (WMU)

In the last 40 years, Vermont has seen a considerable increase in the population size and distribution of eastern moose (*Alces alces americana*). The population, estimated at 20 animals in 1960, was thought to exceed 2,500 in 1998, and continues to grow

at a predicted rate of 1.10 moose/year (Alexander 1993, Alexander et al. 1998). In the same period of time, moose distribution has expanded from Vermont's extreme northeast corner to the entire state. In 1993 the Vermont Department of Fish and Wild-

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life (VTDFW) initiated the first moose hunt in almost a century by issuing 30 harvest permits for one of Vermont's 26 Wildlife Management Units (WMUs). By 1999, the moose hunt was expanded to 10 WMUs, representing approximately 51% of the state, and for the 2000 season 215 permits were issued. With an expanding moose population, public interest in non-consumptive uses of moose, such as viewing and photography, also have risen.

In New England, moose habitat has been described in numerous studies (Cioffi 1981, Monthey 1984, Crossley 1985, Leptich and Gilbert 1989, Pruss and Pekins 1992, Thompson et al. 1995, Alexander et al. 1998, and K. Morris, Maine Department of Inland Fish and Wildlife 1999, unpublished data). Moose were found to require large habitats providing copious amounts of regenerating hardwood as their primary source of annual browse; young balsam fir (*Abies balsamea*) at higher elevations as a source of winter browse; mature spruce (*Picea* spp.) and balsam fir forests to escape the stressful effects of heat in summer and severe weather in winter (Renecker and Hudson 1986, 1990); and macrophyte-rich wetlands as a source of sodium in late spring and summer. Pletscher (1987), while studying nutrient budgets for white-tailed deer in north-central New Hampshire, demonstrated low sodium concentrations in terrestrial vegetation and suggested that deer made up for this deficiency by utilizing natural salt licks, artificial salt licks along salted roads, and aquatic vegetation. Assuming sodium concentration in terrestrial vegetation throughout New England is low, as has been demonstrated for the Lake Superior region in work from Isle Royale (Jordan et al. 1973, Belovsky and Jordan 1981), moose probably make up for sodium deficiencies in the same manner. Wetland areas are also important for calving areas and as refugia from black bear (*Ursus*

americana) predation, and insects. By occupying large home ranges, moose in New England are able to meet their seasonal life requisites, which are often spatially separated.

Because of the presumed abundance and good quality of Vermont's moose habitat, the VTDFW does not routinely inventory or monitor moose habitat. It does, however, collect physical measurements from legally harvested and incidentally killed moose as indicators of population health and habitat condition. While these measurements may indicate that a moose population is approaching carrying capacity or is in decline due to habitat deficiencies, they cannot specify which habitat component is deficient. The present physical condition of Vermont moose suggests that the herd is healthy and the habitat is productive (Alexander et al. 1998). However, with increasing demands on Vermont's forests for recreation, forest products, conservation, and development, their ability to support moose could deteriorate.

A tool that can inventory statewide moose habitat and predict habitat change due to change in forest management practices and natural disturbances will aid in the conservation and management of valuable moose habitats. This tool should be compatible with timber stand classification systems developed for timber management since forestry practices have such a great impact on moose habitat throughout its eastern range (Hurley 1986). The tool also should be simple, inexpensive to apply and capable of analyzing large habitats required by moose. An effective tool to meet all these demands is the moose Habitat Suitability Index (HSI) model (Allen et al. 1987).

The concept of the HSI model began with the development of the U.S. Fish and Wildlife Service (USFWS) sponsored Habitat Evaluation Procedures (HEP) in 1976. The HEP quantified wildlife habitat based

on the Habitat Suitability Index (HSI) and total area of available habitat. They were created in response to the National Environmental Policy Act (NEPA) of 1969, which required that the environmental impacts on wildlife from any activity involving federal funding or a federal permit be described prior to implementation of the project. This act made it necessary for biologists to relate wildlife species to their habitat and to predict species response to habitat alterations (Thomas 1982).

Between 1982 and 1989, the USFWS sponsored the development of over 160 HSI models for mammal, bird, reptile, amphibian, fish, and invertebrate species, and communities. These models translated existing knowledge of a species' habitat requirements into standard, quantitative measures of habitat quality on a scale from 0 (unsuitable) to 1 (optimal). They are used to compare the ability of two or more study areas to provide habitat for a given species or to document habitat change over time within an individual study area. Habitat Suitability Index models also predict the consequences of proposed natural resource management on wildlife habitats and identify suitable areas for development so negative impacts on wildlife habitats can be minimized.

Moose HSI Model II

Two moose HSI models (Model I and Model II) were created by Allen et al. (1987) as part of the USFWS series and have served as the standard for more recent models (Allen et al. 1991, Courtois 1993, Palidwor et al. 1995, Hepinstall et al. 1996, Rempel et al. 1997, Romito et al. 1998, K. Morris, Maine Department of Inland Fish and Wildlife 1999, unpublished data). Model I and II were created for the evaluation of moose habitat in the Lake Superior region and were a product of a modeling workshop in Duluth, Minnesota in 1987. Model I was

designed to evaluate the abundance and quality of growing season and dormant season food and cover in study areas that approximate the size of annual habitats required by moose (~600 ha). Intensive browse data collection is required for Model I. Model II was designed to rapidly evaluate and compare the ability of relatively large areas to provide annual habitat for moose using remotely sensed data.

For this study, the usefulness of Model II for analyzing large tracts of habitat was tested by applying it to 2 of Vermont's 26 WMUs, which is the geographic unit used by the VTDFW for moose management. Model II relates cover-type composition to moose habitat suitability and incorporates 4 cover-type variables that provide annual life requisites for moose. Model variables are: percent area of regenerating forests < 20 years old, used as a source of annual browse (variable 1); non-forested wetlands, used as a source of summer aquatic vegetation (variable 2); spruce/fir forests \geq 20 years old, used as a source of summer and winter cover (suitable stands need \geq 50% spruce/fir canopy) (variable 3); and upland deciduous or mixed forests \geq 20 years old, used for both annual browse and cover (suitable stands must have \geq 25% canopy cover of trees, of which < 50% of the canopy must be spruce/fir) (variable 4) (Table 1). Model variables were based on research conducted by Peek et al. (1976) that described optimal moose habitat for northeast Minnesota. Twenty years was used as the cutoff age for regenerating forests because older trees are assumed to have little value as moose browse.

Model II assumes that ideal year-round moose habitat requires the presence of all 4 habitat components and that model variables are weighted equally. However, if any of the 4 habitat components is missing from the evaluation area, other than wetlands, suitability will equal zero regard-

Table 1. Description of model variables and the life requisites they provide, variable Suitability Indices (SI), and percent area of variables for optimum habitat suitability (Allen et al. 1987, Peek et al. 1976).

Variable #	Variable description (%area)	Life requisites provided by variable	Variable suitability indices (SI)	% Area of variables for optimum habitat suitability
1	Regenerating Forest < 20 years old	forage	SI ₁	40 – 50
2	Non-forested Wetlands	aquatic forage, escape from insects and predation, thermoregulation	SI ₂	5 – 10
3	Spruce / Fir Forest ≥ 20 years old	winter and summer cover	SI ₃	5 – 15
4	Upland Deciduous / Mixed Forest ≥ 20 years old	forage and cover	SI ₄	35 – 55

less of the percent area of the other cover types. It also assumes a positive correlation between species abundance and habitat quality (Allen et al. 1987). The degree of interspersed between food and cover is not addressed in Model II, however, in Vermont where logging operations are relatively small and scattered, and non-forested wetland and mature spruce/fir forests are distributed throughout the state, it is assumed that interspersed is adequate.

Descriptions of preferred browse species and habitats of moose from studies in northern New Hampshire (Miller 1989, Pruss and Pekins 1992) and northern Maine (Cioffi 1981, Monthey 1984, Crossley 1985, Leptich and Gilbert 1989, Thompson et al. 1995) are similar to those described for the Lake Superior region (Allen et al. 1987) for which Model II was designed. Climate, which dictates annual habitat preference, is also similar between these two regions. A classification system developed by Wladimir Köppen shows that climate in the Great

Lakes region and New England is similar based on vegetation types and annual monthly means of temperature and precipitation (Eichenlaub 1979). The U.S. Department of Commerce (1968) shows similarities between the two regions in annual minimum, maximum, and average daily temperatures, annual snowfall, mean annual numbers of days the minimum temperature was below 0°C, mean date for the last 0°C temperature in spring, and mean date for the first 0°C temperature in fall. Because moose habitat composition and climate in Vermont are similar to that of both northern Maine and northern New Hampshire, I consider it appropriate to assess moose habitat in Vermont using Model II.

Specific objectives of this project were to: (1) generate GIS coverages converting vegetation data into 4 cover types upon which Model II is based; (2) apply Model II to 2 WMUs in Vermont to predict habitat suitability; (3) predict within-WMU habitat suitability variation; (4) demonstrate the

change in HSI of WMU I after a 1996 ice storm destroyed over half of the forest canopy at upper elevations; (5) predict change in HSI of WMU E1 after ownership passed from a commercial wood products company to a federal entity; and (6) support model validation for Vermont by correlating HSI values to population data from moose harvests.

STUDY AREA

Wildlife Management Unit E1 and a comparable-sized portion of WMU I were chosen as study areas (Fig. 1) because they both are very important moose habitats in Vermont, however, they vary greatly in vegetation composition, physiographic nature, and density of moose they support. Wildlife Management Unit E1 (680 km²) is located within Essex County in the northeast corner of Vermont. E1 is bordered by Canada to the north, the Connecticut River to the east, Route 105 to the south and Route 114 to the west. It is roughly circular in shape and surrounded by mountains 600

– 1,000 m in elevation except to the south where the Nulhegan Basin lies. The basin is drained by the Nulhegan River, which flows eastward into the Connecticut River. The state's most extensive bogs and softwood swamps are located in the basin, which averages 350 - 450 m in elevation. This WMU is characterized by a mosaic of young, intermediate, and mature stands of trees due to its logging history and diverse geography. Lowland areas are dominated by balsam fir, red spruce (*Picea rubens*), black spruce (*P. mariana*), poplar (*Populus* spp.), alder (*Alnus* spp.), and paper birch (*Betula papyrifera*). Intermediate elevations contain primarily northern hardwood beech (*Fagus grandifolia*) / birch (*Betula* spp.) / maple (*Acer* spp.) forest. Sites above 800 m are predominately in red spruce and balsam fir stands. Deciduous, mixed, and coniferous forests cover approximately 54%, 25%, and 15% of the area, respectively (D. Williams, Spatial Analysis Laboratory, University of Vermont, unpublished data). This WMU has the greatest density of moose and the largest annual moose harvest of all WMUs in the state. Present estimate of moose density is 0.4 moose/km² (C. Alexander, VTDFW, personal communication).

The second study area encompasses a 729 km² portion of WMU I, and lies mostly within Addison County. This portion will be referred to as WMU I for the study. Wildlife Management Unit I is bordered by Route 17 to the north, Route 100 to the east, Route 73 to the south, and Route 116 to the west. It contains much of the northern half of the Green Mountain National Forest and straddles the 1,000 – 1,200 m Green Mountain spine. To the east, the Green Mountains drop steeply into the Mad and White River valleys, and to the west the mountains taper gradually into the Champlain Valley. Wildlife Management Unit I is dominated by mature northern hardwood forests at mid

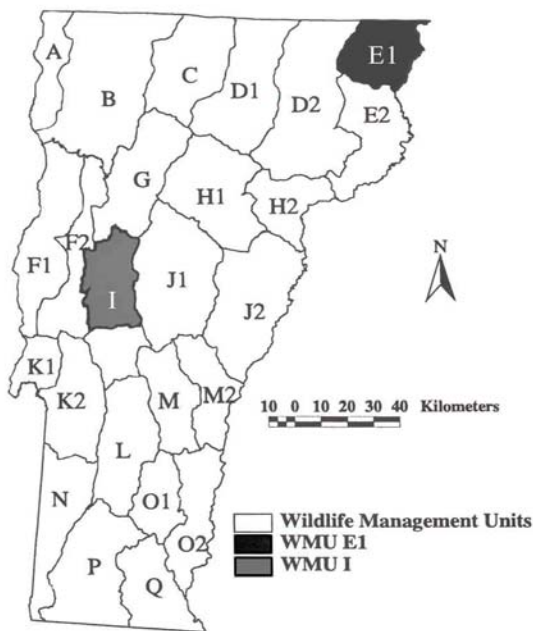


Fig. 1. Location of study areas WMU E1 and WMU I in Vermont.

elevations, paper birch at high elevations, and pockets of spruce/fir on the highest peaks. Unit I has fewer non-forested wetlands than E1. Deciduous, mixed, and coniferous forests cover approximately 66%, 18%, and 10% of the area, respectively (D. Williams, Spatial Analysis Laboratory, University of Vermont, unpublished data). Wildlife Management Unit I is one of 3 additional units opened to hunting in 1999 and has an estimated moose density of 0.1 moose/km² (C. Alexander, VTDFW, personal communication). Although WMU I is more densely populated by people than WMU E1, both areas represent 2 of the largest undeveloped tracts of land in the state.

METHODS

Moose HSI Model II and HSI Calculation

Model II: $HSI = (SI_1 \times SI_2 \times SI_3 \times SI_4)^{1/4}$

In the model, HSI is the habitat suitability index for the study area or evaluation unit and SI_1 , SI_2 , SI_3 , and SI_4 are Suitability Index (SI) values for each of the 4 model variables. The HSI is the geometric mean of the 4 SI values. Percent areas of the 4 model variables are taken from variable cover type maps and plotted on Suitability Index graphs (Figs. 2 and 3) to determine SI values. Suitability index graphs were created for the model following a description of optimal habitat from Peek et al. (1976) (Allen et al. 1987). Percent area of variables falling within optimal ranges will produce a $SI = 1.0$ and percent areas less than or greater than optimal ranges will produce a $SI < 1.0$ (Figs. 2 and 3) (Allen et al. 1987).

Data for each variable were compiled into an ArcView 3.1- based GIS (ESRI, Redlands, California, USA). Data were added to coverages by tablet digitizing with a CalComp Drawing Board II and WinTab digitizer software.

Variable 1 — Percent area of regen-

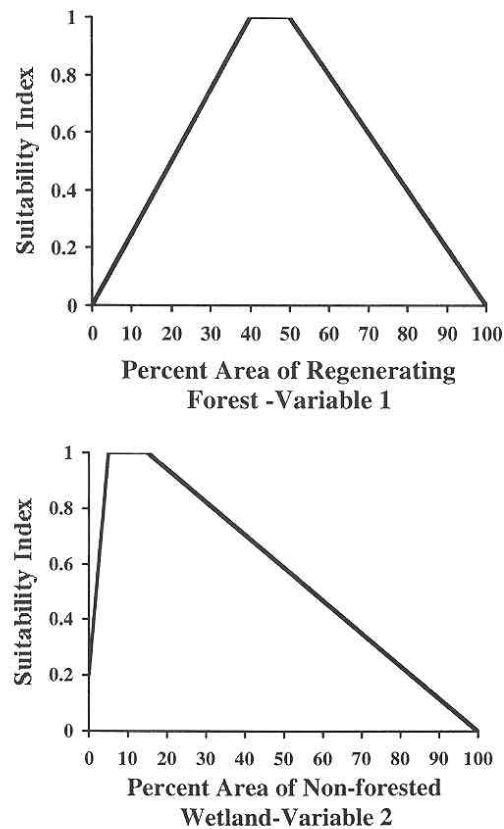


Fig. 2. Suitability index curves showing relationship between percent area of regenerating forest and non-forested wetland variables and suitability index. Optimal coverage of regenerating forest and non-forested wetland is 40-50% and 5-10%, respectively (Allen et al. 1987).

erating forest. The area of regenerating forest within each WMU was determined from numerous data sources. The Vermont Forest Resource Advisory Council (FRAC) quantified “heavy cuts” throughout Vermont between 1977-1996 and reported and mapped their findings (VDFPR 1996). These “heavy-cut” maps were used as base maps for variable 1. “Heavy cuts” were those visually determined from aerial flights or remotely sensed data to have been harvested below “C line”. The C line represents the minimum amount of acceptable growing stock that makes a timber stand worth managing as defined by the

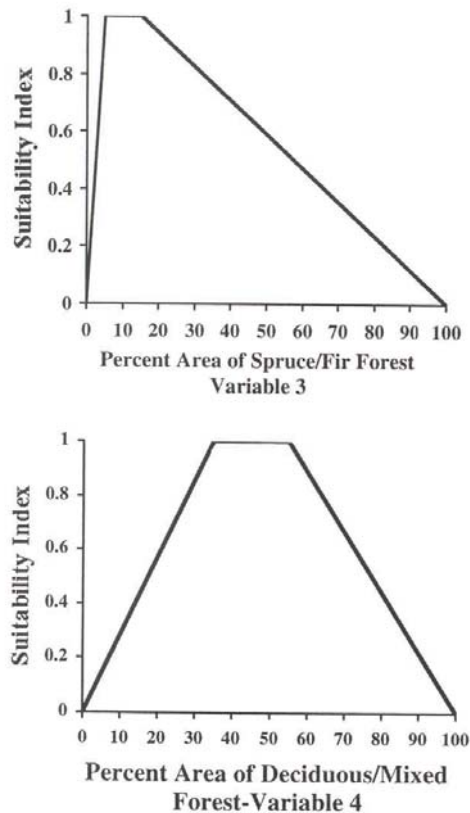


Fig. 3. Suitability index curves showing relationship between percent area of spruce/fir and deciduous/mixed forest variables and suitability index. Optimal coverage of spruce/fir forest and deciduous/mixed forest is 5-15% and 35-55%, respectively (Allen et al. 1987).

U.S. Department of Agriculture silvicultural stocking guides (Long 1997). Stand stocking level is a function of basal area per acre (ft^2) and the number of trees per acre. In New England, stands harvested below the C line can be expected to have large quantities of early successional regeneration from species such as aspen (*Populus* spp.), birch (*Betula* spp.), cherry (*Prunus* spp.), and maple (*Acer* spp.). Heavy cuts were easily discernible from maps because of their regular shape and obvious contrast from adjacent non-cut areas. Ancillary data used to complete the variable 1 map through 1999 for WMU E1 included 1999 digital orthophotography quadrangles (DOQ) and

1997-1999 Act 15 heavy-cut permits. Forest Service stand inventory data, which included all shelterwood, seed-tree, and clearcuts from 1977-March 1998, and 1997-1999 Act 15 heavy-cut permits were used for WMU I. Color-infrared aerial photographs, orthophotography, 1995 DOQs (WMU I), and ground-truthing were used to verify data. The final map displayed areas of regenerating forest as closed polygons. From these maps (Fig. 4), percent area of regenerating forests within the study areas was digitally queried.

Percent area in “heavy cuts” < 23 years old (1977–1999) was used as an estimator of regenerating forests < 20 years old because of data structure. I do not believe the addition of 2 years of data to variable 1 resulted in an overestimation of this variable, but rather made up for the small acreages of regenerating forests that were inadvertently missed while analyzing data.

Variable 2 — Percent area of non-forested wetlands. Non-forested wetlands included in this study followed suggested modifications to Model II by Adair et al. (1991) and wetland classifications from Cowardin et al. (1979). Adair et al. (1991)

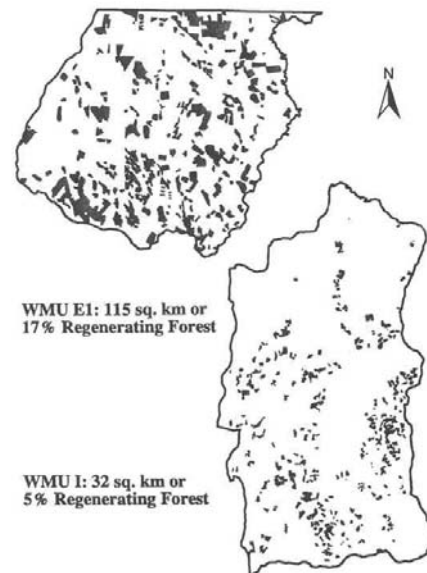


Fig. 4. Variable 1 - regenerating forest.

recommended that only wetlands with limnological conditions favoring macrophyte production should be included in the model. Wetlands included were emergent, unconsolidated bottom, rock bottom, and aquatic bed palustrine, scrub/shrub, dead forested, lower perennial riverine, littoral lacustrine, and beaver ponds. Mylar and digital National Wetland Inventory (NWI) maps were used to determine total area of these non-forested wetland types in each WMU. National Wetlands Inventory data were used because they are readily available to the public, cover the entire United States, and are consistent with their wetland classifications. Suitable wetlands were first identified on NWI mylar maps and then labeled as such on digital maps. Where data were incomplete on digital maps, or had not yet been digitized, data were manually digitized from mylar maps. A coverage of suitable wetland polygons was then generated and percent area digitally queried (Fig. 5).

Variable 3 — Percent area of spruce/fir forests. Variable area was taken from a vegetation grid map of New Hampshire and Vermont created for the USFWS Gap Analysis Project (D. Williams, Spatial Analysis Laboratory, University of Vermont, unpublished data). Data used to create the map included 4 Landsat Thematic Mapper (TM) satellite scenes acquired for spring, summer, and fall of 1992 / 1993, a small portion of the May 1995 scene, and ancillary data. Resolution of the TM data was 30 m. The map was validated through interpretation of aerial videography linked to a Global Positioning System (GPS). The map accurately classified 85% of 907 GPS points examined (D. Williams, Spatial Analysis Laboratory, University of Vermont, unpublished data). Much of the error was associated with classification of mixed forest as either deciduous or coniferous forest. Of the 7 land-cover types classified in this

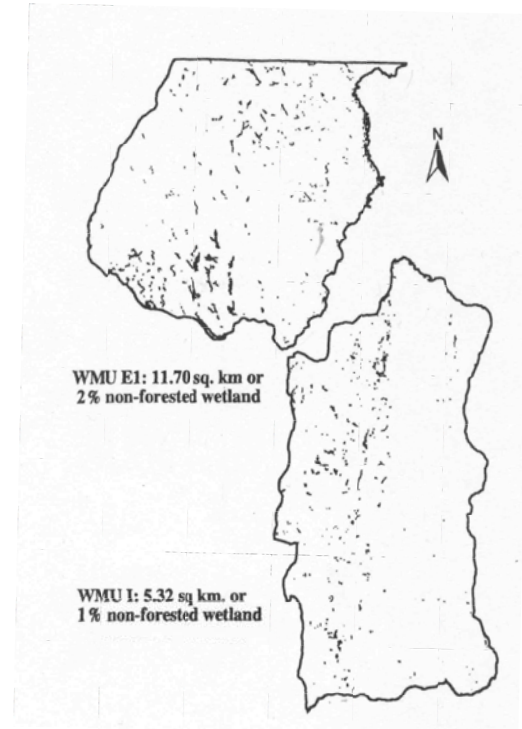


Fig. 5. Variable 2 - non-forested wetland.

mapping project, only deciduous, coniferous, and mixed-forest classifications were pertinent to this study. The others were omitted from analysis. Forests were classified as coniferous or deciduous if either contributed $\geq 65\%$ of stand species, or mixed if neither contributed $\geq 65\%$. The “coniferous forest” classification from this map represented spruce/fir forest for my analysis. Since Model II requires that coniferous or deciduous forests contribute $> 50\%$ of stand species (Allen et al. 1987), areas derived from this vegetation map may underestimate percent area of coniferous and hardwood forests and overestimate percent area of mixed forests.

Using ArcView and ARC/INFO spatial analysis GIS software, the vegetation grid was clipped to the extent of the 2 study areas. Polygon coverages of regenerating forest (variable 1) and non-forested wetland (variable 2) were then erased from the vegetation coverage leaving coniferous, mixed, and hardwood forest cover-types (Fig. 6). Percent area in spruce/fir forest

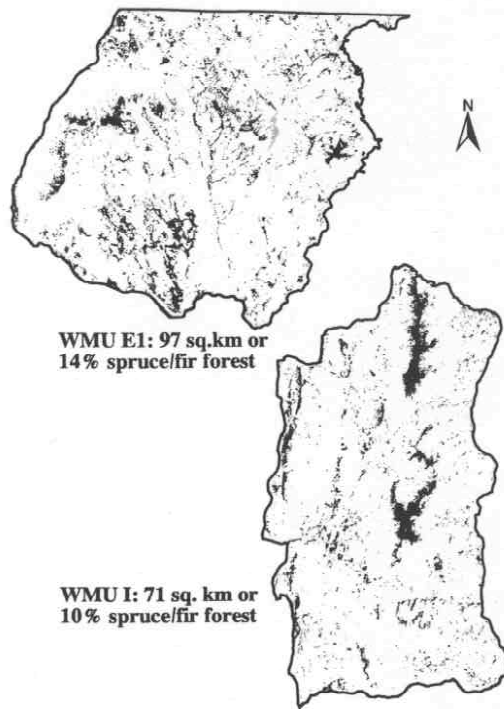


Fig. 6. Variable 3 – spruce/fir forest.

was queried from the resulting coverage.

Variable 4 — Percent area of deciduous/mixed forests. Percent area in upland deciduous/mixed forest was derived in the same manner as variable 3 (Fig. 7).

Within-WMU HSI Variation

To determine within-WMU HSI variation, each WMU was divided into 25-km² hexagonal evaluation units, and a HSI was determined for each unit as previously described. Twenty-five square kilometers was chosen as the evaluation unit size because it approximates the annual home range of moose in New England (Crossley 1985, Miller 1989, Thompson et al. 1995, K. Morris, Maine Department of Inland Fish and Wildlife 1999, unpublished data). Allen et al. (1987) and Schultz and Joyce (1992) recommended that size of the evaluation unit should approximate that of the animals' home range for HSI analysis. A regular hexagonal pattern was chosen for evaluation unit shape because it is the best discon-

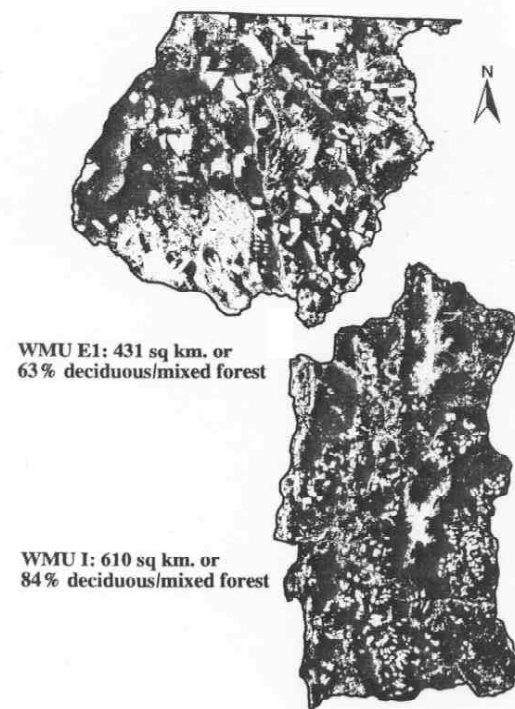


Fig. 7. Variable 4 – deciduous/mixed forest.

tinuous sampling pattern for a spatial function (Olea 1984). Evaluation units were assigned to 3 habitat categories based on HSI values: least suitable habitat (HSI = 0.0–0.31), suitable habitat (HSI = 0.32–0.66), and most suitable habitat (HSI = 0.67–1.0) (Fig. 8).

Effects of Habitat Alteration on HSI of Study Area

The effect of a rapid increase in regenerating forests on HSI was demonstrated by comparing HSI of 81 km² of WMU I before and after heavy ice damaged much of the deciduous forest canopy above 1,000m in 1998 (Fig. 9). The Vermont Department of Forest Parks and Recreation (VDFPR) mapped statewide ice damage into 2 categories labeled “heavy” and “moderate”. Forests were considered “heavily” damaged if > 50% of the forest canopy was damaged. This heavy damage to the forest canopy simulated the effect of harvest practices, which stimulate regeneration in the

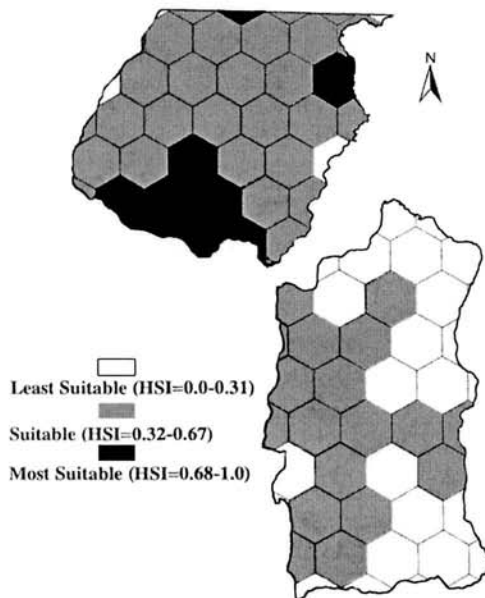


Fig. 8. Relative habitat suitability indices of 25-km² evaluation units for WMUs. “Least suitable” units had suitability indices between 0.0 and 0.31, “suitable” between 0.32 and 0.66, and “most suitable” between 0.67 and 1.0.



Fig. 9. Heavily damaged area in WMU I from January 1998 ice storm (Forest Service Data).

understory, and improve habitat for moose (Monthey 1984, Crête 1988). Therefore, the “heavy” damage areas were treated as regenerating forest for this analysis. Since ice damage was restricted to mature deciduous species, there was a corresponding decrease in deciduous/mixed forest with an increase in regenerating forests. Percent area of spruce/fir and non-forested wetlands remained constant.

The effect of maturation of forest stands by elimination of timber harvest was simulated on 108 km² of land purchased in August 1999 by the USFWS from Champion International Corporation. These lands purchased within WMU E1 were added to the Silvio O. Conte National Fish and Wildlife Refuge. The USFWS is presently drafting a management plan for the region and is exploring several management options. One possibility supported by some conservation groups is to maintain the area as a “natural ecosystem” which could eliminate or significantly reduce the intensity and frequency of timber harvest that creates a mosaic of age classes and cover types that is ideal habitat for moose. As these forests mature, the amount of early successional vegetation would be reduced and habitat quality for moose would decline (Peek et al. 1976, Collins and Schwartz 1998). This management alternative would be a contrast to the steady commercial cutting practices that have maintained this area as the state’s most productive moose habitat. The HSI value under current management of active timber harvest was compared to HSI values following a simulated 20-year no-cut policy. For the simulation, area in regenerating forest of the parcel was reduced from 21% to 1%. This 1% was the amount of regeneration assumed to occur in any non-managed stand due to natural environmental causes. The area allowed to mature was assigned to the spruce/fir or deciduous/mixed forest variables based on its cover

type classification from the vegetation grid map (D. Williams, Spatial Analysis Laboratory, University of Vermont, unpublished data). Area of non-forested wetlands remained constant.

Model Validation

HSI model validation is a process that determines whether a model accurately predicts habitat quality from the animal's perspective. Initial validation of Model II was accomplished by correlating October moose harvest density (moose/km²) to HSI for 25-km² evaluation units within WMU E1. Wildlife Management Unit I was omitted from this analysis because it had been hunted for just 1 year and only 6 moose were harvested. Moose harvest locations recorded for WMU E1 from 1993-1999 were used for analysis. Twenty-five kilometer square evaluation units with > 95% of their areas within WMU E1 were used in the analysis ($n = 21$). One hundred fifty-seven moose harvested were within the 21 evaluation units. The non-parametric Spearman rank correlation coefficient was used for analysis because distribution of evaluation unit HSI values was not normal. For this analysis, it was assumed that moose, during the fall hunting season, are occupying habitats with the greatest HSI values, and therefore moose harvest should be highest in units with the greatest HSI. A positive correlation between HSI and moose harvest would support validation of the model.

Results

Moose HSI Model II revealed large differences in habitat suitability between WMU E1 (HIS = 0.64) and WMU I (HIS = 0.34) based on differences in variable composition (Table 2). Wildlife Management Unit E1 contained 17% regenerating forest (SI = 0.42), 2% non-forested wetland (SI = 0.48), 14% spruce/fir forest (SI = 1.0), and 63% deciduous/mixed forest (S = 0.82). Wildlife Management Unit I contained 4% regenerating forest (SI = 0.11), 1% non-forested wetland (SI = 0.32), 10% spruce/fir forest (SI = 1.0), and 84% deciduous/mixed forest (SI = 0.37). Wildlife Management Unit E1 contained greater amounts of regenerating forest and non-forested wetland, and lesser amounts of deciduous/mixed forest than WMU I. Each WMU contained optimal amounts of spruce/fir forest, less than optimal amounts of regenerating forest and non-forested wetland, and more than optimal amounts of deciduous forests.

Within-WMU HSI variation was found in both study areas between 25-km² evaluation units (Fig. 8). Evaluation units classified as "most suitable" (HIS = 0.67-1.0) had the greatest area of regenerating forest, non-forested wetland, and optimal area in spruce/fir forest, while the "least suitable" (HIS = 0.0-0.31) units had a lesser abundance of regenerating forest and non-forested wetland, and an overabundance of deciduous/mixed forest. Wildlife Management Unit E1 had approximately 20% of its

Table 2. Habitat Suitability Index values for WMU E1 and I (Variable 1 = regenerating forest, Variable 2 = non-forested wetland, Variable 3 = spruce/fir forest, Variable 4 = deciduous/mixed forest).

WMU	Area (km ²)	Percent area of model variables / suitability index (SI)				WMU HSI
		Variable 1	Variable 2	Variable 3	Variable 4	
E1	680	16.90/0.42	1.72/0.48	14.30/1.00	63.40/0.82	0.64
I	729	4.46/0.11	0.73/0.32	9.76/1.00	83.76/0.37	0.34

Table 3. Change in HSI of 81 km² of heavily damaged forest and WMU I following an ice storm in January 1998 (Variable 1 = regenerating forest, Variable 2 = non-forested wetland, Variable 3 = spruce/ fir forest, Variable 4 = deciduous/mixed forest).

Study Area		Percent area of model variables / suitability index (SI)				HSI
		Variable 1	Variable 2	Variable 3	Variable 4	
HID ¹ (B) ²	81	2.95/0.07	0.00/0.20	26.60/0.86	70.10/0.67	0.30
HID ¹ (A) ²	81	55.54/0.89	0.00/0.20	26.60/0.86	17.51/0.51	0.53
WMU I(B) ²	729	4.46/0.11	0.73/0.32	9.48/1.00	78.92/0.47	0.36
WMU I(A) ²	729	10.30/0.26	0.73/0.32	9.48/1.00	73.06/0.60	0.47

¹HID = Heavy Ice Damage.

²B = before ice damage, A = after ice damage.

area in “most suitable” habitat and 80% in “suitable” (HSI = 0.32-0.67) habitat. “Most suitable” habitats were located in the south-central portion of WMU E1 and approximated the boundary of the Nulhegan Basin. One evaluation unit in the northeast corner also contained “most suitable” habitat. Wildlife Management Unit I lacked any units in the “most suitable” category but had approximately 50% of its area in “suitable” habitat. “Suitable” habitats were located in the western half of the study area and in the east-central portion.

The model predicted that HSI increased from 0.30 to 0.53 in 81 km² of WMU I, which was heavily damaged by an ice storm in 1998 (Fig. 9) (Table 3). An increase in percent area of regenerating forest from 3% to 56% caused an increase in SI from 0.07 to 0.9. A corresponding decrease in deciduous/mixed forest from 70% to 18% caused a decrease in SI from 0.67 to 0.51, but caused an increase in the deciduous/mixed forest SI for the entire WMU. Due to ice storm damage, area in regenerating forest doubled in the entire WMU and caused an increase in SI from 0.11 to 0.26. Habitat Suitability Index of the entire WMU increased from 0.36 to 0.47 as a result of the storm.

Within the 108 km² of the Silvio O. Conte National Fish and Wildlife Refuge parcel, habitat suitability was shown to decrease from 0.81 to 0.35 after 20 years of a simulated no-cut policy (Table 4). Over the 20-year simulation, a reduction of percent area of regenerating forest from 21% to 1% was offset by a corresponding 10% increase in both spruce/fir and deciduous/mixed forests. Within the parcel, SI of regenerating forest decreased from 0.53 to 0.03 and SI of spruce/fir and deciduous/mixed forest also declined. Within the entire WMU E1, HSI was predicted to decrease from 0.64 to 0.60.

Correlation of HSI to moose harvest density for 25-km² evaluation units within WMU E1 revealed a Spearman coefficient of $r = 0.53$ ($P = 0.013$) and an increasing trend in moose harvests with an increase in HSI of the evaluation unit (Fig. 10). A HSI of 0.64 for WMU E1 and 0.32 for WMU I compared proportionately to estimated moose density of 0.40 moose/km² and 0.10 moose/km², respectively (C. Alexander, VTDFW, personal communication).

DISCUSSION

Moose HSI Model II predicted differences in habitat suitability between WMU

Table 4. Change in HSI of Silvio O. Conte National Fish and Wildlife Refuge lands and entire WMU E1 following a simulated 20 year no-cut policy (Variable 1 = regenerating forest, Variable 2 = non-forested wetland, Variable 3 = spruce/fir forest, Variable 4 = deciduous/mixed forest).

Study Area	Area (km ²)	Percent area of model variables / suitability index (SI)				HSI
		Variable 1	Variable 2	Variable 3	Variable 4	
Silvio Conte	108	21.20/0.53	4.09/0.85	19.00/0.95	51.63/1.00	0.81
Silvio Conte +20	108	1.00/0.03	4.09/0.85	29.60/0.82	62.24/0.84	0.35
WMU E1	680	16.90/0.42	1.72/0.48	11.32/1.00	63.40/0.82	0.64
WMU E1 +20	680	13.73/0.34	1.72/0.48	13.03/1.00	65.15/0.78	0.60

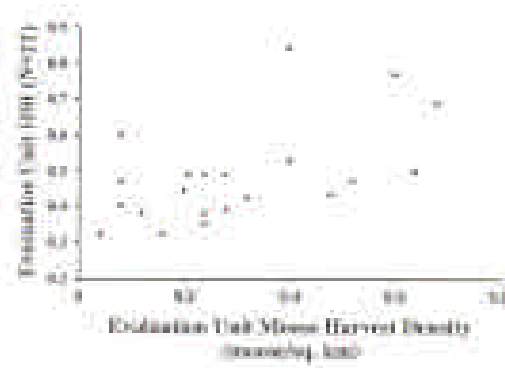


Fig. 10. Moose harvest density versus evaluation unit HSI for WMU E1. Spearman correlation: $r = 0.53$, $P = 0.013$, $n = 21$.

E1 and WMU I that reflect differences in VTDFW moose densities of 0.4 moose/km² and 0.1 moose/km², respectively. Calculated HSI values were 0.64 for WMU E1 and 0.34 for WMU I. This difference in HSI value was due to the greater percentage of regenerating forest and non-forested wetland, and the lesser percentage of mature deciduous/mixed forest in WMU E1 compared to WMU I. On a percentage basis, WMU E1 had 278% more regenerating forest, 136% more non-forested wetland, and 24% less deciduous/mixed forest than WMU I. These data support the theory of Telfer (1978) and Collins and Helm (1997) who have indicated that the abundance of regenerating forest is often the most limiting factor to moose density. These data,

which describe relative moose habitat suitability per WMU, will be useful to wildlife agencies for meeting their moose management objectives and for assisting members of the public in choosing their desired regional moose population levels in states where public opinion is considered for moose management. For instance, within Vermont's "Moose Investigation Project Statement", the VTDFW identifies the need to determine relative habitat suitability per WMU using remotely sensed land-use databases, GIS, and HSI models. The VTDFW also solicits public opinion when making moose management decisions.

Model II also identified variation in habitat suitability within WMUs. The abundance of "most suitable" habitat in WMU E1 was due to a concentration of regenerating forest and non-forested wetland habitats in the Nulhegan Basin. "Suitable" habitat was found throughout the rest of the WMU where lesser amounts of these components exist, and "least suitable" habitat was found on the perimeter of the WMU associated with high concentrations of development and agriculture. WMU I contained no evaluation units with "most suitable" habitat because the WMU as a whole was deficient in regenerating forest and non-forested wetlands. In WMU I "suitable" evaluation units were found to the

west of the Green Mountain spine in association with the highest concentrations of non-forested wetlands and regenerating forest (Figs. 4 and 5). Also, the east central portion of WMU I was heavily cut by the Forest Service in the 1980s and retains a “suitable” classification. Because of its steep mountainous terrain, the remainder of WMU I contains less standing water, is less accessible to logging, and has a “least suitable” classification. Differences in habitat suitability of adjacent evaluation units in both WMUs can be attributed to differences in topography, which determines the ability of the land to develop wetlands and dictates accessibility for logging. In WMU I, suitable habitats are concentrated in flatter areas to the west of the Green Mountain Ridge, and in WMU E1 habitat suitability of areas surrounding the Nulhegan Basin decreases as the basin rises up to the surrounding mountains.

The potential effects of ice damage on habitat suitability were illustrated through HSI analysis before and after an ice storm in January 1998 damaged the deciduous canopy of 81 km² of WMU I (Fig. 9). Increased HSI from 0.30 to 0.53 (an increase of 77%) was due to a significant increase of regenerating forest and a corresponding decrease in deciduous/mixed forest. This same increase in regenerating forest contributed to an increase in HSI of the entire WMU I from 0.36 to 0.47 (an increase of 31%). This effect of ice damage on HSI illustrates how natural events can rapidly affect habitat quality for moose. However, ice storm damage may not cause permanent canopy opening in the affected areas and the resulting increase in production of ground level browse may be short-lived. Studies are presently under way to determine the long-term effects of the 1998 storm on the forest canopy, and these should reveal how long damaged areas will continue to provide regenerating browse. Other

environmental factors such as heavy defoliation by forest insects such as spruce budworm (*Choristoneura fumiferana*), which defoliated 56% of all spruce and balsam fir in Vermont in 1983 (R. Kelley, Vermont Department of Forests, Parks and Recreation, personal communication), tree disease, and wind-throw can have similar effects on moose habitat.

The 108-km² parcel purchased by the USFWS in 1999 from Champion International Corporation contains much of the Nulhegan Basin. The Nulhegan Basin is arguably the most productive moose habitat in the state based on number of moose harvested, automobile-moose collisions, and sightings. Of 187 moose harvests located in WMU E1 from 1993-1997, 30% were within the approximate boundary of the Nulhegan Basin. Model II predicted that after 20 years of a no-cutting policy, HSI of the parcel would decrease from 0.81 to 0.35 (a reduction of 57%), due to a significant reduction in regenerating forest and a corresponding increase in spruce/fir and deciduous/mixed forests. Following 20 years of maturation, this forest will still provide valuable winter cover and non-forested wetland habitats, but would supply limited understory browse. If the suitability of the habitat is reduced by this amount, I project significant declines in the moose population and moose harvest in this area.

Habitat Suitability Index output also was used to support validation of Model II. The ideal method to validate HSI models is to compare model output to known population numbers of target species within the study area. Since these data are usually unattainable, indicators of species abundance are utilized (Clark and Lewis 1983, Laymon and Barrett 1986, Thomas et al. 1991, Robel et al. 1993). Another common method used to validate models is to compare HSI output of known-use sites to random sites in order to test that the model can differentiate be-

tween the two (Allen et al. 1991, Brennan 1991, Apps and Kinley 1998). For this study, moose harvest density was used as an indicator of species abundance for initial validation. A Spearman correlation of HSI output to moose harvest density for 21-WMU E1 evaluation units ($r = 0.53$, $P = 0.013$) indicated the tendency for moose harvest density to increase with an increase in HSI (Fig. 10). A positive relationship between HSI and VTDFW estimated moose densities, for both WMUs, also supports validation of Model II. Additional research to further validate the use of Model II for Vermont includes locating heavy use-sites using GPS collars on moose and correlating these to HSI, and comparing HSI of heavy use-sites to that of random sites. A study to analyze the effects of road density on moose harvest, since hunter access to moose is most likely correlated to road access to hunting areas, also could be conducted.

Results of HSI evaluation only should be used to predict the potential of habitat to support moose and not as a predictor of population density. Too many other factors exist, which can reduce moose abundance even when habitat is favorable, that are not addressed in the model. In Vermont, these include traffic and road density that influence the number of moose/car collisions, deer density and infection rate of brain worm (*Parelaphostrongylus tenuis*), winter severity, illegal harvest, black bear predation on moose calves, the number of hunting permits issued, and inter-specific competition for food.

This study demonstrated that Model II is useful for analyzing large tracts of moose habitat. In view of the rate and scale at which humans alter the environment, it is important to look at habitat from a landscape perspective. Too often we concern ourselves with ecological processes on a small scale, unaware of large changes occurring around us. With advances in higher

resolution satellite imagery and the availability of a greater selection of satellite data scenes, the analysis of large habitats will become simpler. Landsat 7 satellite data are currently available from the United States Geological Survey (USGS) at 30m resolution. Landsat 7 records Enhanced Thematic Mapper Plus (ETM+) data in 7 spectral bands plus an eighth panchromatic band, combines synoptic coverage, high spatial resolution (15 m from the panchromatic band), a high spectral band range (450-2350 nm), increased spatial resolution of the thermal IR band (band 6), and 5% radiometric calibration (USGS 2000, unpublished data). Minimally processed data, known as Level 0-R data, are available at 475 U.S. dollars/scene and Levels 1-R (radiometrically corrected) and 1-G (radiometrically and geometrically corrected) data are available at 600 U.S. dollars/scene. These costs are substantially lower than prices for current Landsat 5 data (USGS, <http://edc.usgs.gov/buspartners/satellite/satellite-program.html>). Because Landsat 7 records image data of the entire world every 16 days, users can choose data from up to 22 different dates of the year for a particular study area. Higher resolution imagery will enhance the ability to differentiate between regenerating and mature forest for HSI model applications for moose.

Suggested Modifications to Model II

Renecker and Hudson (1986, 1990) observed heat stress in moose, characterized by an increase in metabolism and respiration rate, when temperatures exceeded 14°C in summer and -5°C in winter. Such stress can result in depressed foraging activity and weight loss. Telfer (1984) observed that the southern limit of holarctic moose distribution corresponded closely to the 20°C July isotherm and that high temperatures that reduce reproductive performance might restrict the southern expansion

of moose range into areas with adequate habitat otherwise. To reduce effects of heat stress, moose seek shade in dense cover and wet areas to bed, thereby reducing energy expenditure, respiration, and metabolism. From National Oceanic and Atmospheric Administration (NOAA) data (November 1998 – October 1999), I calculated the number of days that temperatures exceeded 20°C between May and September when moose are in summer pelage, and -5°C between October and April when moose are in winter pelage for both WMUs. Approximately 310 days in both Island Pond (WMU E1) and South Lincoln (WMU I) exceeded these limits. Temperatures at higher elevation beneath forest canopy where moose can escape heat would have been slightly lower, but these numbers still establish that moose are subjected to many days of heat stress. I believe there exists a threshold number of days above heat stress thresholds that moose simply cannot tolerate, and that habitat selection in Vermont, and especially in southern New England, is temperature-dependent. The addition of a variable that quantifies the number of days, and the number of hours per day, temperatures exceed heat stress threshold likely would enhance accuracy of this model in New England and help predict the southern limit to moose range. Also, if trends in global warming continue, the management of heat sensitive species such as moose and caribou (*Rangifer tarandus*) will depend on determining the potential of traditional habitats to continue to provide for these animals.

To validate this model with the additional variable for heat stress, moose habitat selection during times of heat stress should be monitored and correlated to HSI. The use of GPS collars would be essential in acquiring these data. A study of moose activity and metabolism during these times also would provide data on behavioral and

physiological changes associated with heat stress. Collars fitted with an activity counter and temperature sensor could gather these data.

MANAGEMENT IMPLICATIONS

The results of this study indicate that in both WMUs, percent area of deciduous/mixed forest exceeds the amount for optimum habitat suitability, percent area of spruce/fir forest exists at optimal amounts, and the area of regenerating forests and non-forested wetlands exist in quantities well below that needed for optimum habitat suitability. Non-forested wetland and regenerating forest are therefore most limiting to moose habitat suitability. With the number of beavers in the state increasing due to a decline in trapping, and legislation protecting wetland habitats, it appears that the present quantity and quality of non-forested wetland habitats will improve. However, a decreasing trend in heavy cutting throughout much of the state since the mid-1980s could reduce the occurrence of regenerating forests. To achieve the goals of moose management in Vermont of maintaining moose populations at or above current densities, and to increase benefits associated with moose such as viewing and hunting, the continued use of forestry practices that create regenerating forests, and the continued protection of non-forested wetland habitat are desirable. Resource managers also should strive to maintain habitat quality within the “suitable” and “most suitable” habitats as identified by Model II. Since timber management has a great impact on moose habitat quality, (Courtois 1993, Palidwor et al. 1995, Rempel et al. 1997, Romito et al. 1998), forest and wildlife managers should strive to integrate the use of moose HSI models at the landscape scale into timber management practices.

ACKNOWLEDGEMENTS

This study was funded by Remo Pizzagalli and the Pope & Young Conservation Fund. Thanks to Cedric Alexander for continued interest and guidance, and to the Vermont Department of Fish and Wildlife, Vermont Department of Forest, Parks & Recreation, National Wetland Inventory, and Vermont Mapping Program for providing data. Thank you David Hirth, Jeffrey Hughes, and Ruth Mickey for guidance as committee members and to the entire University of Vermont Spatial Analysis Lab staff for technical support. Special thanks to Lisa Osborn who offered her endless support throughout the project.

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