TESTING HABITAT SUITABILITY MODELS FOR ROOSEVELT ELK

by

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We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

June 1995

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Department of Animal Science

The University of British Columbia
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Date June 30, 1995
ABSTRACT

Seasonal habitat suitability models for Roosevelt elk, *Cervus elaphus roosevelti*, (Brunt 1991) were tested using two distinctly different study areas on northern Vancouver Island, British Columbia. Locations for 5 radio-collared elk, obtained approximately twice per week by telemetry from May 1992 to August 1993, were used to test the models. I used the adaptive kernel method to estimate seasonal home ranges from each elk's locations. Habitat suitability values for summer, mild winter, and severe winter were calculated across each study area on a geographic information system (GIS), using input variables from forest cover, topology, and understory coverages. I compared the suitability values of elk locations to values within home ranges and across study areas, and the suitability values of seasonal home ranges to those across the study areas. The home ranges were further compared with equal sized, circular areas randomly placed in the study areas. Because elk generally used areas of higher suitability than expected, I concluded that the model had some ability to predict areas which contained suitable elk habitat. I also identified limitations of the model.
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I would like to thank Marco Passeri for his friendship, love and support throughout the study, and his companionship outside the study. I would also like to thank my parents, for without their love and faith in me, none of this would have happened.

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INTRODUCTION

In British Columbia, forest management occurs throughout the province and often conflicts with wildlife management. Such is the case with Roosevelt elk (*Cervus elaphus roosevelti*) on Vancouver Island, British Columbia, whose preferred habitat on rich valley floors also includes the most valuable timber. Although elk bring far less to the economy than do wood products, they are still a major economic benefit for the province. The total monetary value of elk in B.C. in 1993-94, including actual expenditures and willingness to pay by both resident and non-resident hunters, was $22.7 million in 1994 dollars (D. Janz, pers. comm.). In addition, many people enjoy the chance to see or photograph these and other wild animals. Herd sizes are monitored by the B.C. Ministry of Environment, Lands and Parks (MOELP) to relate population response to environmental and habitat conditions, and to set quotas for limited entry hunting on the Island. Both elk and forestry are important to British Columbians, and the need for elk habitat should be considered in logging plans. Habitat models could provide the necessary information to help forest managers maintain adequate elk habitat so that elk and forestry may coexist.

Habitats used by elk in particular areas have been determined by radio-telemetry studies (Witmer and deCalesta 1983, Marcum and Scott 1985, Edge *et al.* 1987, Brunt *et al.* 1989, Edge and Marcum 1989, Merrill 1991, McCorquodale 1993), by examining elk sign (Schwartz and Mitchell 1945; Marcum and Scott 1985; Edge and Marcum 1989), or by observing tame (Irwin and Peek 1983; Parker *et al.* 1984) or wild (Schwartz and Mitchell 1945; Knight 1970; Hanley 1984) elk. However, all these methods are labour intensive and site-specific. For this reason, Brunt (1991)
developed habitat suitability index (HSI) models for Roosevelt elk on Vancouver Island. Theoretically, these models could be used anywhere on Vancouver Island to predict how suitable the habitat is for elk.

The development of HSI models began in the mid-1970s so that wildlife managers could determine which species and habitats were present on lands within their jurisdictions and make more informed decisions about land use (Berry 1986). HSI and other wildlife-habitat models have been developed for species which are managed for hunting, such as black bear *Ursus americanus* (Clark et al. 1993), brown bear *Ursus arctos* (Schoen et al. 1992), and Columbian black-tailed deer *Odocoileus hemionus columbianus* (Eng and Schieck 1992). Other HSI models have been developed to manage endangered species such as the northern spotted owl *Strix occidentalis caurina* (Laymon and Reid 1986), and to predict how habitat will be affected by resource industries such as mining (Lancia et al. 1986).

The HSI models for Roosevelt elk were first tested by Brunt (1991) in the southern part of Vancouver Island using newly transplanted migratory elk (low elevation in winter, and high elevation in summer), and the summer model was investigated in central Vancouver Island with non-migratory elk (Sovka 1993). Brunt’s (1991) transplanted elk would not be familiar with their surroundings; therefore, they may not have selected the optimum habitat, thus affecting the results of model testing. Further testing was needed in both summer and winter, in different areas than where the models were developed, and with established elk herds. My study was designed to test both the summer and winter models on the northern end of the Island (the limit of the subspecies’ natural range) in 2 areas with contrasting topography, and where the elk
were believed to be non-migratory. I believe that these 3 studies were sufficient to validate (or invalidate) the models for Vancouver Island because they include elk with both migration strategies and they sample areas from different parts of the island.

Validation of a model tests its ability to predict states or events (Marcot et al. 1983, Bunnell 1989). Ideally, it should be validated with new data (Lancia et al. 1982) to assess model performance and reliability (Berry 1986, Laymon and Barrett 1986, Schamberger and O'Neill 1986, Bunnell 1989). Although models can improve understanding or predictive abilities, they are still incomplete pictures of reality (Bunnell 1973) because mathematical equations cannot explain all the variables in the real world. Thus, in model testing we merely look at the model's validity - its outcome. There is no way to test for the model's veracity - whether the entire model is true.

The HSI value is determined from an assessment of the physical and biological attributes of the habitat in a patch and is assumed to be proportional to the patch's carrying capacity for an animal species (Berry 1986). With large animals such as elk, their home ranges generally include more than 1 habitat patch, so carrying capacity of small individual habitat patches cannot be measured. The HSI value given to a habitat patch thus represents the expected value of that patch to the animal, relative to other habitat types. Animals should select higher quality habitat whenever possible to increase their fitness (Schamberger and O'Neill 1986). To obtain an indication of habitat use by elk, I examined the locations and home ranges of radio-collared elk and compared their HSI values to those of the available habitat types in the study areas. The null hypotheses for the validation tests stated that the HSI values of areas used by elk did not differ significantly from those of the available area. I investigated Johnson's
(1980) second and third order of selection (i.e. the area selected by the elk for their home range, and patterns of use within that home range).

METHODS

Study Areas

Benson

The Benson River valley lies on northern Vancouver Island about 40 km south of Port McNeill (Figure 1). My study area extended from the headwaters of the river to Kathleen Lake, bounded approximately by the height of land on either side of the valley. The elevation rises from 80 m to 1400 m above sea level. The valley lies within the Very Wet Maritime Coastal Western Hemlock Zone (CWH) below 800-900 m, and within the Mountain Hemlock Zone (MH) at higher elevations (T. Lewis pers. comm.). Logging has occurred in the valley for half a century, with substantial harvesting activity in the past 2 decades. Part of the timber on the valley bottom has been set aside as Elk Winter Range, and the remaining area is a mosaic of clearcuts, second growth, mature timber, and old growth. There is an extensive network of logging roads.

Nahwitti

The Nahwitti River valley lies in the Very Wet Maritime CWH zone, on the north coast of Vancouver Island about 90 km west of Port Hardy (Figure 1). My study area extended from Nahwitti Lake to the ocean, and into the plateau on either side of the valley at least half way to the next major valley. The valley is surrounded by the low hills of the Nahwitti plateau, with elevation rising from sea level to 660 m. Logging has
occurred mostly in the past 15 years, and road access is limited. Here also, a section of old growth has been set aside as Elk Winter Range.

Figure 1: Location of study areas on northern Vancouver Island, B.C.
Roosevelt elk are a popular game species and hunting in both valleys is managed by MOELP. Wolf predation in the Nahwitti valley may have depleted the number of Roosevelt elk. When wolf numbers declined and access due to logging increased, hunting was suspended by MOELP to allow the population to recover. In the Benson, I estimated the population from an aerial census. I used maximum age-sex class counts from sightings to estimate the population in the Nahwitti, where I believe the entire population sometimes came together in one group.

**Radio Telemetry**

MOELP personnel darted 3 adult (> 3 years) female elk in the Benson from a helicopter and fitted them with Telonics (Telonics Telemetry-Electronics Consultants, Mesa, Arizona) or Lotek (Lotek Engineering, Newmarket, Ontario) radio collars. The Nahwitti elk were captured in a corral trap and 2 adult females were collared, also by MOELP. I used a Telonics Yagi antenna and receiver to locate animals approximately twice per week from May 1992 to August 1993 (Table 1). Beyer and Haufler (1994)

Table 1: Total number of radio locations for each collared adult female Roosevelt elk between May 1992 and August 1993.

<table>
<thead>
<tr>
<th>Study Area</th>
<th>ID #</th>
<th># Locations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benson</td>
<td>241</td>
<td>150</td>
</tr>
<tr>
<td>Benson</td>
<td>249</td>
<td>148</td>
</tr>
<tr>
<td>Benson</td>
<td>849</td>
<td>79 *</td>
</tr>
<tr>
<td>Nahwitti</td>
<td>441</td>
<td>132</td>
</tr>
<tr>
<td>Nahwitti</td>
<td>461</td>
<td>127</td>
</tr>
</tbody>
</table>

* elk #849 died in January 1993.
suggest varying the time of day (or night) for locations; however, for safety reasons I was constrained primarily to hours when MacMillan Bloedel or Western Forest Products (WFP) personnel were in radio contact, or to times at night when I could be accompanied by someone else.

I used the loudest signal method (Springer 1979) to determine the direction to take a compass bearing. The loudest signal, however, usually came from an arc of < 30°, so the bearing was taken at its centre. Triangulation, with a minimum of 3 and a maximum of 10 bearings, was used to determine an animal's location. The time between each bearing was kept short to reduce error due to animal movement (Schmutz and White 1990; Saltz 1994). I continued to take bearings, and draw them on a map in the field, until I had at least 3 strong signals with bearings which converged on an area approximately < 2 ha. The location was taken as the approximate centre of this area, with more weight given to bearings with stronger signals, and less to probable outliers.

An estimate of triangulation precision (error in the locations) was made using the average distance from the mapped point to the known location of all collared animals sighted just after triangulations were completed. I expected the true location of the animal to be within a circle of that radius, centred on the triangulated point. For 41 locations in the Benson and 63 in the Nahwitti, the collared elk were sighted before triangulation was complete, and the locations were drawn on the field map as points. Errors in these locations were from 2 sources: my ability to place the point on the map, and any inaccuracies in the map itself.
The locations were categorized as summer 1992, winter, or summer 1993. I used a combination of migration times from other Roosevelt elk herds on the Island, and plant phenology to determine the shifts between seasons. Summer began on April 15, and winter began on November 15.

Home Ranges

The home range of an animal is the area traversed by that individual in its normal activities of food gathering, mating, and caring for young (Burt 1943). Several methods of calculating the home range from a set of animal locations exist. I compared the adaptive kernel method (Worton 1989) in the program KERNELHR (Seaman and Powell 1991) to the harmonic mean method (Dixon and Chapman 1980) in Program Home Range (Ackerman et al. 1990). I believe the home ranges that I calculated using the adaptive kernel method fit the data and the topography better than did those using the harmonic mean method (which included high elevation areas that elk never were observed to use). The adaptive kernel method is a robust estimator of the utilization distribution because it does not assume any underlying distribution, and it is also very good at estimating areas of concentrated activity (Worton 1987). Furthermore, Program Home Range required input of an arbitrary smoothing constant which affected the resulting home range size (D. Sovka, pers. comm.). In KERNELHR, the optimal smoothing constant was chosen automatically by cross validation (Worton 1989), which provides an obvious advantage over the harmonic mean method (Larkin and Halkin 1994).

I used KERNELHR to calculate home ranges from the animal locations for each individual, in each season. I avoided pooling locations across individuals (Aebischer et
al. 1993) and seasons (Schooley 1994) so that behavioural variation among individuals and annual variation among seasons would not be lost. Programs written by F. Hovey (SFU) were used to import the resulting density probability grid into Stanford Graphics 2.1 as a matrix, and to provide the density levels for 95% contours. These contours enclosed an area within which the probability of locating the animal was 95%, and I considered this to be the home range. The contours were saved as polygons in text files (DXF) readable by a geographic information system.

Elk #849 died at the beginning of January, after only 14 winter locations. I included the last 6 summer locations in the home range calculation because the minimum number of locations for the adaptive kernel method was 20. Therefore, results for elk #849's winter home range should be interpreted conservatively.

**Geographic Information System (GIS)**

To analyze the spatial data, I used the GIS Terrasoft 10 (Digital Resource Systems Limited, Nanaimo, B.C.) and Idrisi 4.0 (Clark University Graduate School of Geography, Worcester, Massachusetts). For the Benson and Nahwitti, topographic features including roads, rivers, streams, lakes, and contours were available on 1:20 000 digital "Terrain Resource Information Management" (TRIM) maps from MOELP. Dr. Terrence Lewis (Consulting in Soils and Land Use, Courtenay, BC) created understory based habitat maps of the study areas from 1:15 000 aerial photographs and site visits. For the Benson, I digitized the map into the GIS, and for the Nahwitti, Lewis' photo-interpretation linework was digitally mapped with a stereo analytic plotter (Darren Ham, Dept. of Geography, UBC) and entered into the GIS. MacMillan Bloedel and MOELP provided digital forest cover maps for the Benson and Nahwitti.
respectively, both of which I updated to 1993 and adjusted to the same coordinate system (UTM NAD83) as the TRIM map using The Geographic Calculator 2.0 (Blue Marble Geographics, Gardiner, Maine). Finally, I digitized elk locations and home ranges.

To calculate the suitability values, I used raster (grid cell based) rather than vector (line based) analysis for 4 reasons:

1) the accuracy of the elk locations was about 30 to 40 m, and with my chosen pixel size of 20 m, no accuracy was lost;
2) the accuracy of the habitat and forest cover maps after being merged with the TRIM map was probably no better than 20 m;
3) two of the variables (aspect and elevation) originated as raster layers; and
4) it is a much faster method, requiring less disk space.

Model

Separate model algorithms were created for summer, mild winter, and severe winter. Basically, the models use 5 habitat factors (forage, cover, interspersion, aspect and elevation) as input variables, the last 2 of which are used as modifiers in winter.

Forage

Preferred elk forage (Brunt 1990) consists of a combination of trees (the most important species are western hemlock and amabilis fir), shrubs (e.g., dull oregon grape, Pacific ninebark, red elderberry, huckleberry/blueberry, willow, salmonberry), ferns (e.g., deer and sword), and herbs (e.g., bunchberry, twinflower, sedges, and grasses) [Latin names for plants are given in Appendix 2]. Season dictates the
proportions of each group found in the diet. For example, conifers are nearly absent from the summer diet, but considered to make up almost half the diet in winter (Brunt 1990).

Forage values (Table 2) varying between 0.0 and 1.0 (with 1 being ideal) were based on habitat types, and then modified by overstory conditions. The modifier values (Table 3) are an index of canopy closure.

Cover

Elk use cover for at least 3 reasons: to avoid extreme temperatures, to take advantage of lesser snow accumulations in winter, and to avoid predators or human harassment. Brunt (1991) combined snow interception cover with thermal cover, and I will refer to the combination as thermal cover. Because cover is either present or absent, cover values (Table 2) were either 0.99 or 0.0 (the value 1 would cause division by zero in the algorithm). Brunt (1991) assumed that thermal cover was adequate in forested stands >10 m in height and with >70% mean canopy closure, while security cover was adequate in any stand >3 m in height. I used age of a forest stand to estimate tree height and canopy closure; security cover values in those stands < 8 years old, and thermal cover values in stands < 20 years old were multiplied by 0.0 to indicate the absence of cover.

The habitat mapping done by T. Lewis identified more habitat types than did Brunt's understory mapping. Lewis correlated his system to Brunt's where possible, and estimated the forage and cover values for those habitat types not listed by Brunt (see Table 2). One discrepancy between the two systems is that whereas Brunt uses
Table 2. Cover and potential forage suitability values by habitat type (Brunt 1991, Lewis, unpubl.). See Appendix 1 for explanation of habitat types.

<table>
<thead>
<tr>
<th>Lewis' Habitat Type</th>
<th>Brunt's Primary Understory</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>S11</td>
<td>Bog/Wetland</td>
<td>0.00</td>
<td>0.00</td>
<td>0.99</td>
<td>0.90</td>
</tr>
<tr>
<td>S1HA, MH1, M1, M1c, M1s</td>
<td>Huckleberry-Moss</td>
<td>0.99</td>
<td>0.99</td>
<td>0.20</td>
<td>0.30</td>
</tr>
<tr>
<td>P</td>
<td>Lichen-Pink mountain heather</td>
<td>0.99</td>
<td>0.00</td>
<td>0.10</td>
<td>0.20</td>
</tr>
<tr>
<td>S2f, S12f</td>
<td>Lichen-Salal</td>
<td>0.99</td>
<td>0.00</td>
<td>0.20</td>
<td>0.10</td>
</tr>
<tr>
<td>M3, M3c, M5</td>
<td>Rosy twistedstalk-5 leaved bramble</td>
<td>0.99</td>
<td>0.00</td>
<td>0.30</td>
<td>0.30</td>
</tr>
<tr>
<td>S1ch, S2, S12, S10, S12ch, M2</td>
<td>Salal-Huckleberry</td>
<td>0.99</td>
<td>0.00</td>
<td>0.40</td>
<td>0.20</td>
</tr>
<tr>
<td>S3, S3b, S4</td>
<td>Salmonberry</td>
<td>0.99</td>
<td>0.00</td>
<td>0.80</td>
<td>0.80</td>
</tr>
<tr>
<td>A</td>
<td>Slide Complex</td>
<td>0.00</td>
<td>0.00</td>
<td>0.50</td>
<td>0.99</td>
</tr>
<tr>
<td>S1c, S13, S13l</td>
<td>Sword Fern</td>
<td>0.99</td>
<td>0.99</td>
<td>0.80</td>
<td>0.70</td>
</tr>
<tr>
<td>S5, S7**</td>
<td>Skunk Cabbage</td>
<td>0.99</td>
<td>0.00</td>
<td>0.75</td>
<td>0.80</td>
</tr>
<tr>
<td>S6</td>
<td>Skunk Cabbage</td>
<td>0.99</td>
<td>0.00</td>
<td>0.40</td>
<td>0.60</td>
</tr>
<tr>
<td>M4</td>
<td>Skunk Cabbage</td>
<td>0.99</td>
<td>0.00</td>
<td>0.10</td>
<td>0.60</td>
</tr>
<tr>
<td>MH2</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.14</td>
<td>0.20</td>
</tr>
<tr>
<td>AT</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.10</td>
<td>0.20</td>
</tr>
<tr>
<td>S8</td>
<td>Sphagnum</td>
<td>0.00</td>
<td>0.00</td>
<td>0.25</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>[with Labrador tea]</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S9</td>
<td>Sphagnum [treeless]</td>
<td>0.00</td>
<td>0.00</td>
<td>0.90</td>
<td>0.90</td>
</tr>
<tr>
<td>S15</td>
<td>Deer Fern</td>
<td>0.99</td>
<td>0.99</td>
<td>0.50</td>
<td>0.60</td>
</tr>
<tr>
<td>CP</td>
<td>Sphagnum-deer fern</td>
<td>0.99</td>
<td>0.00</td>
<td>0.70</td>
<td>0.75</td>
</tr>
<tr>
<td>W</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.40</td>
<td>0.50</td>
</tr>
<tr>
<td>R, NV, Talus</td>
<td>-</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

* A=Security Cover, B=Thermal/Snow Interception Cover, C=Potential Winter Forage, D=Potential Summer Forage

** Forage and cover values for remaining habitats, which were not given by Brunt (1991), were estimated by T. Lewis.
Table 3: Forage modifier values from Brunt (1991).

<table>
<thead>
<tr>
<th>HABITAT</th>
<th>FORAGE MODIFIER VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Logged ≤ 2 years previously</td>
<td>0.40</td>
</tr>
<tr>
<td>Logged 3 - 5 years previously</td>
<td>0.75</td>
</tr>
<tr>
<td>Logged 6 - 15 years previously</td>
<td>1.00</td>
</tr>
<tr>
<td>Logged 16 - 20 years previously(^1)</td>
<td>0.50</td>
</tr>
<tr>
<td>Logged 21 - 50 years previously(^1)</td>
<td>0.10</td>
</tr>
<tr>
<td>Logged &gt; 50 years previously(^1)</td>
<td>see unlogged</td>
</tr>
<tr>
<td>Unlogged - deciduous dominated overstory(^2)</td>
<td>0.75</td>
</tr>
<tr>
<td>Unlogged - conifer dominated overstory(^3)</td>
<td>0.50</td>
</tr>
<tr>
<td>Bog/Wetland, Rock outcrop, and Slide Complex</td>
<td>1.00</td>
</tr>
</tbody>
</table>

\(^1\)From Brunt (pers. comm.).
\(^2\)Deer fern, Salmonberry, and Swordfern understory types.
\(^3\)All other understory types with the exception of Bog/Wetlands, Rock outcrops, and Slide complexes.

elevation/aspect modifiers to identify snowpack zones, Lewis used montane (M) areas to make this distinction. In some cases, Lewis' classification would more accurately identify certain habitats. For example, snow accumulation zones and areas with regular thermal inversions are distinguished as montane by Lewis, whereas Brunt, who uses elevation to identify montane habitats, might not separate these areas from the surrounding sub-montane habitat (T. Lewis, pers. comm.).

For polygons which contained combinations of habitats listed in Table 2, I calculated mean forage values, taking into account the proportion of each habitat type in the polygon. Lewis distinguished 3 levels of heterogeneity by his classification.
method; for example, the label S3S5 was a 50:50 ratio of the 2 habitat types S3 and S5, S3/S5 was a 65:35 ratio, and S3//S5 was an 85:15 ratio. I took cover values from the major habitat type (the first type listed in the label).

Interspersion

The interspersion of forage and cover appears to be critical to elk (Thomas et al. 1979; Skovlin 1982; Witmer et al. 1985; Brunt 1990). While the best forage grows in areas with little or no canopy cover (natural openings, clear cuts, and young forests), the most valuable cover occurs when the canopy closes (mature forests or old growth). To take advantage of the best forage and the best cover, elk would need to live along a boundary between different aged forests (Skovlin 1982). Elk will use a good forage area if it is close (< 140 m) to cover, while forage located far (> 300 m) from cover is almost never used (Brunt 1991). Interspersing different types or ages of forests increases the number and types of these boundaries, thus elk use would become more extensive in such areas.

Interspersion values are determined for the model using the distance to high quality cover (0.99) or to forage (> 0.50) areas (Table 4). I created the areas in each category by placing 140, 250 and 300 m buffers around high quality cover and forage areas in the GIS.

Aspect/Elevation

During winter, the depth and persistence of snow affects the winter suitability values because it buries forage and increases locomotion costs at a time when food is
Table 4. Interspersion modifier values from Brunt (1991).

<table>
<thead>
<tr>
<th>DISTANCE FROM COVER OR PREFERRED FORAGE AREAS (m)</th>
<th>MODIFIER VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>0*</td>
<td>1.0</td>
</tr>
<tr>
<td>&lt;140</td>
<td>1.0</td>
</tr>
<tr>
<td>141 - 249</td>
<td>0.6</td>
</tr>
<tr>
<td>250 - 300</td>
<td>0.4</td>
</tr>
<tr>
<td>&gt;300</td>
<td>0.1/0.01**</td>
</tr>
</tbody>
</table>

* Site qualifies as cover or a preferred forage area
** 0.1 for cover; 0.01 for food

limited and energy demands are high (Parker et al. 1984, Brunt 1991). Aspect and elevation combine to give a good indication of snow conditions. Snow tends to be deeper and more persistent on north slopes at high elevations than on south slopes at lower elevations. Using the GIS, I created elevation and aspect raster layers with 20 x 20 m pixel resolution from contours and used these to assign modifier values (Table 5).

Table 5. Aspect/elevation modifier values used in the mild and severe winter models from Brunt (1991).

<table>
<thead>
<tr>
<th>ELEVATION (m)</th>
<th>290-70° (NORTH)</th>
<th>71-110° (EAST)</th>
<th>110-250° (SOUTH)</th>
<th>250-290° (WEST)</th>
<th>FLAT</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-350</td>
<td>0.6</td>
<td>0.8</td>
<td>1.0</td>
<td>0.8</td>
<td>1.0</td>
</tr>
<tr>
<td>351-550</td>
<td>0.4</td>
<td>0.6</td>
<td>0.8</td>
<td>0.6</td>
<td>0.8</td>
</tr>
<tr>
<td>551-1050</td>
<td>0.2</td>
<td>0.4</td>
<td>0.6</td>
<td>0.4</td>
<td>0.6</td>
</tr>
<tr>
<td>&gt;1050</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Habitat Suitability Calculations

Using the same (20 x 20 m) pixels as the slope and aspect calculations, I created the following raster layers:

- SFOR = summer forage value (modified for logging)
- WFOR = winter forage value (modified for logging)
- TCOV = thermal cover value (modified for logging)
- SCOV = security cover value (modified for logging)
- SUMDIST = interspersion value: distance to summer forage of value ≥ 0.5
- WINDIST = interspersion value: distance to winter forage of value ≥ 0.5
- TDIST = interspersion value: distance to thermal/snow interception cover
- SDIST = interspersion value: distance to security cover
- ASP_ELEV = aspect/elevation modifier value

Brunt's (1991) model provides an HSI value for each pixel within a habitat patch. Each patch (i.e. an area which contains a homogeneous combination of mapped variables) is rated on a scale from 0.0 to 1.0 based on its estimated value for elk. I used Brunt's (1991) algorithms (below) to calculate the suitability values for each pixel, which I then put into a new raster layer for each seasonal model. The 3 seasonal models (Brunt 1991) are:

**Summer Habitat Suitability** = \( \exp(0.5\ln(1-\exp(0.7\ln(1-SFOR) + 0.15\ln(1-TCOV) + (0.15\ln(1-SCOV)))) + 0.25\ln(SUMDIST) + 0.125\ln(TDIST) + 0.125\ln(SDIST)) \)

**Mild Winter Habitat Suitability** = \( \exp(0.5\ln(1-\exp(0.7\ln(1-WFOR) + ((0.2\ln(1-TCOV)) + (0.1\ln(1-SCOV)))) + 0.25\ln(WINDIST) + 0.125\ln(TDIST) + 0.125\ln(SDIST)) \times ASP\_ELEV^{0.25} \)

**Severe Winter Habitat Suitability** = \( \exp(0.5\ln(1-\exp(0.5\ln(1-WFOR) + ((0.4\ln(1-TCOV)) + (0.1\ln(1-SCOV)))) + 0.20\ln(WINDIST) + 0.20\ln(TDIST) + 0.1\ln(SDIST)) \times ASP\_ELEV^{1.0} \)

Figure 2 illustrates how each of the input variables contribute to the summer suitability model (winter models are the same except for the final multiplication of the aspect/elevation modifier).
The raster maps of habitat suitability values consisted of pixels, each containing a suitability value (between 0.0 and 1.0). These values were used to calculate mean suitability values of areas, or to represent the suitability value at an elk location which fell within a pixel. For some tests, suitability values were grouped into 1 of 5 classes:

- 0.00 - 0.20 (Very Low)
- 0.21 - 0.40 (Low)
- 0.41 - 0.60 (Medium)
- 0.61 - 0.80 (High)
- 0.81 - 1.00 (Very High)

Using the original continuous data, or choosing a larger number of classes, would have made the results very difficult to interpret. As the number of categories increases, the frequency of locations within each category decreases and it becomes more difficult to resolve differences in the animals' behaviour. However, using too few classes would allow a very large difference in quality within the same class. An odd number of classes makes interpretation clearer by providing a "middle" category, and I chose a compromise of 5 categories for comparative purposes.

**Validation of Brunt's Models**

To validate Brunt's models, I investigated elk use and the predicted HSI values of the study areas. Assuming that the study area is large relative to the home range, a model is validated if predicted high suitability habitats are used by elk proportionally more often than they occur in the study area. Because the winter of 1992-93 was mild, I have no data to test the severe winter model, so I attempted to validate only the summer and mild winter models. I made the assumption that elk will use areas of higher quality whenever possible; therefore, I expected elk to spend more time in
Figure 2: Diagram of input variables for Brunt’s (1991) summer suitability model. The thickness of the lines relates to the relative input of the variable.
habitats with higher predicted HSI values than in those with lower ones. Because the 5 suitability classes are not necessarily available in the same amount, I would not always expect increasing use from the lowest to the highest class. However, the difference between the proportion of available habitat in each class and the proportion of time spent in each class should increase from negative to positive as the suitability moves from the lower classes to the higher classes (Figure 3).

![Suitability Class Diagram]

**Figure 3:** Expected difference between the proportion of habitats used by elk and that of the expected use if elk are using habitat classes in proportion to their availability.

In an attempt to validate Brunt's seasonal models, I employed 3 methods of testing use vs. availability at Johnson's (1980) level 2 selection (locations vs. study area, home ranges vs. study area and home ranges vs. random circles) and 1 method at Johnson's (1980) level 3 selection (locations vs. home ranges).
Use vs. Availability - Level 2 Selection

For each season and each individual, I compared the suitability values of elk use (both locations and home ranges) to what was available in the study area. Habitat availability was estimated to be the total proportion of each habitat suitability class in the study area (calculated with the GIS).

1) Locations vs. Study Area

For the elk locations, a chi-square test was used to test the null hypothesis: proportional use of suitability classes by elk does not differ from the proportions available in the study area. Expected locations were calculated as the percentage of the study area within each class, multiplied by the total number of elk locations per individual per season. Some classes were grouped together to ensure that no expected frequency was < 1.0, and no more than 20% of the expected frequencies were < 5.0 (Cochran 1954).

2) Home Ranges vs. Study Area

The chi-square test cannot be performed with home ranges because they are measured in units of area, not frequency data which the test requires. Therefore, to compare home ranges to the study area, I used only graphs to illustrate the habitat classes used by elk and those available in the study area.

3) Home Ranges vs. Random Circles

The previous test estimated availability from the proportions that each habitat type (i.e. suitability class) made up of the entire study area. Another method is to
estimate availability from random dots on a map of the study area (Marcum and Loftsgaarden 1980). However, neither of these approaches takes into account the spatial relationships among the habitats. Both assume an animal is not restricted from moving anywhere within the study area to gain resources.

Not only is the total amount (area) of habitat important for survival and reproduction, but so is the dispersion, both absolute (throughout the study area) and relative (with respect to other classes of habitat), of the valuable habitats. Suitable habitat for non-migratory elk must meet their year-round needs. It should also be continuous, or in patches which are relatively close so that they benefit (through a net gain in energy or decreased chance of predation) by using them. The farther apart valuable habitat patches are, the less useful they are to an animal because of energetic costs of locomotion and predation risks while travelling among them.

To allow a more realistic assessment of habitat availability for elk, I placed circles of equal area to each elk’s 95% home range, randomly throughout the study area to represent a random selection of seasonal ranges. A circle was chosen as the shape to place around randomly selected coordinates on the map, eliminating a source of bias due to orientation. I compared an observed elk’s seasonal range with a random sample of 50 equal-sized circles within the study area.

For each individual’s seasonal range (summer 1992, winter, summer 1993), and for each random circle, I calculated a mean HSI value. I also calculated a grand mean and standard error of all circle means, and ranked the seasonal range means along with the circle means. From the rankings, I obtained a probability estimate of potential home ranges (i.e. circles) which have lower means than the one chosen by the elk.
Assuming high quality habitat patches are smaller than the home range and are heterogeneously distributed (Wilson et al., in prep.), I would expect this probability to be high (i.e., > 80%) if the model is valid. This procedure is similar to a Monte Carlo simulation, except that only 50 home ranges were simulated (1000 is suggested as a minimum; Manly 1991, Wilson et al., in prep.). While I would have preferred to do 1000 simulations for each individual/season, it was not feasible due to computer time constraints. I compared runs of 25, 50, 75, and 100 circles, and only the 25 circles differed; therefore, I chose to use 50 as a minimum estimate.

Use within the Home Range - Level 3 selection

While the previous tests examined Johnson's (1980) level 2 selection (choice of a home range from within a larger available area), it is useful also to examine level 3 - selection of habitats within the home range (Aebischer et al. 1993, Carroll et al. 1995). To do this, I compared HSI values at locations used by elk to those available in the seasonal range. For each individual in each season, I performed a chi-square test with the observed value being the number of elk locations in each suitability class, and the expected being the proportion of each suitability class in the seasonal range multiplied by the total number of locations. This tested the null hypothesis: proportional use of suitability classes by elk does not differ from the proportions available in the seasonal range. As before, I expected the actual sites used by elk to have higher suitability values than seasonal ranges because the latter may contain areas not actually used by elk.
RESULTS

Population Estimates

Estimates of the total population of the Benson valley have been as high as 80 animals in 1991 (D. Janz, pers. comm.). However, aerial counts made on 14 January 1993 indicated at least 41 elk, found singly or in groups of 2, 8, 13, or 15, were present in the study area. Estimates of the population in the Nahwitti study area were 13 in 1990, 19 in 1991 (Rick Davidge, pers. comm.), 25 in 1992, and 34 in 1993 (my estimates based on maximum age-sex counts).

General Habitats and Movements of Elk

In general, elk were found in riparian areas and wetlands, as well as in clearcuts, young regenerating stands, and old growth on valley bottoms and lower slopes. There was no seasonal migration by collared animals, although logging truck drivers in the Benson reported seeing elk in higher elevation areas adjacent to the Benson valley only in summer. While snow was present in winter, the collared elk used clearcut or relatively open slopes at slightly higher elevations than they used throughout the rest of the year.

The collared elk were found mostly in groups, that ranged in size from 2 to 34 individuals. There was some evidence that females moved away from the group to areas of little use to give birth in spring. I identified one calving spot in a small brushy draw on a clearcut sidehill.
Telemetry Accuracy

To estimate accuracy of the locations I used only sightings of collared elk which occurred immediately after triangulation was complete. From 19 such sightings in the Benson, the location precision was 0.43 ha, and in the Nahwitti, the precision from 5 sightings was 0.28 ha.

Seasonal Ranges

While the sizes of the 2 study areas were similar, the seasonal ranges in the Nahwitti were larger in general than those in the Benson, especially 3 of the 4 summer ranges (Table 6).

Table 6: Sizes (ha) of study areas and seasonal 95% ranges used by collared elk.

<table>
<thead>
<tr>
<th>Area</th>
<th>Season</th>
<th>Elk #241</th>
<th>Elk #249</th>
<th>Elk #849</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benson</td>
<td>Summer 1992</td>
<td>288</td>
<td>242</td>
<td>1482</td>
</tr>
<tr>
<td></td>
<td>Winter 1992/93</td>
<td>259</td>
<td>253</td>
<td>663</td>
</tr>
<tr>
<td></td>
<td>Summer 1993</td>
<td>259</td>
<td>305</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>Total = 14504</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nahwitti</td>
<td>Summer 1992</td>
<td>3236</td>
<td>2380</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter 1992/93</td>
<td>1419</td>
<td>1732</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Summer 1993</td>
<td>961</td>
<td>4147</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total = 15259</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Seasonal Models

Compared to the Benson, the Nahwitti contained very little of the low suitability classes (tan and brown in Figures 4 and 5). The areas of high suitability (green areas)
in the Benson and Nahwitti are aggregated mostly on the valley bottoms near the rivers. In the Benson, the class covering the largest area is the 0.21 - 0.40 class in the summer model, and the 0.00 - 0.20 class in the mild winter model. In the Nahwitti, the 0.41 - 0.60 class covers the largest area for both seasonal models (Table 7). In both study areas, the predicted suitability of the study area, in general, decreased from summer to mild winter. The severe winter model was not tested; however, it is interesting to note the decrease in higher suitability areas from the mild to severe winter maps (Figures 4 and 5) since it is likely the amount of high quality severe winter habitat which limits a population in the long term.

Table 7: Availability of suitability classes for the 2 study areas as determined by the HSI summer and mild winter models.

<table>
<thead>
<tr>
<th>Suitability Class</th>
<th>Nahwitti Summer</th>
<th>Mild Winter</th>
<th>Benson Summer</th>
<th>Mild Winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Very Low</td>
<td>2410 (16.6)*</td>
<td>3117 (21.5)</td>
<td>3195 (20.9)</td>
<td>8350 (54.7)</td>
</tr>
<tr>
<td>Low</td>
<td>1499 (10.3)</td>
<td>1856 (12.8)</td>
<td>8184 (53.6)</td>
<td>3643 (23.8)</td>
</tr>
<tr>
<td>Medium</td>
<td>7000 (48.3)</td>
<td>7369 (50.8)</td>
<td>586 (3.8)</td>
<td>1210 (7.9)</td>
</tr>
<tr>
<td>High</td>
<td>2706 (18.7)</td>
<td>1743 (12.0)</td>
<td>1815 (11.9)</td>
<td>1180 (7.7)</td>
</tr>
<tr>
<td>Very High</td>
<td>785 (5.4)</td>
<td>315 (2.2)</td>
<td>1130 (7.4)</td>
<td>528 (3.5)</td>
</tr>
<tr>
<td>Water</td>
<td>104 (0.7)</td>
<td>104 (0.7)</td>
<td>349 (2.3)</td>
<td>349 (2.3)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>14504</strong></td>
<td><strong>15259</strong></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*area in hectares (and percentage of total area).
Figure 4: Available areas in each HSL class for the Benson study area from severe winter, mild winter, and summer models.
Figure 5: Available areas in each HSI class for the Nahwitti study area from the summer, mild winter, and severe winter models.
Tests of the Model

Level 2 selection

1) Locations vs. Study Area

For all elk in all seasons in both the Benson and Nahwitti, the distribution of locations over the 5 suitability classes was significantly different ($\alpha = 0.05$) from what was available in the study area (Table 8). In all cases, the elk tended to use a greater proportion of the higher suitability classes (High and Very High) and a lesser proportion of the lower suitability classes (Very Low and Low) relative to what were available in the study area.

Table 8: Results of chi-square tests for locations vs. study area. Proportions and total number of observed locations are included. Expected locations = total locations X proportions of study area in HSI class (from Table 7).

<table>
<thead>
<tr>
<th>Elk ID</th>
<th>Season</th>
<th>V Low</th>
<th>Low</th>
<th>Medium</th>
<th>High</th>
<th>V High</th>
<th>Total</th>
<th>$\chi^2$</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benson</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>241</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sum92</td>
<td>0.03</td>
<td>0.02</td>
<td>0.23</td>
<td>0.47</td>
<td>0.26</td>
<td>66</td>
<td>198</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.12</td>
<td>0.14</td>
<td>0.14</td>
<td>0.51</td>
<td>0.09</td>
<td>43</td>
<td>45</td>
<td>2</td>
</tr>
<tr>
<td>Winter</td>
<td>0.00</td>
<td>0.00</td>
<td>0.26</td>
<td>0.50</td>
<td>0.24</td>
<td>0.24</td>
<td>42</td>
<td>173</td>
<td>2</td>
</tr>
<tr>
<td>249</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sum92</td>
<td>0.02</td>
<td>0.08</td>
<td>0.23</td>
<td>0.43</td>
<td>0.25</td>
<td>65</td>
<td>96</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.00</td>
<td>0.00</td>
<td>0.32</td>
<td>0.41</td>
<td>0.27</td>
<td>41</td>
<td>132</td>
<td>2</td>
</tr>
<tr>
<td>Winter</td>
<td>0.14</td>
<td>0.12</td>
<td>0.16</td>
<td>0.47</td>
<td>0.12</td>
<td>0.47</td>
<td>43</td>
<td>83</td>
<td>2</td>
</tr>
<tr>
<td>849</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sum92</td>
<td>0.02</td>
<td>0.32</td>
<td>0.06</td>
<td>0.22</td>
<td>0.38</td>
<td>65</td>
<td>70</td>
<td>2</td>
</tr>
<tr>
<td>Winter</td>
<td>0.07</td>
<td>0.21</td>
<td>0.07</td>
<td>0.29</td>
<td>0.36</td>
<td>0.36</td>
<td>14</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Nahwitti</td>
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<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sum92</td>
<td>0.09</td>
<td>0.05</td>
<td>0.29</td>
<td>0.42</td>
<td>0.15</td>
<td>55</td>
<td>31</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.00</td>
<td>0.09</td>
<td>0.26</td>
<td>0.49</td>
<td>0.17</td>
<td>35</td>
<td>33</td>
<td>2</td>
</tr>
<tr>
<td>Winter</td>
<td>0.00</td>
<td>0.08</td>
<td>0.49</td>
<td>0.36</td>
<td>0.08</td>
<td>0.08</td>
<td>39</td>
<td>33</td>
<td>3</td>
</tr>
<tr>
<td>461</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Sum92</td>
<td>0.04</td>
<td>0.06</td>
<td>0.25</td>
<td>0.47</td>
<td>0.19</td>
<td>53</td>
<td>51</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.03</td>
<td>0.06</td>
<td>0.31</td>
<td>0.34</td>
<td>0.25</td>
<td>32</td>
<td>22</td>
<td>2</td>
</tr>
<tr>
<td>Winter</td>
<td>0.00</td>
<td>0.05</td>
<td>0.54</td>
<td>0.33</td>
<td>0.08</td>
<td>0.08</td>
<td>39</td>
<td>30</td>
<td>3</td>
</tr>
</tbody>
</table>
2) Home Ranges vs. Study Area

The seasonal ranges in the Benson and the Nahwitti appear to be centred around areas where the predominant colours are green and yellow (the top three suitability classes), whereas they tend to exclude the bottom two classes - tan and brown (Figures 6 and 7). While not as dramatic as with location data, in most cases the elk chose less of the lower quality habitat, and more of the higher quality habitat in both the Benson (Figure 8) and the Nahwitti (Figure 9), relative to what were available. Winter ranges in the Benson included greater proportions of the lower suitability classes than did summer ranges. However, in the Nahwitti, the distribution of suitability class proportions changed very little from summer to winter, and the most frequently used HSI class was medium (0.41 - 0.60).

3) Home Ranges vs. Random Circles

In the Benson, all seasonal ranges had mean suitability values > 2 standard errors above the grand mean of all circles (Table 9). All summer ranges were ranked either first or second among the random circles, meaning the probability of finding an equal sized area that has a mean HSI value < that of the summer range was < 0.98. The probability of finding such an area for winter ranges was between 0.74 and 0.88.

In the Nahwitti the probability of finding a random circle with a mean HSI value < that of the seasonal range was decreased to between 0.06 and 0.80. Only the 1993 summer ranges had mean suitability values that were higher than the grand mean of the circles, and both were > 2 standard errors from their respective means (Table 9). These results do not show elk seasonal ranges to be different from
Figure 6: Examples of seasonal ranges on suitability maps for (a) summer and (b) mild winter (Benson).
Figure 7: Examples of seasonal ranges on suitability maps for (a) summer and (b) mild winter (Nahwitt).
Figure 8: Used (seasonal range) and available (study area) areas in each HSI class for the Benson study area. Numbers in graph titles are elk ID's. VL=very low; L=low; M=medium; H=high; VH=very high.
Figure 9: Used (seasonal range) and available (study area) areas in each HSI class for the Nahwitti study area. Numbers in graph titles are elk ID's. VL=very low; L=low; M=medium; H=high; VH=very high.
what could be chosen at random from the study area. However, the Nahwitti study area has a higher average suitability than does the Benson. Therefore, grand means of random circles were approximately 0.2 higher in the Nahwitti, which moves them into a higher suitability class. The variation around the grand means was also much lower in the Nahwitti as shown by the standard errors of the means (Table 9).

Table 9: Comparison of mean HSI for seasonal ranges and grand mean of all corresponding circles. (P = probability of finding circles with a higher mean HSI than the seasonal range used by elk.)

<table>
<thead>
<tr>
<th>Elk ID #</th>
<th>Season</th>
<th>Grand Mean (Circles)</th>
<th>SE* (Circles)</th>
<th>Mean HSI of Seasonal Range</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Benson</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>241</td>
<td>Sum92</td>
<td>0.32</td>
<td>0.013</td>
<td>0.69</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.33</td>
<td>0.017</td>
<td>0.65</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.29</td>
<td>0.016</td>
<td>0.44</td>
<td>0.12</td>
</tr>
<tr>
<td>249</td>
<td>Sum92</td>
<td>0.31</td>
<td>0.015</td>
<td>0.67</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.33</td>
<td>0.014</td>
<td>0.66</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.28</td>
<td>0.017</td>
<td>0.43</td>
<td>0.16</td>
</tr>
<tr>
<td>849</td>
<td>Sum92</td>
<td>0.35</td>
<td>0.007</td>
<td>0.52</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.29</td>
<td>0.013</td>
<td>0.36</td>
<td>0.26</td>
</tr>
<tr>
<td>Nahwitti</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>441</td>
<td>Sum92</td>
<td>0.53</td>
<td>0.004</td>
<td>0.48</td>
<td>0.94</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.52</td>
<td>0.011</td>
<td>0.60</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.54</td>
<td>0.008</td>
<td>0.48</td>
<td>0.88</td>
</tr>
<tr>
<td>461</td>
<td>Sum92</td>
<td>0.53</td>
<td>0.006</td>
<td>0.52</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>0.52</td>
<td>0.003</td>
<td>0.54</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>0.52</td>
<td>0.008</td>
<td>0.47</td>
<td>0.80</td>
</tr>
</tbody>
</table>

* standard error of the grand mean of all circle means.
Level 3 selection

Locations vs. Seasonal Ranges

The locations show that even within a seasonal range, elk rarely used lower quality habitat. For example, in Figure 10a, a patch of low quality habitat (tan) juts into the seasonal range from the left, and the locations show that this area was generally unused by the elk. Figures 10b and 11 also show that locations were in higher quality habitats within the seasonal range. In both the Benson and Nahwitti, 11 of 14 chi-square tests (Table 10) showed the proportions of elk locations in each HSI class to be significantly different from those of the corresponding seasonal range (the exceptions were summer 1992 for elk 241 and 249 in the Benson, and summer 1993 for elk 441 in the Nahwitti). In general, there was a greater proportion of the higher suitability classes, and a lesser proportion of the lower suitability classes used by the elk than what were proportionally available in the seasonal ranges.

Table 10: Results of chi-square tests of locations vs. seasonal ranges for each animal/season. Observed locations are in Table 8. Expected locations = total locations X proportions of range in HSI class from Figures 8 and 9.

<table>
<thead>
<tr>
<th>Elk ID</th>
<th>Benson Season</th>
<th>$\chi^2$</th>
<th>df</th>
<th>Elk ID</th>
<th>Nahwitti Season</th>
<th>$\chi^2$</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>241</td>
<td>Sum92</td>
<td>6.1*</td>
<td>3</td>
<td>441</td>
<td>S'92</td>
<td>21.4</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>9.9</td>
<td>3</td>
<td></td>
<td>S'93</td>
<td>4.8*</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>40.8</td>
<td>4</td>
<td></td>
<td>Win</td>
<td>12.8</td>
<td>4</td>
</tr>
<tr>
<td>249</td>
<td>Sum92</td>
<td>2.7*</td>
<td>4</td>
<td>461</td>
<td>S'92</td>
<td>25.0</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Sum93</td>
<td>9.8</td>
<td>3</td>
<td></td>
<td>S'93</td>
<td>7.4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>14.1</td>
<td>4</td>
<td></td>
<td>Win</td>
<td>15.2</td>
<td>4</td>
</tr>
<tr>
<td>849</td>
<td>Sum92</td>
<td>16.9</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>4.2</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* No significant difference ($\alpha = 0.05$).
Figure 10: Illustrative examples of elk use within seasonal ranges in (a) summer and (b) mild winter (Benson).
Figure 11: Illustrative examples of elk use within seasonal ranges in (a) summer and (b) mild winter (Nahwitti).
DISCUSSION

Sample Size

While the sample size (n = 5 collared elk) seems small, a) I am not inferring anything about elk, in general, from them but using them to test the model's predictive ability, and b) they represented the behaviour of a larger number of elk (12-32) that probably had very similar home ranges. Roosevelt elk live in groups, and through sightings and aerial censuses, I estimated that the whole population in the Nahwitti (except adult males) and 1/3 of the population in the Benson had seasonal ranges that were similar to the collared elk.

Independence

Researchers often assume that independence is lost when one individual is sampled more than once (Hurlbert 1984) or, in home range calculations, if the time interval between locations is too short (Swihart and Slade 1985; Reynolds and Laundre 1990). In my study, I used each individual as a separate test of the model, so repeated sampling from each individual was necessary. For the chi-square test, locations are assumed to be independent. One view of independence is that the animal has sufficient time between consecutive locations to traverse its home range (Swihart and Slade 1985). I felt that my sampling schedule (locations were generally 2-5 days apart) allowed this, and I recorded elk moving from one end of the home range to the other between consecutive locations. Furthermore, in the chi-square tests, I considered the number of suitability classes (not locations) as the sample size. Hence, increasing the
number of locations does not increase the degrees of freedom, but it does increase the accuracy of the estimate of habitat use.

While I believe my locations were independent, independence was not essential for the home range calculations. Autocorrelated data collected at short time intervals can still be appropriate for obtaining valid home range estimates, and at the same time maximize the information available about habitat selection (Reynolds and Laundre 1990). By compiling the set of locations, or calculating a home range, I was trying to estimate the total area used by that individual over the duration of the season, which can also be thought of as a trajectory through time and space (Aebischer et al. 1993). In the ideal situation, the animal would be tracked continuously so that its exact route is known, as would the time spent at each point on its trajectory. Radio-locations taken from the ground sample this trajectory. As long as locations are spaced either randomly or relatively regularly in time, the sample can be considered a good estimate of habitats used.

Telemetry Error

The ad hoc method (Nams and Boutin 1991) of triangulation that I used seemed most appropriate even though no statistical method of assessing error was used. Factors which increase error include increased distance from the animal, topographic or vegetative barriers, atmospheric conditions, and the time between bearings (Harris et al. 1990), as well as intersection angle of the bearings (Saltz 1994). In both areas, the error around each triangulated point was small compared to the average patch size (Benson = 44 ha, Nahwitti = 54 ha) of the most coarsely mapped input variable - the habitat map. Furthermore, the accuracy of the locations was similar to the accuracy of
the map layers in the GIS, and I checked each location which was near a boundary in
the habitat or forest cover maps to ensure it fell in the proper polygon. For these
reasons, I believe the location error was not significant.

**Seasonal Ranges**

The average size of seasonal ranges in the Benson area (468 hectares) fell
within the range of sizes found in other elk studies: 637 ha for migratory elk on
southern Vancouver Island (Brunt 1991) and 290 ha for resident elk in California
(Franklin et al. 1975). However, the seasonal ranges of the Nahwitti elk were much
larger on average (2,313 ha) than in the Benson, and closer in size to the average
range of resident elk in both Sovka's (1993; 3,000 ha) and Brunt's et al.'s (1989; 1,710
ha) studies, and to those reported for Rocky Mountain elk (Cervus elaphus nelsoni;
1,880 and 3,020 ha; Pederson et al. 1980). Such a large difference in seasonal range
size between the Benson and Nahwitti could indicate that the Benson has higher
quality elk habitat, because home range size tends to increase with decreasing food
density (McNab 1963; McCorquodale et al. 1989) and forage is the most influential
factor in Brunt's (1991) models.

The general habitats selected by all collared elk, including riparian areas,
wetlands, clearcuts, young regenerating stands, and old growth on valley bottoms and
lower slopes, were similar to those used by elk in previous studies (Schwartz and
Mitchell 1945, Pederson et al. 1980, Collins and Urness 1983, Irwin and Peek 1983,
1993, Sovka 1993). These habitats tend to provide preferred forage for elk, such as

**Model Validation**

"The validation process in some way compares model predictions to observations of species' responses (or to prior knowledge), determines the strong and weak points of the model according to specified criteria, and guides further empirical studies or model development and revision" (Marcot et al. 1983:317).

This statement identifies each of the important steps in validating an HSI model. Brunt (1991) first used prior knowledge of elk habitat use to develop the seasonal models, then he and Sovka (1993) compared model predictions to elk locations and home ranges to determine that the models have some predictive capability. My results also validate the models. Each study provided information which could be used in the future to revise or simplify the models.

Elk locations should be more accurate as indicators of selection than are seasonal ranges because the seasonal ranges are extrapolations from the locations, thus there were probably areas within the seasonal ranges where elk were never found. Therefore, using seasonal ranges rather than locations to compare elk use to availability in the study area is probably more conservative.

The results of all tests of the model applied to the Benson, and all but the home ranges vs. random circles test in the Nahwitti, validated the models by showing that the elk were using more of the high quality and less of the low quality habitat relative to what was available. In the Nahwitti, the mean HSI values of the home ranges were generally no better than those of similar sized areas selected at random from within the study area. Not all locations were found in high quality habitat, but I expected to find
some locations in lower quality areas if the elk were forced there by predators or human harassment, or if they were travelling between high quality patches. Thus, one would not expect a perfect fit to the model, and working with statistical significance levels of 95% is overly conservative for wildlife managers when 75-80% would suffice for large scale planning (Hurley 1986). Wiser management decisions can be made by using models, even if they are imperfect (Chalk 1986).

There are several possible explanations for finding no difference between the seasonal ranges and the study area (represented by circles) in the Nahwitti. First, the adaptive kernel method of calculating home ranges includes areas peripheral to the locations which may be of low quality and not used by the elk at all; therefore, the estimated home range may be of lower quality than the true home range. This seemed to be more a problem in the Nahwitti, and was especially evident in the southern end of some seasonal ranges where the river runs east-west. The shape of the "kernel" in KERNELHR is determined by the mean squared error (MSE) in the X and Y directions. The program chooses a smoothing parameter which minimizes the MSE, and when the locations span a greater distance in one direction, the kernels, and thus the home range, are extended in that direction (i.e. the kernels become elongated instead of circular; Worton 1989). In the Nahwitti the seasonal ranges were extended in the north-south direction (Figures 7 and 11). This appears realistic in the part of the valley that runs north-south, but not when the valley runs east-west. This problem might be overcome by choosing a smoothing constant such that the area around each location was circular instead of allowing KERNELHR to choose the optimal one.
A second alternative would be to use the minimum convex polygon (MCP) instead of the adaptive kernel method. I tried this method with the 1992 summer locations of elk #441 which showed the worst result in the tests of seasonal ranges vs. random circles. The adaptive kernel summer range had a higher HSI value than only 6% of the corresponding circles, whereas the MCP summer range was higher than 58% of the circles (Figure 12).

![Figure 12: Mean HSI values of elk #441's summer 1992 adaptive kernel and Minimum Convex Polygon ranges (black) and corresponding random circles (white).](image)

The third explanation is that the elk's seasonal ranges were relatively large compared to the total Nahwitti study area (the largest filled 29% of the study area). In this case, any circle of equal size to the elk range would contain part of the seasonal range because of the latter's shape, size and central placement in the study area. Fourth, due to budget constraints, the habitat mapping was not done to the finest detail possible in the Nahwitti. The Nahwitti study area in general had higher HSI values (mean summer HSI = 0.49, mild winter = 0.42) than did the Benson (summer = 0.34, mild winter = 0.26). The large expanses of the Nahwitti plateau which run along each
side of the study area have a large amount of “medium” suitability in summer, but they were not used by collared elk. My feeling is that the plateau may have been given too high an HSI value because it was considered one broad mosaic instead of many small patches of different habitat. Last, although this “circle method” was used to incorporate some of the spatial components of the habitat suitability map into the test, averaging suitability values of the seasonal ranges and the circles may have resulted in a failure to identify high quality habitat. For example, a homogeneous area of suitability value 0.45 may not be as valuable for elk as would an equal sized area with half being valued at 0.05 and half at 0.85, yet both would have the same mean. Presumably there is some point at which an area changes from “sufficiently high suitability to satisfy the needs of elk” to “insufficient”. In my example, if that threshold was 0.50, the homogeneous area could not support elk at all, whereas half of the heterogeneous area could.

The placement of the study area boundaries may affect the results of a use-availability study for Johnson’s (1980) level 2 selection, especially when the pattern of habitat patches is aggregated (Porter and Church 1987). Ideally, the study area should extend as far as it would be possible for elk to travel - in this case, perhaps all of Vancouver Island. In reality, due to their gregariousness, they are not likely to travel outside of the range of the population into which they are born. An area outside this is either not available to them, or is available but not selected. I believe the boundaries of my study area in the Benson were realistic because much of the boundary was at the height of land, a natural barrier. However, in the Nahwitti I would have preferred (a
posteriori) a larger study area because the seasonal ranges covered a larger portion of
the study area, and the rolling topography did not provide any obvious barriers.

Uncertainty in the extent of the true available area can be reduced by
considering 2 different levels of selection (Aebischer et al. 1993; Carrol et al. 1995).
The study area could be very different from what elk perceive as the area available to
them. Reducing the available area to the extent of the home range, increases the
probability that elk are familiar with the area. An unused area within the home range
may be avoided, whereas an unused area within the study area (but outside the home
range) may be unavailable. On the other hand, elk have already selected the home
range, presumably because of its high quality, so using this as the available area would
result in a more conservative test than one using the study area. Therefore, testing at
both levels seems appropriate.

In both study areas, there were large areas of high HSI value that were not used
by the collared elk, and some areas of low HSI value that were used. The latter case
suggests that some factors are missing from the model (see "Problems with the
models"). The former has many possible explanations. The HSI does not include any
effects of competitors, predators, parasites, exploitation, or harrassment by humans
(Schamberger and O'Neill 1986). In the Benson, there were other groups of elk
separate from the collared elk. This, along with the presence of wolves (Canis lupus),
cougars (Felis concolor), hunters, and both commercial and recreational traffic could
have affected which areas were used by collared elk. Therefore, use of an area by elk
does not always indicate that the area is of high HSI value, nor does non-use indicate
low HSI values (especially since one cannot be certain that an area is not used by some elk).

Animals of different age and sex may have different movements and patterns of range use (Harris et al. 1990), so conclusions cannot be drawn from the collared animals about the entire elk population. Only adult females were used to test the model, but elk are gregarious, and age-sex class counts of other individuals observed with the collared elk lead me to believe that other adult females and juveniles had very similar home ranges to the collared elk. Adult males were observed with the female-young groups during the rut (autumn), and occasionally during the rest of the year.

Problems with the Models

If a model's predictions are accurate, some confidence is placed in its predictive ability, but no conclusions can be drawn about its veracity. In fact, predictions which are clearly wrong can lead us to a better understanding of the system being modeled (Bunnell 1973) because they can help to identify gaps in our knowledge. While my data generally seem to fit the model, the results are not absolutely clear, and this has given me insights into possible problems with either the model itself or with my method of testing the model.

I believe significant improvements to the models could be made in how cover influences the HSI values. Polygons were given cover values of either 0 or 0.99, indicating that cover was either absent or present. I felt that in some cases there should have been intermediate values for security cover. For example, in a large cutblock with undulating topography, the cover would have been rated "0" because the trees were not tall enough to hide the elk, yet the elk could be completely hidden.
behind a log, a shrub, or a small rise. Combinations of undulating topography (which could be identified on aerial photographs) and height of shrubs (which would be related to the date of logging) could have been used to improve the models by providing intermediate values for security cover. Brunt (1991) discussed the importance of both thermal and snow interception cover, yet his model combined the two because his study area did not include any second growth old enough to qualify as thermal cover, but too young to qualify as snow interception cover. In the Benson, this type of forest stand was present and probably should have been distinguished in the model. I suggest that this modification be made if the model is used again. Furthermore, a problem arose with cover values in stands that were mosaics of 2 different habitat types because I gave these polygons the cover value of the predominant habitat type; however, an intermediate value may have been more accurate. To compound the security cover problem, darkness may provide adequate security in clearcuts at night (Beyer and Haufler 1994). This would explain why "pit-lamping" is so successful for poachers, and why I was able to get within 25 m of elk groups in a clearcut at night, whereas during the daylight this was rarely possible.

The ability to see long distances may also give elk a sense of security. While snow was present in the Benson, collared elk stayed on a large clear-cut side hill with very little vegetative cover. Schwartz and Mitchell (1945) also found that elk used logged areas in winter, and in fact most elk and elk tracks seen during an aerial census of northern Vancouver Island at this time were on clearcut or relatively open side slopes of valleys. Wolves are known predators of elk on Vancouver Island (Scott and Shackleton 1980) and I found their sign in the Benson in winter. A small patch of
bushes (i.e. ~ 0.1 ha) in that same clear-cut side hill was also chosen as a calving spot by one of my collared elk. Perhaps in both cases, the elk needed extra time to flee from predators (because of the presence of snow or young), and having a clear vantage point to see any threat well in advance, might have been more advantageous than being in dense cover where a predator could surprise them. On the other hand, open clearcuts in winter could be the only place where food is found in sufficient quantity. There, full light allows maximum summer growth of shrubs and small conifers which provide most of the winter diet (Brunt 1990), and unless directly threatened by a predator, elk may not move through snow to safer cover because of energetic constraints. Furthermore, winter temperatures on these slopes (east and west facing) could be higher than on the valley floor due to exposure to sunlight on the slopes and to cold air pooling on the valley floor. During the time when snow was present, elk #241 and #249 and other members of the group (N = 5 to 13) chose the side slopes, possibly for one of the above reasons. The average HSI value of their locations at this time was 0.19 and the minimum 0.06. Their choice of low suitability slopes over nearby areas of significantly higher suitability leads me to conclude that some factor or combination of factors (discussed above) is either misclassified or missing from the mild winter suitability model.

Management Implications

To have confidence in applying the models to forest management, data for severe winter should be used to test the severe winter model. Knight (1970) found that Rocky Mountain elk used open areas in mild winters, but used timbered areas in severe winters. In any winter, the lack of high quality forage and increased energetic costs of
thermal regulation and movement through snow probably create a net loss of energy for elk (Janz 1983), and a severe winter would make this problem more extreme. The amount of high quality, severe winter habitat may be the limiting factor to the long term survival of a population. In this case, management decisions for an area should maximize the high quality habitat delineated by the severe winter model. Due to recent mild winters on Vancouver Island, however, the severe winter model has not been tested (this study, Sovka 1993, Brunt 1991).

While Brunt's (1991) models appear to predict which habitats are suitable for elk, the HSI values would have to be updated along with the forest cover maps as stands are harvested and succession proceeds. The understory-based habitat map, which is essential to the HSI models for elk, is not normally available to forest managers, and is expensive to create. Thus, the models may not be practical at this time in their present form. However, I believe that there is still valuable information to be gained from them. Forest managers should be aware of any old growth areas which have high HSI values, especially in severe winters, because logging would substantially reduce these values by removing thermal and snow interception cover. Also, if they are aware of how each variable in the model influences the HSI value, then they will have a better idea of which areas will be suitable for elk, even without running (or updating) the models.

Monitoring wildlife populations is the key to adaptive resource management (Salwasser 1985), and a healthy, stable elk population should indicate that the area provides good elk habitat. Also, recording the location of elk sign and sightings can help delineate preferred habitats. The stand prescription controls the vegetative
substrates upon which wildlife species can find food and cover resources (Salwasser 1985), so forest managers have the ultimate responsibility to ensure that habitats for all species in their areas are maintained, not just for popular animals like elk, deer, bears, and spotted owls.
LITERATURE CITED


Salwasser, H. 1985. Integrating wildlife into the managed forest. For. Chron. 61: 146-149.


### Appendix 1: Understory-based habitat types.

<table>
<thead>
<tr>
<th>Habitat Label</th>
<th>Habitat Type</th>
<th>Trees</th>
<th>Understory</th>
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<th>Tropho-tope**</th>
</tr>
</thead>
<tbody>
<tr>
<td>CP</td>
<td>Pine-redcedar-cypress woodland</td>
<td>pine, redcedar, yellow cedar, western hemlock</td>
<td>salal, deer fern, goldthread</td>
<td>5-6</td>
<td>B</td>
</tr>
<tr>
<td>S1CH</td>
<td>salal-moss, cedar-hemlock phase</td>
<td>open redcedar-western hemlock (amabilis fir)</td>
<td>salal, (Vaccinium), moss</td>
<td>4-5</td>
<td>C</td>
</tr>
<tr>
<td>S1HA</td>
<td>salal-moss, hemlock-amabilis fir phase</td>
<td>western hemlock, amabilis fir</td>
<td>moss, (alaskan blueberry, red huckleberry, salmonberry, deer/sword/spiny wood fern, 3-leaved foam flower)</td>
<td>4-5</td>
<td>C</td>
</tr>
<tr>
<td>S1C</td>
<td>colluvial phase of S1</td>
<td>western hemlock, amabilis fir</td>
<td>moss, Vaccinium</td>
<td>4-5</td>
<td>C</td>
</tr>
<tr>
<td>S2</td>
<td>salal-folisol over rock</td>
<td>open, scrubby redcedar &amp; western hemlock</td>
<td>salal, very sparse herb layer</td>
<td>2-3</td>
<td>B</td>
</tr>
<tr>
<td>S2F</td>
<td>same as S2, Douglas fir phase</td>
<td>same, includes Douglas Fir</td>
<td>same as S2, also lichen and bare rock</td>
<td>2-3</td>
<td>B</td>
</tr>
<tr>
<td>S3</td>
<td>alluvial sword/fem-foamflower</td>
<td>Sitka spruce, western hemlock, amabilis fir</td>
<td>Higher terraces and microsites: Red huckleberry, alaskan blueberry, sword/deer/spiny wood fern, 3-leaved + cut-leaved foamflower Low terraces: salmonberry, elderberry, devil's club, ferns (oak, lady, maidenhair), twisted stalk, false bugbane, bedstraw, hedge-nettle, coast boykinia, pink fawn lily</td>
<td>5</td>
<td>D</td>
</tr>
<tr>
<td>S3B</td>
<td>beach phase of S3</td>
<td></td>
<td>see S3 higher terraces</td>
<td>4</td>
<td>D</td>
</tr>
<tr>
<td>S4</td>
<td>alluvial alder-spruce-herb</td>
<td>red alder (Sitka spruce)</td>
<td>salmonberry, elderberry, stink currant, youth-on-age, sword fern, hedge-nettle, (cow parsnip, lady fern, bleeding heart, bedstraw, purple sweet cicely, Pacific oenanthe, 3-leaved + cut-leaved foamflower, grasses)</td>
<td>5</td>
<td>E</td>
</tr>
<tr>
<td>S5</td>
<td>wet alluvial spruce-redcedar-skunk cabbage</td>
<td>Sitka spruce, redcedar, (western hemlock)</td>
<td>same as S3, but more lady fern, also skunk cabbage, (slough sedge, nodding trisetum)</td>
<td>6</td>
<td>E</td>
</tr>
<tr>
<td>S6</td>
<td>redcedar-skunk cabbage swamp forest</td>
<td>redcedar (spike-topped) poor western hemlock and Sitka spruce, all on raised microsites</td>
<td>Raised Microsites: salal, (Vaccinium, Pacific menziesia), deer fern, bunchberry, false Solomon's seal, twayblades Depressional Microsites: skunk cabbage, goldthread</td>
<td>7</td>
<td>D</td>
</tr>
<tr>
<td>S7</td>
<td>shore pine - redcedar, sedge - skunk cabbage</td>
<td>shore pine, redcedar</td>
<td>skunk cabbage, sedge</td>
<td>8</td>
<td>D</td>
</tr>
<tr>
<td>S8</td>
<td>shore pine bog</td>
<td>shore pine</td>
<td>Labrador tea, sphagnum moss</td>
<td>7</td>
<td>B</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Associated Plants</td>
<td>Code</td>
<td>Location</td>
<td></td>
</tr>
<tr>
<td>---</td>
<td>------------------------------------------------------------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------------------------------------------------</td>
<td>------</td>
<td>----------</td>
<td></td>
</tr>
<tr>
<td>S9</td>
<td>open bog</td>
<td>nil</td>
<td>8</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>S10</td>
<td></td>
<td>redcedar, western hemlock</td>
<td>4</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>S11</td>
<td>sweetgale-hardhack-sedge fens</td>
<td>sparse small red cedar</td>
<td>8</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>S12</td>
<td>limestone holly fern</td>
<td>same as S2</td>
<td>3-4</td>
<td>D-E</td>
<td></td>
</tr>
<tr>
<td>S12F</td>
<td></td>
<td>redcedar, Douglas fir, western hemlock</td>
<td>3-4</td>
<td>D-E</td>
<td></td>
</tr>
<tr>
<td>S13</td>
<td>colluvial salmonberry-swordfern</td>
<td>western hemlock, amabilis fir, (redcedar, Sitka spruce)</td>
<td>4-5</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>S13L</td>
<td></td>
<td>same as S13, also thimbleberry</td>
<td>4-5</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>montane Vaccinium moss</td>
<td>western hemlock, amabilis fir, (yellow cedar in climax)</td>
<td>4</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>M1C</td>
<td></td>
<td>same as M1</td>
<td>4</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>M2</td>
<td>montane salal</td>
<td>yellow cedar, western hemlock, suppressed mountain hemlock</td>
<td>3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>M3</td>
<td>montane oakfern</td>
<td>same as M1, but old growth is larger and taller</td>
<td>5</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>M3C</td>
<td></td>
<td>same as M3</td>
<td>5</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>M4</td>
<td>wet montane skunk cabbage - marshall marigold</td>
<td>western hemlock, yellow cedar, small mountain hemlock, all on raised microsites</td>
<td>6</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>M5</td>
<td>montane Devil's club</td>
<td>western hemlock, amabilis fir, yellow cedar</td>
<td>5</td>
<td>D</td>
<td></td>
</tr>
<tr>
<td>MH1</td>
<td>closed mountain hemlock forest</td>
<td>closed canopy of mountain hemlock &amp; yellow cedar, shrubby amabilis fir</td>
<td>4</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>MH2</td>
<td>rocky mountain hemlock forest</td>
<td>same as MH1</td>
<td>3</td>
<td>B</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>mountain hemlock parkland</td>
<td>stunted mountain hemlock &amp; yellow cedar in clumps openings dominated by heather or sedge</td>
<td>oval-leaved &amp; alaskan blueberry, black crowberry, red mountain heather, cassiope, copperbush, bunchberry, goldthread</td>
<td>various</td>
<td></td>
</tr>
<tr>
<td>---------</td>
<td>--------------------------</td>
<td>------------------------------------------------------------------------------------------</td>
<td>------------------------------------------------------------------------------------------------------</td>
<td>---------</td>
<td></td>
</tr>
<tr>
<td>A</td>
<td>snow avalanche track</td>
<td>Sitka alder, or stunted mountain hemlock &amp; yellow cedar</td>
<td>lush herbs and ferns</td>
<td>4-5</td>
<td>D</td>
</tr>
<tr>
<td>T</td>
<td>talus</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>NV</td>
<td>non vegetated</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>AT</td>
<td>alpine tundra</td>
<td>-</td>
<td>heathers, lichens</td>
<td>various</td>
<td></td>
</tr>
<tr>
<td>W</td>
<td>wetland (montane / sub-alpine)</td>
<td>(yellow cedar)</td>
<td>sphagnum, sedges</td>
<td>8</td>
<td>D</td>
</tr>
<tr>
<td>R</td>
<td>bare rock</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Soil moisture regime: 0 (very dry) to 8 (very wet).
** Soil nutrient regime: A (very poor) to E (very rich).
### Appendix 2: Common and scientific names of plant species listed.

#### Trees:
- alder, red: *Alnus rubra*
- balsam fir: *Abies amabilis*
- cedar, western red: *Thuja plicata*
- cedar, yellow: *Chamaecyparis nootkatensis*
- Douglas fir: *Pseudotsuga menziesii*
- hemlock, mountain: *Tsuga mertensiana*
- hemlock, western: *Tsuga heterophylla*
- pine, shore: *Pinus contorta*
- spruce, Sitka: *Picea sitchensis*

#### Shrubs:
- blueberry, alaskan: *Vaccinium alaskaense*
- blueberry, oval-leaved: *Vaccinium ovalifolium*
- copperbush: *Cladothamnus pyroliflorus*
- crowberry, black: *Empetrum nigrum*
- currant, stink: *Ribes bracteosum*
- devil's club: *Oplopanax horridus*
- elderberry, red: *Sambucus racemosa*
- hardhack: *Spiraea douglasii*
- heather, red mountain: *Phyllococe emeptriformis.*
- heather, white mountain: *Cassiope mertensiana*
- huckleberry, red: *Vaccinium parvifolium*
- Labrador tea: *Ledum groenlandicum*
- Oregon grape, dull: *Mahonia nervosa*
- Pacific menziesia: *Menziesia ferruginea*
- Pacific ninebark: *Physocarpus capitatus*
- salal: *Gaultheria shallon*
- salmonberry: *Rubus spectabilis*
- sweet gale: *Myrica gale*
- thimbleberry: *Rubus parviflorus*
- willow: *Salix spp.*

#### Herbs:
- baneberry, red: *Actaea rubra arguta*
- bedstraw, sweet-scented: *Galium triflorum*
- bleedingheart, Pacific: *Dicentra formosa*
- bracken: *Pteridium aquilinum*
- bramble, 5-leaved: *Rubus pedatus*
- bugbane, false: *Trautvetteria caroliniensis*
- bunchberry: *Cornus unalaschkensis*
- burnet, great: *Sanguisorba officinalis*
- clintonia: *Clintonia uniflora*
- clubmoss: *Huperzia selago*
coast boikinia
Boikinia occidentalis

cow parsnip
Heracleum sphondyllum

false hellabore
Veratrum viride eschscholtzii

fern, deer
Blechnum spicant

fern, holly
Polystichum lonchitis

fern, lady
Athyrium filix-femina

fern, maidenhair
Adiantum pedatum aleuticum

fern, oak
Gymnocarpium dryopteris

fern, spiny wood
Dryopteris assimilis

fern, sword
Polystichum munitum

fireweed
Epiobium angustifolium

foamflower, 3-leaved
Tiarella trifoliata

foamflower, cut-leaved
Tiarella laciniata

goldthread
Coptis aspleniiifolia

hedge-nettle
Stachys cooleyae

lilly, pink fawn
Erythronium revolutum

marigold, marsh
Caltha leptosepala biflora

orchid, slender rein
Platanthera stricta

Pacific oenanthe
Oenanthe sarmentosa

polypody
Polypodium hesperium

sedges
Carex, spp.

shooting star
Dodecatheon jeffreyi

skunk cabbage
Lysichiton americanum

slough sedge
Carex obnupta

Solomon's seal, false
Maianthemum dilatatum

spleenwort, green
Asplenium viride

spleenwort, maidenhair
Asplenium trichomanes

sweetcicely, purple
Osmorhiza purpurea

trisetum, nodding
Trisetum cernuum

twayblades
Listera spp.

twineflower
Linnacea borealis

twisted stalk
Streptopus spp.

yellow wood violet
Viola glabella

youth-on-age
Tolmiea menziesii

wintergreen
Pyrola asarifolia