WINTER HABITAT SELECTION BY ELK (CERVUS ELAPHUS) IN THE LOWER FOOTHILLS OF WEST-CENTRAL ALBERTA

University of Alberta

Winter Habitat Selection by Elk (Cervus elaphus) in the
Lower Foothills of West-Central Alberta

by

Paul Francis Jones

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Masters of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Winter Habitat Selection by Elk (Cervus elaphus) in the Lower Foothills of West-Central Alberta submitted by Paul Francis Jones in partial fulfillment of the requirements for the degree of Masters of Science in Wildlife Ecology and Management.

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Foothills Model Forest is one of eleven Model Forests that make up the Canadian Model Forest Network. As such, Foothills Model Forest is a non-profit organization representing a wide array of industrial, academic, government and non-government partners, and is located in Hinton, Alberta. The three principal partners representing the agencies with vested management authority for the lands that comprise the Foothills Model Forest, include Weldwood of Canada (Hinton Division), the Alberta Department of Environmental Protection and Jasper National Park. These lands encompass a combined area of more than 2.75 million hectares under active resource management.

The Canadian Forest Service of Natural Resources Canada is also a principal partner in each of the eleven Model Forest organizations and provides the primary funding and administrative support to Canada's Model Forest Program.

The Foothills Model Forest mission: "We are a unique community of partners dedicated to providing practical solutions for stewardship and sustainability of our forest lands."

Abstract

I examined winter habitat selection by elk (Cervus elaphus) at three spatial scales in west-central Alberta from December 1, 1994 to March 21, 1995. Elk selected habitats at each of the three scales examined. Elk selected home ranges that had lower road densities, higher seismic line densities and whose vegetation composition was more heterogeneous. At a stand level elk utilized the grass/meadow habitat in greater proportion than its availability. Selection of site characteristics was noted for different activities. For both the feeding and bedding sites, elk selected characteristics that were different from the immediately available habitat.

A winter habitat suitability index model was tested as part of this study. Each component and individual variables did not perform well. The food and hiding cover components did not perform significantly better between the used locations and available vegetation data. The thermal cover component performed better on the available vegetation data than the used locations. Alternatives to each component were given as well as a model based on pooling all locations and using stepwise logistic regression.

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1.0 Introduction

Elk (Cervus elaphus) are considered ecological generalists because of their ability to adapt to and successfully colonize a diversity of habitats. The elks' ability to adjust to local micro- environments (i.e. vegetational structure and forage and cover availability) have allowed for its adaptation and successful colonization of North America (Morgantini 1988). Land managers must account for adaptations by elk to local conditions when management decisions are made regarding habitat. Site specific habitat requirements of elk are needed before any informed decisions can be made.

Basic ecological information on elk within the lower foothills of west-central Alberta is essentially unknown. Quinlan et al. (1990) identified a need for research into the distribution, home range size, and habitat use by elk on Weldwood's Forest Management area (FMA). Getting site specific information on habitat selection would allow resource managers to make better informed decisions regarding habitat management for elk. This information would also allow for the testing of an elk winter HSI model developed by Buckmaster et al. (1995) to assist Weldwood of Canada's (Hinton Division) forest resource managers in their management of elk habitat.

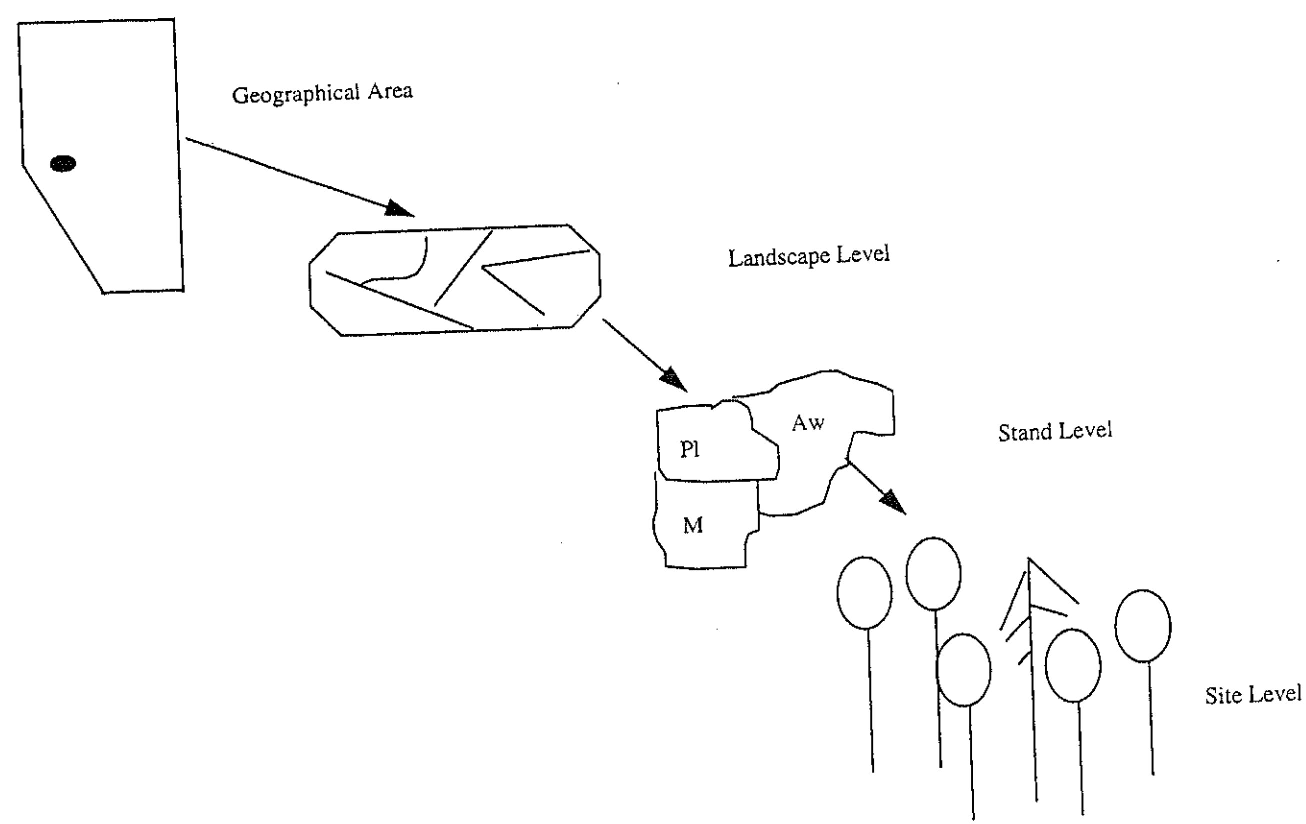
1.1 Habitat Selection

Selection is the process whereby an animal chooses a resource to satisfy its life requirements, and ultimately to increase individual fitness (Johnson 1980, Thomas and Taylor 1990, Manly et al. 1993). Choice of habitat is governed by energy requirements, thermal conditions, reproductive requirements, and intra- and interspecific competition (Litvaitis et al. 1986, Morrison et al. 1992). For example, when selecting a home range an animal will select an area that contains a high proportion of resources necessary for survival, while within that home range the animal will select habitat types based on food availability, predation risk, and intra- and interspecific competition (Pedlar et al. 1997). Habitat selection may occur at multiple scales ranging from the geographical range of a species to the selection of food items from within a feeding site (Johnson 1980, Manly et al. 1993).

Johnson (1980) defined four levels of habitat selection: (1) selection of a physical or geographical range, (2) selection of a home range within that geographical range, (3) selection of habitat components within the home range, and (4) selection of food items at a particular feeding site (Figure 1). Lofroth (1993) expanded Johnson's (1980) fourth-order selection to include any habitat component that a species requires (e.g. for mating, calving, shelter and escaping predators). Numerous studies deal with habitat selection by elk, but most have addressed habitat selection at only one level.

Landscape level selection involves the selection of a home range within the geographical or physical area. This definition closely resembles Johnson's (1980) second order selection. Specifically, landscape selection involves assessing the relative abundance or composition of each habitat type within the animal's home range. For elk it is generally believed that an area containing a 60:40 ratio of forage to cover, in the proper spatial

Figure 1 A hierarcial depiction of habitat selection by elk within the lower foothills of west-central Alberta.



arrangement, is optimal habitat (Thomas et al. 1979, Smith 1985, Brown 1994, Buckmaster et al. 1995). One quarter of the cover should be thermal cover, one half should be hiding cover, with the remaining quarter being either thermal or hiding, depending on which is more limited in the area (Brown 1994, Buckmaster et al. 1995). The selection of a home range by elk is also governed by road density. Elk habitat effectiveness is reduced as the density of roads open to motorized vehicles increases (Wisdom et al. 1986, Thomas et al. 1988).

Johnson's (1980) 3rd order selection, or the selection of habitat components or types within the home range, will be referred to as stand level selection for the purpose of this study. The majority of studies of habitat selection by elk have been examined at the stand level. In general, the selection of habitat types by elk at the stand level has been governed by season, activity, climatic conditions, and location. Various studies have reported different habitat selection patterns. In Idaho, Irwin and Peek (1983) determined that elk selected grass-shrub and serial shrub communities in spring for feeding, while Lees (1989) found that in west-central Alberta, elk used right-of-ways year round as feeding areas. In Montana, Lyon and Jensen (1980) stated that elk entered clear-cut openings in search of forage of higher quality and quantity, while a study in Alberta reported that elk used clear-cuts for both foraging and bedding (Morgantini et al. 1994). Irwin and Peek (1983) stated that elk preferred to bed within pole-timber stands on ridges. This was supported by Beall (1976) who found elk to bed within timber clumps on or near ridge tops, with elk selecting the south side of the stand during the day and the north side of the stand during the evening.

Site level selection or Johnson's 4th order selection can be viewed as the selection of habitat characteristics required to satisfy different activities (e.g. feeding or bedding) (McCorquodale 1987, Lofroth 1993). Few studies have examined elk feeding and bedding sites at a site scale. In western Montana, Edge et al. (1987) determined that elk locations did not differ from available sites, in terms of habitat characteristics, and that the more important variables were slope, amount of forage area within 200 m of each location and distance to open roads and human disturbance. When comparing elk bedding sites to available sites, Brown (1994) in his study in Arizona noted that elk selected bedding sites in areas with high canopy closure, greater total diameter at breast of height, few limbs below 6.5 ft, and clear of rocks.

Selection of feeding and bedding sites by elk is also governed by the spatial arrangement of vegetation communities and level of disturbance. Evidence suggests that elk use of forage areas dramatically decreases as the distance surpasses 100 yards from the forest-cover edge, while optimal use of forest cover for bedding occurred within 300 yards of the forage-cover edge (Nietfeld et al. 1985, Wisdom et al. 1986). Lees (1989) stated elk preferred areas where human activity was the lowest. Conversely, Edge et al. (1987) determined that the mean distance from roads was less than the mean for random sites, suggesting that elk were not avoiding the roads or human disturbance. However, they believed this was due to the low traffic volume in their study area and suggested that elk avoidance of roads depends on traffic volume (Edge et al. 1987).

Variation in habitat exists at a variety of levels allowing selection to occur at several scales (Dunning et al. 1992, Pedlar et al. 1997). All levels of selection are connected, but the higher the level the more general the habitat attributes. The change in habitat attributes at each scale or level may change the criteria for selection. All organisms and individuals perceive the environment differently, and comparisons and inferences regarding habitat selection should take into account the scale at which selection is made (Manly et al. 1993) and differences among individuals and species (Kotliar and Wiens 1990). Understanding how habitat selection by a species changes with spatial scale may allow for the long term management of a species at local and broad scales (Baker et al. 1995).

1.2 Elk Habitat Suitability Index Model

With increasing demands on resource development, resource managers face the challenge of maintaining wildlife habitat requirements while making land use decisions. Since the 1970's several modelling techniques have been developed to aid decisions regarding land allocation and the protection of wildlife habitat (Berry 1986). One technique has been the development of single-species models (Berry 1986). Single-species models include habitat suitability index (HSI) models, habitat effectiveness models (HEM), and cummulative effect models (USDI 1981, Berry 1986, Houthansen et al. 1994).

Weldwood of Canada's (Hinton Division) forest resource managers have adopted the HSI model approach to integrate wildlife needs into multiple-use forest management (Bonar et al 1990, Beck and Beck 1995, Farr 1995). Initially, Weldwood selected 30 species based on social or economic importance (e.g. elk), rare species or as indicator species (Bonar et al 1990). Each HSI habitat model would be linked to a habitat supply analysis model developed for the area (Beck and Beck 1995, Farr 1995). The objective is to allow forest managers to predict habitat availability for each species based on different forest management scenarios, and therefore allow forest resource managers to balance fibre production with wildlife habitat (Farr 1995).

Habitat suitability index models were developed by the U.S. Fish and Wildlife Service as part of the habitat evaluation procedures (HEP) to assess the environmental impacts of proposed water and land resource development projects (USDI 1981, Cole and Smith 1983, Bart et al. 1984, Berry 1986). Habitat suitability index models are hypothetical models constructed through the synthesis of current scientific knowledge and expert opinion (Brennan et al. 1986, Morrison et al. 1992). Habitat suitability index models work by evaluating habitat components from 0 to 1, where a rating of 1 is considered optimal habitat and a rating of 0 as poor habitat (USDI 1981, Wisdom et al. 1986). Each component is then combined into an overall index value for that area.

An HSI model for elk winter range was developed by Buckmaster et al. (1995) for west-central Alberta. The model was based on a review of elk ecology studies and refined through expert opinion. The model addresses three components: (1) food, (2) thermal cover, and (3) hiding cover requirements. Each component is characterized by vegetative variables related to the life requisite (e.g. % grass cover for food, % canopy closure for thermal cover) and the spatial relationship between each component (e.g. food distance from thermal and hiding cover). The variables, relationships and equations are summarized in Appendix A. The model has not been field tested. In order for the model to be a useful tool for forest managers, the model should be tested to ensure that it reflects actual habitat preference from an animal's perspective and that the assumptions in the model are valid (Bunnell 1989, Thomasma et al. 1991, Morrison et al. 1992).

1.3 Objectives

In this study, I examined habitat selection by elk in the lower foothills of west-central Alberta at three spatial scales, and tested the performance of a winter HSI model.

In the first part of this study I examined habitat selection by elk at the landscape (2^{nd} order), stand (3^{rd} order), and site level (4^{th} order). My first objective is to determine if elk selected home ranges based on the habitat components of the area. The null hypothesis is that the habitat composition of elk home ranges will not differ from random home ranges. My second objective is to determine if elk were selecting specific habitat types within their home ranges. The null hypothesis is that elk will select habitats within their home range in proportion to their availability.

At the site level I examined habitat selection at three sub-levels. My third objective is to determine whether elk were selecting habitat characteristics at sites to meet the requirements of different life requisites (i.e. feeding and bedding). I tested the null hypothesis that the mean spatial and non-spatial characteristics at elk feeding sites were not significantly different than those found at elk bedding sites. My fourth objective is to determined whether or not elk select specific sites within the immediately available area on the basis of their non-spatial and spatial attributes. The null hypotheses are that the non-spatial and spatial characteristics at elk feeding and bedding sites do not differ from the non-spatial and spatial characteristics at immediately available vegetation plots. My fifth objective is to determine the influence of temperature on the selection of bedding sites. The null hypothesis is that the mean spatial and non-spatial attributes at bedding sites made on warm, mild, and cold days are not significantly different.

In the second part of this study I tested the ability of each component of the elk winter range HSI model to accurately differentiate between plots where elk were located and those representing available habitat. For each component of the model, I tested the null hypothesis that the HSI values for the used locations is not significantly different than the HSI values for the available sites. Inherent in the hypothesis is the assumption that the life requisites of food, thermal cover, and hiding cover are limiting factors for elk (Buckmaster et al. 1995). From the hypothesis and assumption it can be deduced that elk preference for each habitat component of the model will increase with an increase in HSI value (Thomasma et al. 1991). No population estimates or densities were obtained during this study and therefore these tests are preliminary and should be considered part of the model's development and refinement (Bunnell 1989, Morrison et al. 1992, Farr 1995). Proposed revisions for each component, based on visual inspection and statistical analysis are given.

2.0 Study Area and Methods

2.1 Study Area

The study area is located in west-central Alberta along the north and south facing slopes of the Athabasca River Valley near Hinton, Alberta (53°25'N, 117°35'W) (Figure 2). The area is located within the Lower Foothills Subregion (Beckingham et al. 1996). The area rises in elevation from 500m to 1150m (Beckingham et al. 1996). The area is predominatly mature mixedwood stands of trembling aspen (Populus tremuloides), lodgepole pine (Pinus contorta), white and black spruce (Picea glauca and P. mariana respectively), and balsam poplar (Populus balsamifera). There are also large open meadows (on the Athabasca Ranch) and regenerating cutblocks. Low-bush cranberry (Viburnum edule), prickly rose (Rosa acicularis), green alder (Alnus crispa), Canada buffalo-berry (Shepherdia canadensis), marsh reed grass (Calamagrostis canadensis), and hairy wild rye (Elymus innovatus) are common understorey species (Beckingham et al. 1996).

The winter climate for the Lower Foothills Subregion is less influenced by cold Arctic air masses but is moderated by warm chinook winds (Beckingham et al. 1996). Monthly

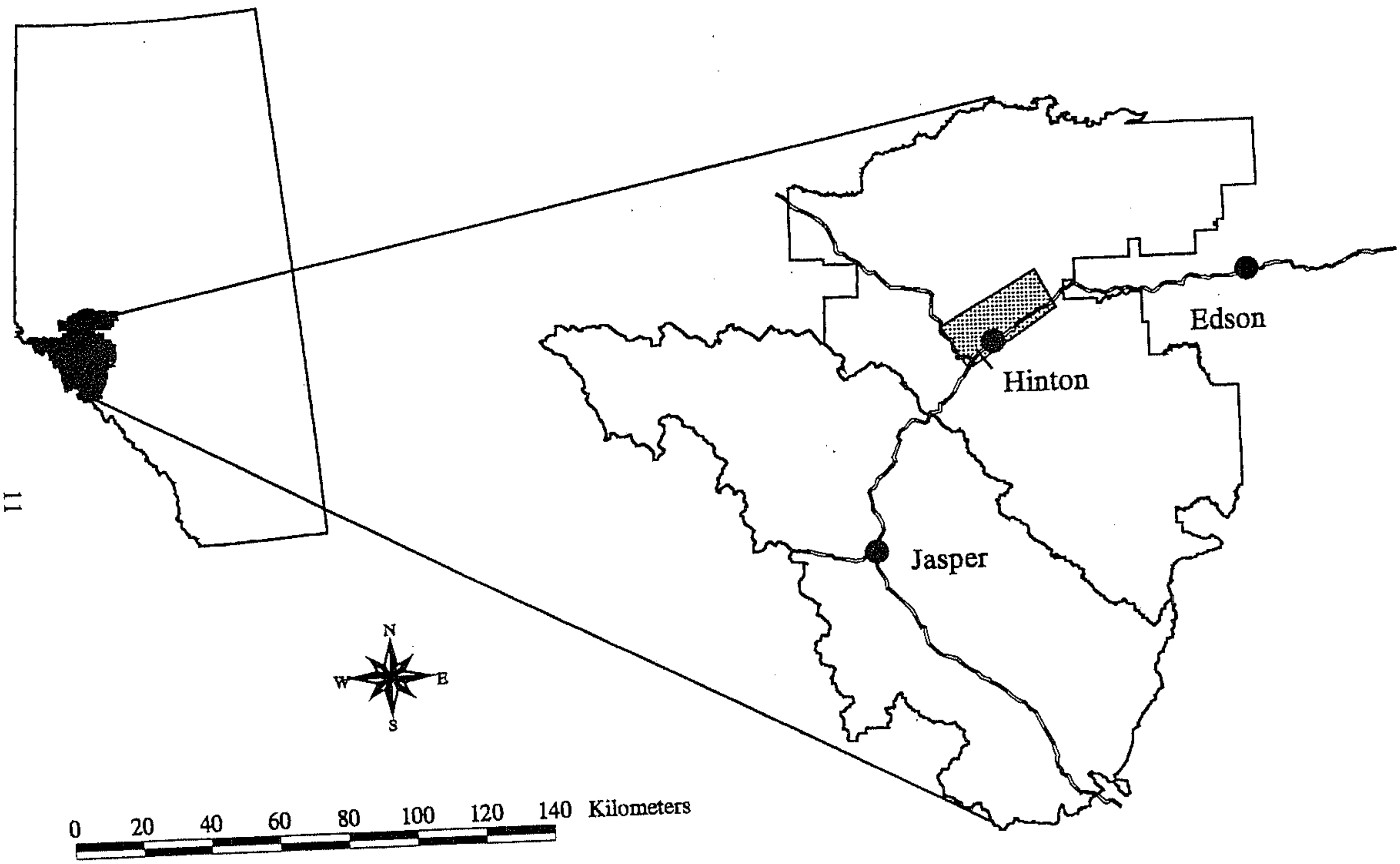


Figure 2 Study area located within the boundaries of the Foothills Model Forest in west-central Alberta

mean temperatures for the winter (December to March) of 1994-1995 are comparable to those of the previous 2 years (Figure 3). Snow fall levels for the winter (December to March) of 1994-1995 were less than the 2 previous years (Figure 4). Climatic data was obtained from the Brule weather station located just outside the west boundary of the study area.

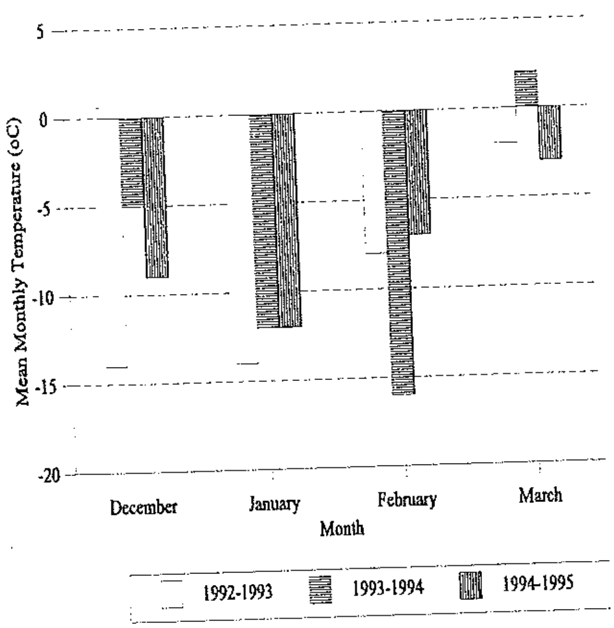
2.2 General Methods

2.2.1 Elk Capture

Elk were captured using 4-8 collapsible clover traps baited with salt blocks or alfalfa (Thompson et al. 1989). Traps were placed in areas of known elk use and checked twice a day. Captured elk were fitted with a Lotek LMRT-4 radio collar containing a mortality sensor and a head up/head down activity sensor. Eleven elk were captured from May 1, 1994 to August 30, 1994 using collapsible clover traps. Of the 11 elk captured, 5 elk cows (4 adults and 1 yearling) and 2 adult bulls were fitted with a Lotek radio collar (Table 1). One yearling bull escaped during handling, prior to a transmitter being placed on the animal, 1 elk cow escaped before processing, and 2 elk calves were released. In addition to elk being captured, 20 deer, 5 bears, and 19 horses were captured and released. The 1994 trapping season resulted in a capture rate of 42.3 trap nights per elk, and an overall capture rate of 8.45 trap nights per animal. During this trapping period no mortalities were encountered.

In addition to the elk fitted with radio collars during the spring/summer of 1994, Foothills

Figure 3 Mean monthly temperatures for the winters of 1992-1993 to 1994-1995.



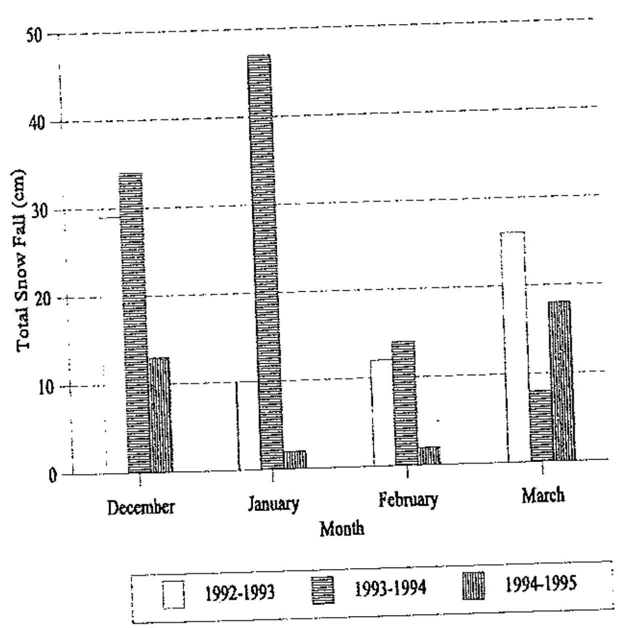


Figure 4 Total monthly snow fall (cm) for the winters of 1992-1993 to 1994-1995.

Table 1 Radio collar frequencies, capture dates, sex, estimated age at capture, and total number of locations for collared elk during the winter 1994 -1995.

Elk	Frequency	Capture Date	Sex	Age*	# of Locations
F1805	151.805	08/04/93	F	A	14
F1814	151.814	03/10/93	F	A	22
F1823	151.823	08/04/93	F	Y	29
F1834	151.834	08/15/93	F	A	28
F1844	151.844	03/10/93	F	A	22
F1885	151.885	06/30/94	F	A	23
F1895+	151.895	02/16/94	F	Y	0
F1904	151.904	07/12/95	F	Y	26
F1914	151.914	07/25/94	F	A	25
F1935	151.935	06/21/94	F	A	4
F1945	151.945	08/06/94	F	A	27
M1955	151.955	06/21/94	M	A	0
M1975	151.975	07/06/94	M	A	18

* A = Adult, Y = Yearling
+ died 06/02/94

Model Forest staff collared 4 additional elk of which 1 died 4 months after collaring (Table 1). Alberta Fish and Wildlife also collared 2 elk cows in the spring of 1993 using aerial (helicopter) darting (Table 1). The total sample size for the winter of 1994/95 was 12 animals.

2.2.2 Radio Telemetry and Monitoring

Telonics TR-2 receiver with scanner and a 3 element yagi antenna were used to receive signals from radio collared elk. The locations were taken from the ground from fixed bearing sites, with animal locations determined from 3-5 intersecting compass bearings. The time interval between bearings was usually less than 25 minutes. Attempts were made to minimize distance between receiver and collared elk without disturbing the elk. All bearings were plotted on 1:15000 airphotos while in the field. Due to the topography in the study area, I tried to visit each fix to confirm elk activity at that point (84% confirmed). A GPS reading was taken at the confirmed site or at the center of the polygon for non-confirmed sites, and differentially corrected to determine the UTM coordinates for each location.

Elk were located at least twice a week from December 1,1994 to March 21, 1995, subject to field restrictions. To reduce autocorrelation of successive locations, individual animals were located at least 72 hours apart ($\bar{x}$ = 95.5 hours) (Swihart and Slade 1985, McNay et al. 1994). The necessity of obtaining approximately 20 locations per animal over the winter period prohibited a complete randomized design. Upon sighting a collared elk, while visiting the fix site or while in the field, the location, activity, number of elk, date and time were recorded. Also, while visiting fix sites the predominant activity for that location was recorded and the location marked in the field.

2.2.3 Site Location

Feeding and bedding locations were determined by one of three methods: a) through radio telemetry on collared elk, b) visual sightings of non-collared elk feeding or bedding, or c) discovery of feeding or bedding sites while performing radio telemetry on collared elk. Feeding and bedding sites were located from December 1, 1994 to March 21, 1995. Only one bed or feeding site was measured per group of animals.

2.2.4 Vegetation Characterization

For all feeding and bedding sites and the vegetation plots, a number of vegetative and spatial variables were determined. Vegetation plots were used to estimate habitat availability in the immediate vicinity of the elk location. A vegetation plot was located 300 m from the bed or feeding site, in a random direction (Brown 1994). Vegetation variables were assessed in a 0.04 ha circular plot (radius 11.3m). All measurements were taken between June 01, 1995 and September 01, 1995, except percent canopy closure which was measured in the spring of 1995. Vegetation measurements followed the guidelines by Bessie (1995). Table 2 is a summary of the variables and methods used to estimate them.

Table 2 Variables measured at elk feeding and bedding sites and their respective vegetation plots.

Variable	Units	Method
Grass Cover	%	Estimated using a 0.5 m^2 quadrant located at 3.5m, 7.0m, and 10.5m along 4 transects. The mean of the 12 samples was used as the percent cover for the site
Herb Cover	%	Estimated using a 0.5 m^2 quadrant located at 3.5m, 7.0m, and 10.5m along 4 transects. The mean of the 12 samples was used as the percent cover for the site
Shrub Cover	%	Estimated using the line intercept method
Canopy Closure	%	Estimated using a spherical densiometer. A reading was taken at each cardinal direction and then averaged into one estimate for the site. All vegetation (limbs and stems) were recorded as canopy
Spruce, Pine, and Fir in Canopy (SPF)	%	Estimated by tallying the number of trees by class in the canopy within the plot. The percentage was determined by dividing the number of SPF trees in the canopy by the total number of trees in the canopy
Spruce and Fir in Canopy (SPFR)	%	Estimated by tallying the number of trees by class in the canopy within the plot. The percentage was determined by dividing the number of SPFR trees in the canopy by the total number of trees in the canopy
Stem Density	# / ha (*1000)	Estimated by tallying the number of stems $\geq$ 3m tall within the 0.01 ha plot. The number of stems for the plot was then converted to the number of stems per ha (*1000)
Overstorey Tree Height	m	Estimated using a clinometer. Tree height was the height of the average dominant trees in the plot
Elevation	m	Determined for each plot using a GPS unit. UTM co-ordinates and elevation were taken at each plot and then differentially corrected to increase accuracy (Trimble Navigation, Ltd. 1992)

For each plot, a number of spatial variables were estimated based on activity type (feeding or bedding). Distances were estimated from maps produced by overlaying the plot locations with Weldwood of Canada's (Hinton Division) forest cover, road and seismic line data using ARC/INFO. Table 3 provides a definition for each spatial variable.

2.3 Habitat Selection

2.3.1 Landscape Level Selection

The 95% adaptive kernal (ADK) home ranges were estimated for 9 of the 12 collared elk using the program CALHOME (Kie et al. 1996) (see Appendix B for a summary of the home ranges and distibution of elk in the study area). The 95% ADK UTM coordinates for the 9 elk home ranges were imported into ARC/INFO for spatial analysis. The forest cover (Phase III data), roads, seismic lines, and harvest data were clipped and summarized for each home range.

To determine availability of habitat at the landscape scale, 9 circular buffers equal to the mean area of the 9 elk home ranges, and a circular buffer equal in area to each elk's home range (n=9) were created in ARC/INFO. Each buffer was randomly determined but had to fall completely within the study area boundary. The forest cover, roads, seismic lines, and harvest data were clipped and summarized for each buffer (n=18). Incomplete forest cover data occurred for both the elk home ranges and the buffers. To fill in the missing data for the home ranges and buffers, maps of each were plotted. Using data from

Table 3 Definitions of the spatial variables measured for each elk feeding and bedding location and their respective vegetation plot.

Variable	Definition
Major Roads	Any hard packed road, open year round and maintained
Minor Roads	Roads that are not maintained year round and are usually only accessible by 4x4 during the winter
Seismic Line	General term given to include seismic lines, cut lines, power lines and gas line right-of-ways
Thermal Cover (D2)	A stand with >70% canopy closure (D density) with a height class of 2 (12.1 - 18.0 m) or better (Buckmaster el al. 1995)
Thermal Cover (C2)	A stand with >50% canopy closure (C density) and a height class of 2 (12.1 - 18.0m) or better
Hiding Cover	A stand of trees $\geq$ 3 m tall with a density class of B (>30%) (Buckmaster el al. 1995)
Forage Areas	A stand with less than 51% combined canopy closure of trees and tall shrubs over 3 m in height.

vegetation plots, air photos, and personal knowledge of the area, the data for missing stands was determined.

Stands, based on forest cover type, for each home range and buffer were classified into food, thermal cover and hiding cover separately. Table 4 provides a definition for each habitat category. A stand could be classified into more than one type because elk are able to utilize certain stands for more than one purpose. For example a stand with a canopy closure of density class 3 and a tree height of class 3 would be classified as both thermal cover (class C2) and as hiding cover. Therefore percent food, thermal cover and hiding cover will not sum to 100%. For each home range and buffer the road density, seismic line density, patch density, and mean patch size were calculated (Table 4). Finally the percent of each home range and buffer previously harvested (between 1957 and 1985) was determined.

To evaluate habitat selection I compared the composition of the elk home ranges to the equal mean area buffers using the Kruskal-Wallis test. I also determined selection by comparing the mean composition of the elk ranges to the equal sized buffers using the Wilcoxon Matched-Pairs Sign test. Non-parametric tests were used after determining the distribution of data was non-parametrically distributed.

2.3.2 Stand Level Selection

Locations contained within the 95% ADK home range for each elk (n=9 elk) were placed

Table 4 Definitions of landscape variables used in the analysis of winter habitat selection by elk.

Variable	Definition
Food	A stand with canopy closure no greater than B density
Thermal Cover (D2)	A stand with canopy closure of D density and a tree height of class 2 or greater
Thermal Cover (C2)	A stand with canopy closure of C density or greater and a tree height of class 2 or greater
Hiding Cover	A stand with canopy closure of B density or greater and a tree height of class 0 or greater
Harvested	The proportion of the home range or buffer previously logged
Road Density	The distance (km) of roads found within the home range or buffer
Seismic Line Density	The distance (km) of seismic lines found within the home range or buffer
Patch Density	Number of forest cover stands ($\geq$ 1 ha) per km^2
Mean Patch Size	The mean size of forest cover stands

into 1 of 10 habitat types: grass/meadow, regenerating cut, water, sapling, pole, open, mature, closed mature, open old-growth, closed old-growth, or other. White and Garrott (1990) recommended determining habitat selection at an individual level because different animals may use the habitat differently. However, the number of relocations for each animal was inadequate for analysis at an individual level. Therefore, locations from each collared animal were pooled.

Habitat availability was determined by averaging the percent composition of each habitat type within each elk's home range. A chi-square test was used to determine if elk were using each habitat type in proportion to its availability (Neu et al. 1974). If the null hypothesis that elk were using the habitat in proportion to its availability was rejected, a Bonferroni Z statistic was calculated for each habitat type to determine if it was used more or less than expected (Neu et al. 1974).

2.3.3 Site Level Selection

Selection by elk at the site level was determined by using the vegetation and spatial data (section 2.2.4) recorded at feeding , bedding, and vegetation plots. A 1-way ANOVA was used to determine if the mean spatial and non-spatial attributes at elk feeding sites were significantly different than the mean spatial and non-spatial attributes found at elk bedding sites. For each spatial and non-spatial attribute, the means for the elk feeding and bedding sites were compared to the means at their respective vegetation plots using a paired t-test. I placed the bedding sites into one of three classes based on the estimated temperature for the day that the bed was made. Beds were placed into one of the following temperature classes: (1) warm (≥ -8°C), (2) mild (≤ -9°C but ≥ -14°C) or (3) cold (≤ -15°C). Only fresh beds were used for the analysis. A 1-way ANOVA was used to determine if the mean spatial and non-spatial attributes at the bedding sites made during the 3 different temperature classes were significantly different.

2.4 Elk Habitat Suitability Index Model

2.4.1 Overall Model Performance

Overall model performance was assessed by testing the assumption that elk preference for each "life requisite" (Table 5) increased with an increase in HSI value. An HSI value was calculated for each elk location and its respective vegetation plot. The variables associated with food were applied to the feeding sites and their respective vegetation plots, while the variables associated mainly with thermal cover and hiding cover were applied to the bedding sites and their respective vegetation plots separately. The variables associated with hiding cover were applied to the bedding data under the assumption, that while bedded, elk were maximizing hiding cover.

A habitat preference index was calculated for each life requisite of the model using 10 equal HSI value classes ranging from 0.0 to 1.0 (Thomasma et al. 1991). The preference index was calculated as:

$$PI = \frac{\%\ \text{elk plots within an HSI class}}{\%\ \text{available vegetation plots within an HSI class}}$$

Table 5 Habitat suitability variables for each life requisite for the elk winter HSI model (Buckmaster et al. 1995) and the additional variables.

Life Requisite	Variable Code	Variable
Food	S2	Grass cover (%)
	S5	Food distance from thermal cover edge (km)
	S6	Herbaceous cover (%)
	S7	Shrub cover (%)
	S8	Food distance from hiding cover edge (m)
	S9	Food distance from access (m)
Thermal Cover	S1	Canopy cover (%)
	S3	Overstorey tree height (m)
	S4	Spruce, pine and fir in the canopy (%)
	S10	Cover distance from access (m)
	S12	Spruce and fir in the canopy (%)
	S15	Thermal cover distance from food (m)
Hiding Cover	S10	Cover distance from access (m)
	S11	Coniferous cover + 0.25 deciduous cover (%)
	S13	Average tree height (m)
	S14	Hiding cover distance from food (m)
Additional	S16	Distance to minor roads (m)
	S17	Distance to seismic (m)
	S18	Food distance to thermal cover (type C-2) (m)
	S19	Elevation (m)
	S20	Stem density (stems/ha)

I tested for a positive correlation between the PI and the HSI value class. In addition, I determined if there was a significant difference in the mean of HSI values for the elk locations and the vegetation plots for each life requisite using a paired t-test. I also determined if there was a correlation between the HSI values of the used site and the HSI value of the corresponding vegetation plot. The correlation was performed to determine if the vegetation plots were independent of the used sites.

Revisions to the HSI model were proposed based on visual comparison of the original model's suitability relationships and possible alternative equations. Revised habitat suitability relationships and equations were applied to the appropriate data set and a paired t-test was performed to test if there was a significant difference between the distribution of HSI scores between the used sites and the vegetation plots. A Wilcoxon test was performed to determine if there was a significant difference in HSI scores between the original model and the revised model.

2.4.2 Individual Model Variable Performance

Stepwise logistic regression was used to determine the significance of each variable, in differentiating between the elk used sites and the vegetation plots for the life requistes of food and thermal cover. Initially, variables were entered and retained in the logistic regression model if they were significant at p=0.05. Then variables that were significant at the p=0.05 level were entered and retained in the logistic regression model if they were significant at the p=0.01 level. The relationship of each predictor variable, significant at the p=0.01 level, to the dependent variable was obtained by performing separate linear and logistic regression analysis to plot the probability of use (Brennan et al. 1986, Thomasma et al. 1991).

2.4.3 Alternative Model

An alternative model to the HSI model was developed using stepwise logistic regression. Plots used by elk (i.e. feeding and bedding sites) were pooled and compared to the pooled vegetation plot data using stepwise logistic regression. Variables were entered and retained in the model if they were significant at p=0.05. The model is based on the resource selection probability function taking the form:

$$W(Y) = \frac{\exp(B_o + B_1X_1 + \ldots\ldots + B_pX_p)}{1 + \exp(B_o + B_1X_1 + \ldots\ldots + B_pX_p)}$$

where W(Y) = the estimated probability that the area represents elk habitat given a vector, Y, of habitat measurements; B_o = constant, B = the regression coefficients, and X = the predictor variables in the model (Brennan et al. 1986, Manly et al. 1993).

3.0 Results

3.1 Habitat Selection

3.1.1 Landscape Level Selection

The mean 95% ADK home range size for the 9 collared elk was 2304 ha (SE=402) (Appendix B). Individual home ranges ranged from 1224 ha to 5299 ha. Four of the habitat variables examined at the landscape level were significantly different between the elk home ranges and the circular buffers of equal mean area (Table 6). Elk home ranges had a lower mean road density, but a greater mean seismic line density than the circular buffers. The elk home ranges had smaller mean patch sizes and a greater number of patches per km^2. There was no significant difference in the composition of the home ranges and buffers in terms of food and cover composition.

Four of the variables examined at the landscape level were significantly different between the paired elk home ranges and circular buffers (Table 7). The elk home ranges had a lower mean road density and a higher mean seismic line density than the paired circular buffers. The elk home ranges also had a greater proportion of their area as thermal cover (D2) than the buffers. In addition, elk home ranges had a smaller mean patch size than the circular buffers. There was no significant difference between the elk home ranges and paired circular buffer in terms of food and hiding cover.

3.1.2 Stand Level Selection

For all elk home ranges combined (n=9), the dominant habitat was closed old-growth comprising 26% (53.94 km^2) of the combined home ranges (Table 8). Sapling and water habitat types were the least prevalent (2% and 3% respectively). Grass/meadow accounted for 7% (13.63 km^2) of the combined home ranges, while regenerating cuts accounted for 10% (20.49 km^2). For all elk combined (n=9), grass/meadow was usedmore than expected (Table 8). All other habitat types were used in proportion to

Table 6 Mean attributes for elk home ranges and equal mean area buffers. P values are the results from Kruskal-Wallis tests.

Variable	Elk Home Range[a] Mean $\pm$ SE (n)	Mean Area Buffer [b] Mean $\pm$ SE (n)	P Value
Food (%)	49.22 $\pm$ 1.93 (9)	48.47 $\pm$ 6.95 (9)	0.453
Thermal Cover (D2) (%)	1.21 $\pm$ 0.28 (9)	0.57 $\pm$ 0.20 (9)	0.106
Thermal Cover (C2) (%)	43.28 $\pm$ 2.17 (9)	41.92 $\pm$ 6.17 (9)	0.427
Hiding Cover (%)	88.16 $\pm$ 1.28 (9)	82.21 $\pm$ 4.88 (9)	0.508
Harvested (%)	10.50 $\pm$ 3.37 (9)	7.92 $\pm$ 4.10 (9)	0.269
Road Density (km/km^2)	0.32 $\pm$ 0.05 (9)	0.82 $\pm$ 0.22 (9)	0.005
Seismic Line Density (km/km^2)	3.18 $\pm$ 0.16 (9)	2.48 $\pm$ 0.24 (9)	0.038
Patch Density (# / km^2)	42.99 $\pm$ 6.12 (9)	21.67 $\pm$ 4.85 (9)	0.012
Mean Patch Size (km^2)	0.03 $\pm$ 0.004 (9)	0.06 $\pm$ 0.009 (9)	0.007

a = mean home range size = 2304 ha (for individual home range sizes see Appendix B)
b = mean area buffer size = 2304 ha.

Table 7 Mean attributes for elk home ranges and paired circular buffers. P values are the results from Wilcoxon Matched-Pairs Sign tests.

Variable	Elk Home Range[a] Mean ± SE (n)	Paired Circular Buffer[b] Mean ± SE (n)	P Value
Food (%)	49.22 ± 1.93 (9)	54.14 ± 6.93 (9)	0.214
Thermal Cover (D2) (%)	1.21 ± 0.28 (9)	0.81 ± 0.23 (9)	0.028
Thermal Cover (C2) (%)	43.28 ± 2.17 (9)	38.41 ± 5.28 (9)	0.441
Hiding Cover (%)	88.16 ± 1.28 (9)	78.42 ± 6.04 (9)	0.124
Harvested (%)	10.50 ± 3.37 (9)	10.13 ± 4.12 (9)	0.953
Road Density (km/km^2)	0.32 ± 0.05 (9)	1.05 ± 0.27 (9)	0.015
Seismic Line Density (km/km^2)	3.18 ± 0.16 (9)	2.20 ± 0.26 (9)	0.028
Patch Density ($\# / km^2$)	42.99 ± 6.12 (9)	25.61 ± 4.49 (9)	0.051
Mean Patch Size (km^2)	0.03 ± 0.004 (9)	0.06 ± 0.012 (9)	0.008

a = for individual home range size see Appendix B
b = size of circular buffers paired with individual home range sizes (see Appendix B)

Table 8 Habitat use at a stand level by elk (n=9)[a] in west-central Alberta during the winter of 1994 - 1995.

Habitat	Available (%)	Observed (n)	Expected (n)	X^2	Bonferroni 95% Confidence Interval	Use
Grass / Meadow	6.6	43	13	64.94	0.130 - 0.290	More
Regenerating Cut	9.8	21	20	0.03	0.043 - 0.161	Equal
Water	1.9	0	4	3.83	0.000 - 0.000	No Use
Sapling	2.7	4	5	0.39	-0.007 - 0.047	Equal
Pole	9.8	12	20	3.22	0.012 - 0.104	Equal
Open Mature	7.6	18	16	0.37	0.032 - 0.144	Equal
Closed Mature	16.0	40	33	1.56	0.117 - 0.273	Equal
Open Old-growth	11.5	15	24	3.17	0.022 - 0.124	Equal
Closed Old-growth	25.9	39	53	3.77	0.113 - 0.267	Equal
Other	8.2	13	17	0.85	0.016 - 0.110	Equal

a = pooling all elk locations and defining the area of availability as the mean of each habitat type found within each elk's 95% ADK home range their availability.

3.1.3 Site Level Selection

3.1.3.1 Activity Dependent Habitat Selection

A total of 111 feeding sites were located. This sample size was reduced to 96 sites after 15 sites were removed due to autocorrelation. A total of 64 bedding sites were located. The data set was reduced to 62, after 2 locations were removed due to autocorrelation. Autocorrelation occurred when two or more collared animals were seen feeding or bedded within the vicinity of each other. Only one location was used in this instance. All of the non-spatial variables were compared between the two activity types, while only the spatial variables distance to major roads, minor roads, and seismic lines were compared.

Five of the non-spatial variables were significantly different between the elk feeding and bedding sites (Table 9). Elk feeding sites had a lower mean percent canopy closure, percent shrub cover, stem density and tree height. Elk feeding sites also had a higher mean percent grass cover than the bedding sites. In terms of the spatial variables compared, only one variable was significant (Table 10). Elk feeding sites were significantly closer to seismic lines than bedding sites.

3.1.3.2 Use Versus Availability

3.1.3.2.1 Feeding Locations

All of the non-spatial habitat attribute variables were significantly different between the

Table 9 Mean non-spatial attributes at elk feeding and bedding sites. P-values are the result of 1-way ANOVA's.

	Elk Feeding Sites		Elk Bedding Sites		
Variable	Mean ± SE	(n)	Mean ± SE	(n)	P Value
Canopy Closure (%)	31.34 ± 3.45	(96)	64.68 ± 4.03	(62)	<0.001
Grass Cover (%)	59.73 ± 3.37	(96)	34.95 ± 3.30	(62)	<0.001
Herb Cover (%)	19.00 ± 1.16	(96)	16.85 ± 0.89	(62)	0.185
Shrub Cover (%)	15.15 ± 1.49	(96)	27.37 ± 1.76	(62)	<0.001
Spruce, Pine,& Fir in the canopy (%)	28.17 ± 4.20	(96)	38.53 ± 5.07	(62)	0.120
Spruce & Fir in the canopy (%)	26.23 ± 4.13	(96)	28.73 ± 4.50	(62)	0.692
Stem Density (# / ha x 1000)	1.31 ± 0.19	(96)	2.03 ± 0.17	(62)	0.008
Tree Height (m)	5.57 ± 0.72	(96)	13.38 ± 0.86	(62)	<0.001
Elevation (m)	1060.38 ± 8.25	(96)	1061.34 ± 8.90	(62)	0.939

Table 10 Mean spatial attributes at elk feeding and bedding sites. P-values are the results of 1-way ANOVA's. Variables are "distance to" in meters.

	Elk Feeding Sites		Elk Bedding Sites		
Variable	Mean ± SE	(n)	Mean ± SE	(n)	P Value
Major roads	1093 ± 66.06	(96)	1244 ± 87.46	(62)	0.164
Minor roads	601 ± 70.05	(96)	763 ± 69.90	(62)	0.121
Seismic	102 ± 11.30	(96)	165 ± 19.59	(62)	0.004

elk feeding sites and vegetation plots, except for percent herbaceous cover (Table 11). Elk feeding sites had significantly less canopy closure, less spruce, pine, and fir, and less spruce and fir in the canopy than the vegetation plots. Elk feeding sites had a significantly lower tree height and stem density than did the vegetation plots. Elk feeding sites had a greater percent grass cover and less percent shrub cover than the vegetation plots. Elk feeding locations were found at a significantly lower elevation than the vegetation plots.

Only two of the six spatial variables were significantly different between elk feeding sites and the vegetation plots (Table 12). Distance to seismic lines was significantly less for feeding sites when compared to the vegetation plots. Elk feeding sites were located significantly further from hiding cover than the vegetation plots.

3.1.3.2.2 Bedding Locations

Elk selected bedding sites whose non-spatial characteristics were significantly different from the available habitat (Table 13). Elk bedding sites had a significantly higher percent grass cover, significantly less spruce, pine and fir, and spruce and fir in the canopy than did the vegetation plots. Also, elk selected bedding sites that had significantly fewer stems per ha than the vegetation plots.

In terms of spatial attributes, elk exhibited no selection when choosing bedding sites (Table 14). There was no significant difference between elk bedding sites and the

Table 11 Mean non-spatial attributes at elk feeding and vegetation plots. P values are results from paired t-test.

	Elk feeding sites		Vegetation plots		
Variable	Mean ± SE	(n)	Mean ± SE	(n)	P value
Canopy Closure (%)	31.34 ± 3.45	(96)	63.72 ± 3.55	(96)	< 0.001
Grass Cover (%)	59.73 ± 3.37	(96)	32.61 ± 3.20	(96)	< 0.001
Herb Cover (%)	19.00 ± 1.16	(96)	19.85 ± 1.01	(96)	0.574
Shrub Cover (%)	15.31 ± 1.50	(96)	26.25 ± 1.95	(96)	< 0.001
Spruce, Pine,& Fir in the canopy (%)	28.17 ± 4.20	(96)	44.70 ± 4.06	(96)	0.004
Spruce & Fir in the canopy (%)	26.23 ± 4.13	(96)	40.17 ± 3.99	(96)	0.012
Stem Density (# / ha x 1000)	1.31 ± 0.19	(96)	3.24 ± 0.29	(96)	< 0.001
Tree Height (m)	5.46 ± 0.72	(96)	12.44 ± 0.78	(96)	< 0.001
Elevation (m)	1060 ± 8.25	(96)	1065 ± 8.32	(96)	0.006

Table 12 Mean spatial attributes at elk feeding and vegetation plots. P values are the results from paired t-test. Variables are "distance to" in meters.

	Elk feeding sites	Vegetation plots	
Variable	Mean ± SE (n)	Mean ± SE (n)	P value
Major road	1093 ± 66.06 (96)	1088 ± 64.50 (96)	0.829
Minor road	601 ± 70.05 (96)	635 ± 72.24 (96)	0.139
Seismic	102 ± 11.30 (96)	164 ± 12.34 (96)	< 0.001
Thermal Cover (C-2)	160 ± 14.35 (96)	158 ± 18.25 (96)	0.932
Thermal Cover (D-2)	2351 ± 177.08 (96)	2376 ± 180.27 (96)	0.240
Hiding Cover	71 ± 7.68 (96)	48 ± 8.06 (96)	0.024

Table 13 Mean non-spatial attributes at elk bedding and vegetation plots. P values are results from paired t-test.

	Elk bedding sites	Vegetation plots	
Variable	Mean ± SE (n)	Mean ± SE (n)	P value
Canopy Closure (%)	64.68 ± 4.03 (62)	71.74 ± 4.01 (62)	0.157
Grass Cover (%)	34.95 ± 3.30 (62)	25.35 ± 2.92 (62)	0.016
Herb Cover (%)	16.85 ± 0.89 (62)	17.71 ± 1.29 (62)	0.56
Shrub Cover (%)	27.37 ± 1.76 (62)	28.26 ± 2.13 (62)	0.698
Spruce, Pine,& Fir in the canopy (%)	38.53 ± 5.07 (62)	54.21 ± 5.15 (62)	0.023
Spruce & Fir in the canopy (%)	28.73 ± 4.50 (62)	46.66 ± 5.08 (62)	0.005
Stem Density (# / ha x 1000)	2.03 ± 0.17 (62)	3.17 ± 0.27 (62)	0.001
Tree Height (m)	13.38 ± 0.87 (62)	13.75 ± 0.78 (62)	0.701
Elevation (m)	1061 ± 8.90 (62)	1060 ± 8.43 (62)	0.522

Table 14 Mean spatial attributes at elk bedding and vegetation plots. P values are the results from paired t-test. Variables are "distance to" in meters.

	Elk bedding sites	Vegetation plots	
	Mean ± SE (n)	Mean ± SE (n)	P value
Major road	1244 ± 87.46 (62)	1229 ± 84.34 (62)	0.550
Minor road	763 ± 69.90 (62)	757 ± 72.24 (62)	0.830
Seismic	165 ± 19.59 (62)	155 ± 19.50 (62)	0.684
Forage Cover	71 ± 11.14 (62)	69 ± 13.63 (62)	0.880

vegetation plots in terms of the distance to major and minor roads, and the distance to seismic lines. There was no significant difference between the distance from the bedding site to foraging areas and the distance from the vegetation plots to foraging areas.

3.1.3.3 Selection of Bedding Sites Based on Temperature

Fresh bedding sites known to have been made on a specific day were divided into 1 of 3 temperature classes to determine if elk selected different habitat characteristics based on temperature. Only 1 of the non-spatial variables was significantly different between the 3 temperature classes (Table 15). Percent herb cover was lower for bedding sites made on cold days than on bedding sites made on mild or warm days. There was no significant difference between bedding sites made on warm, mild, or cold days in terms of the spatial variables (Table 16).

3.2 Elk Habitat Suitability Index Model

3.2.1 Overall Model Performance

3.2.1.1 Food Model

HSI values were calculated for 96 elk feeding sites and 96 adjacent vegetation plots based on the variables and relationships for the life requisite of food (Buckmaster et al. 1995) (Figure 5). The PI index and HSI classes were not significantly correlated ($r= -0.098$, $p=0.79$) (Figure 6). The mean HSI value for the feeding sites was not significantly different than the mean for the adjacent vegetation plots ($t=-0.75$, $p=0.46$) (Table 17).

Table 15 Mean non-spatial attributes at bedding sites made during different temperature class. P-values are the result of 1-way ANOVA's.

	Temperature Class[a]			
	Warm	Mild	Cold	
Variable	Mean ± SE (n)	Mean ± SE (n)	Mean ± SE (n)	P-value
Canopy Closure (%)	69.17 ± 6.58 (19)	58.19 ± 7.57 (16)	65.89 ± 8.57 (18)	0.59
Grass Cover (%)	32.16 ± 4.06 (19)	33.38 ± 6.72 (16)	39.94 ± 7.46 (18)	0.63
Herb Cover (%)	18.37 ± 1.59 (19)	19.00 ± 1.35 (16)	13.11 ± 1.45 (18)	0.01
Shrub Cover (%)	25.16 ± 2.69 (19)	28.06 ± 3.65 (16)	27.83 ± 3.73 (18)	0.79
Spruce, Pine,& Fir in the canopy (%)	30.68 ± 7.85 (19)	39.75 ± 10.14 (16)	51.22 ± 11.06 (18)	0.32
Spruce & Fir in the canopy (%)	25.47 ± 6.86 (19)	35.88 ± 9.41 (16)	31.72 ± 9.81 (18)	0.70
Stem Density (# / ha x 1000)	2.35 ± 0.30 (19)	1.87 ± 0.37 (16)	1.74 ± 0.25 (18)	0.33
Tree Height (m)	12.94 ± 1.45 (19)	13.12 ± 1.48 (16)	13.95 ± 1.90 (18)	0.89
Elevation (m)	1066 ± 17.34 (19)	1046 ± 16.26 (16)	1059 ± 15.41 (18)	0.69

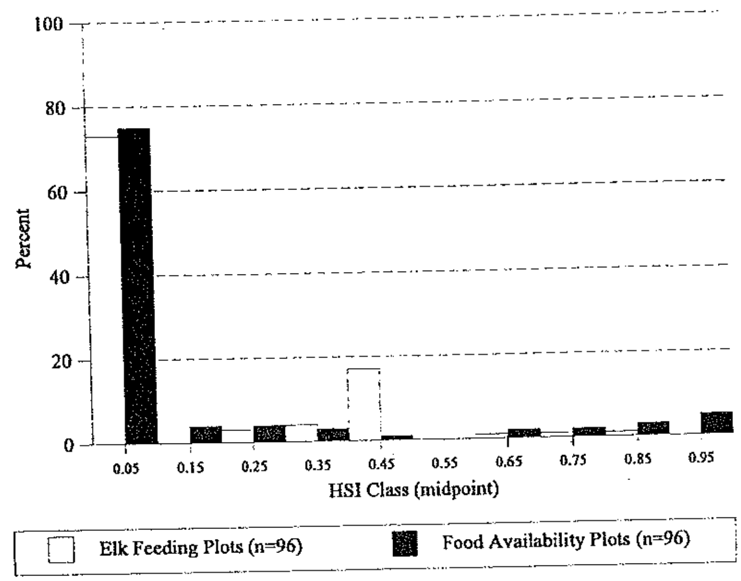
a = warm (≥ -8°C), mild (≤ -9°C but ≥ -14°C) and cold (≤ -15°C)

Table 16 Mean spatial attributes for elk bedding sites made during different temperature class. P-values are the results of 1-way ANOVA's. Variables are "distance to" in meters.

	Temperature Class[a]			
	Warm	Mild	Cold	
Variable	Mean ± SE (n)	Mean ± SE (n)	Mean ± SE (n)	P-value
Major road	1187 ± 164.29 (19)	1413 ± 176.42 (16)	1208 ± 176.40 (18)	0.6
Minor road	737 ± 124.96 (19)	688 ± 120.41 (16)	808 ± 142.18 (18)	0.81
Seismic	164 ± 41.27 (19)	177 ± 36.00 (16)	136 ± 32.93 (18)	0.73
Food	94 ± 19.63 (19)	45 ± 17.14 (16)	72 ± 22.56 (18)	0.25

a = warm (≥ -8°C), mild (≤ -9°C but ≥ -14°C) and cold (≤ -15°C)

Figure 5 The distribution (%) of HSI classes between the elk feeding plots and available vegetation plots.



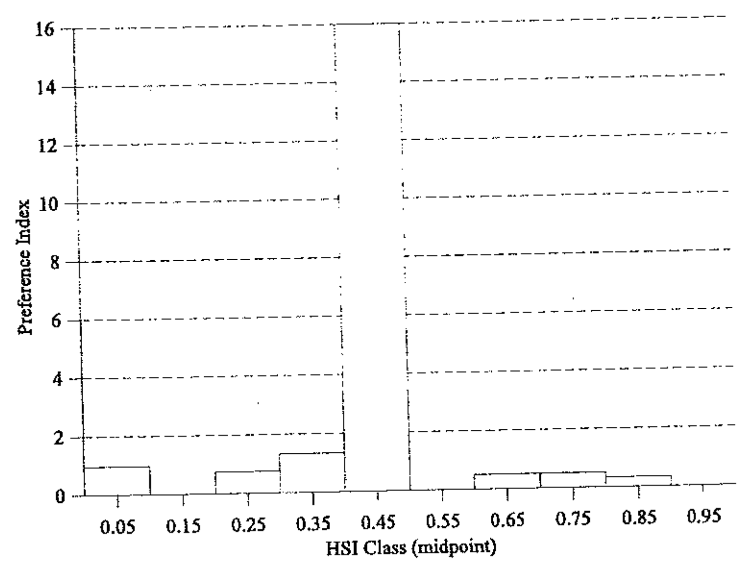


Figure 6 Preference index for 10 HSI classes for food model

Table 17 Original (Buckmaster et al. 1995) and alternative elk HSI model for the life requisite of food.

Model	Function	n[a]	Used mean	Used SE	Available mean	Available SE
Original	$(S2+0.5S6+0.25S7)^{b}$ x S5 x S8 x S9	96	0.13	0.02	0.14	0.03
FM-2	$(S2+0.5S6+0.25S7)^{b}$ x $S5^{c}$ x S8 x S9	96	0.68	0.03	0.42	0.03
FM-3	$S5^{c}$ x S8 x S9	96	0.98	0.01	0.88	0.03

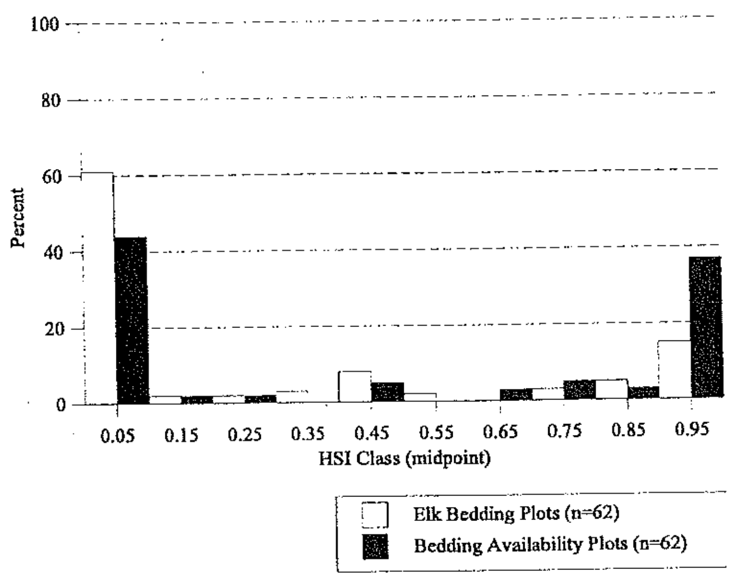
a = number of pairs
b = maximum value is 1.00
c = modified definition of thermal cover to a stand with a canopy of C density from D density

There was a significant correlation between the used sites HSI values and the available sites HSI values ($r=0.788$, $p<0.001$). The significant correlation was due to the fact that variable S5 was 0 for the majority of the used and available sites. This resulted in the HSI values being 0 for both the used and available sites. The model performed poorly for both the used and available sites because of the distance to thermal cover variable (S5). The original model defined thermal cover as a stand of tree height 12m or greater and a canopy closure of >70% (Buckmaster et al. 1995). Model performance was significantly improved when S5 was defined as a stand with tree height of 12m or greater and a canopy closure of > 50%. The modified model (FM-2) resulted in a significantly higher mean HSI value than the original model when applied to the used sites ($z=-8.01$, $p<0.001$) (Table 17). The modified model (FM-2) also resulted in a significantly higher mean HSI value for the used sites than for the available sites ($t=7.01$, $p<0.001$) (Table 17). Model performance was further enhanced when only for the the spatial variables were included in the equation (FM-3). There was a significant difference between the mean HSI values for the used sites and the mean for the available sites ($t=3.63$, $p<0.001$) (Table 17). The spatial model (FM-3) had a mean HSI value of 0.98 which was significantly higher than the revised model (FM-2) mean of 0.68 ($z=-7.01$, $p<0.001$).

3.2.1.2 Thermal Cover Model

HSI scores were calculated for 62 elk bedding sites and 62 adjacent vegetation plots based on the variables and relationships for the life requisite of thermal cover (Buckmaster et al. 1995) (Figure 7). The PI index and HSI classes were not significantly

Figure 7 The distribution (%) of HSI classes for elk thermal cover plots and available vegetation plots.



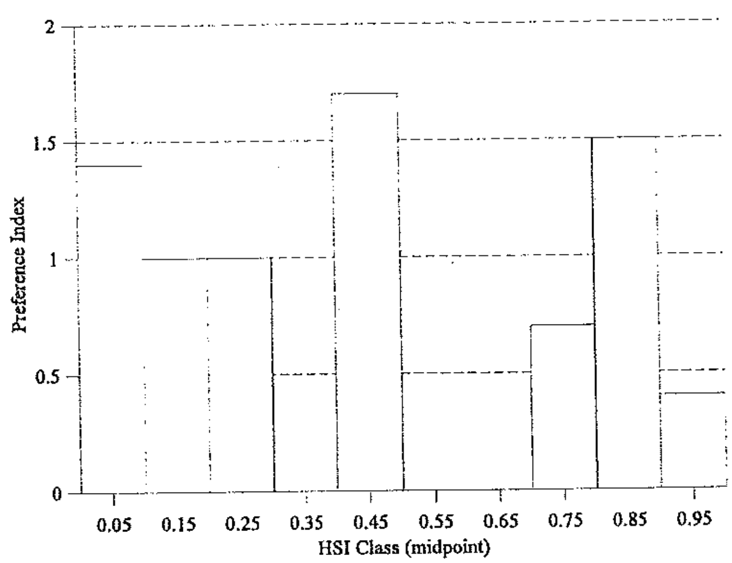


Figure 8 Preference index for 10 HSI classes for the thermal cover model.

correlated (-0.254, p=0.48) (Figure 8).

The mean HSI value for the available sites was significantly higher than the mean for the used sites (t=-2.75, p<0.01) (Table 18). There was not a significant correlation between the HSI values for the used sites and the HSI values for the available sites (r=0.107, p=0.41). When variables S4 and S12 were removed from the equation, there was a significant difference between the mean HSI values for the used sites based on the modified model (TC-2) and the mean HSI values for the used sites based on the original model (z=-5.23, p<0.001) (Table 18). When TC-2 is applied to both the used sites and the available sites there is not a significant difference between mean HSI values (t=-1.56, p=0.12) (Table 18). If only the spatial variables are included in the equation (TC-3), the mean for the TC-3 model when applied to the used sites is significantly higher than the mean HSI values for model TC-2 for the used sites (z=-4.60, p<0.001) (Table 18). The spatial model did not result in a significant difference between mean HSI values of the used and available sites (t=0.001, p=1.00). Even though the mean HSI score could be significantly increased by modifying the equation, the used sites had either a lower or non-significantly different mean HSI values than the available sites.

3.2.1.3 Hiding Cover Model

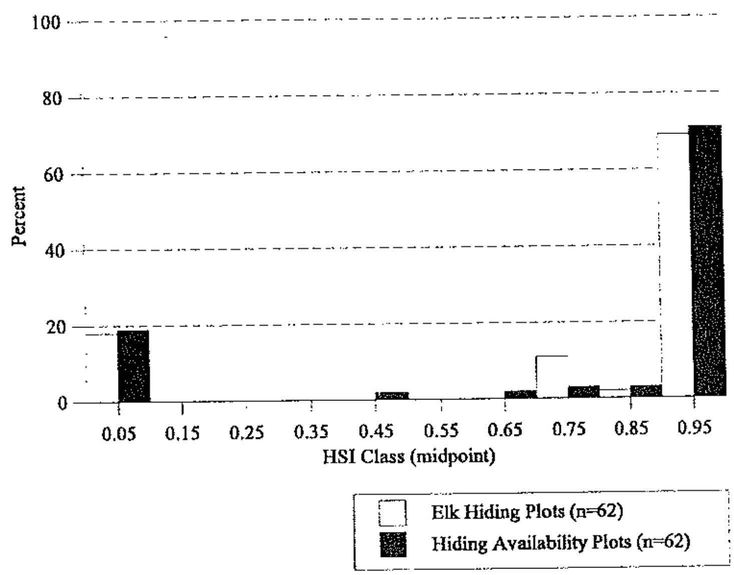
HSI scores were calculated for 62 bedding sites and 62 adjacent vegetation plots based on the variables, relationships, and equation for the life requisite of hiding cover (Buckmaster et al. 1995) (Figure 9). The variables and relationships for hiding cover was

Table 18 Original (Buckmaster et al. 1995) and alternative elk HSI models for the life requisite of thermal cover.

Model	Function	n[a]	Used mean	Used SE	Available mean	Available SE
Original	S1 X S3 x S4 x S10 x S12 x S15	96	0.28	0.05	0.48	0.06
TCM-2	S1 X S3 x S10 x S15	96	0.68	0.06	0.78	0.05
TCM-3	S10 x S15	96	1.00	0.01	1.00	0.01

a = number of pairs

Figure 9 The distribution (%) of HSI classes for elk hiding cover and available vegetation plots.



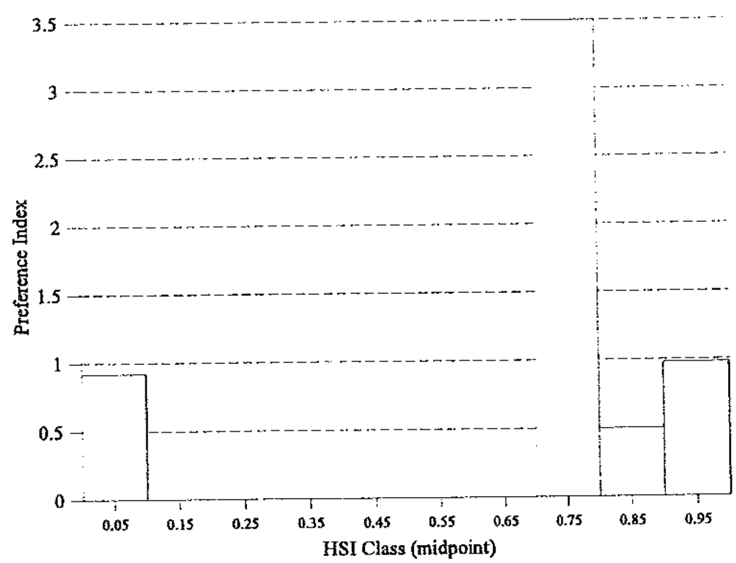


Figure 10 Preference index for 10 HSI classes for the hiding cover model.

applied to the bedding data with the assumption, that while bedded, elk were also maximizing hiding cover. The PI index and HSI classes were not significantly correlated (r=0.361, p=0.31) (Figure 10).

The mean HSI value for the used sites was not significantly different than the mean for available sites (t=0.200, p=0.84) (Table 19). There was not a significant correlation between the mean HSI values for the used plots and the mean HSI values for the available plots (r=0.185, p=0.14). No alternative models were proposed because of the high HSI score produced for the used sites ($\bar{x}$=0.80) based on the original models habitat relationships and equation.

3.2.2 Individual Model Variable Performance

3.2.2.1 Food Model Variables

All of the variables contained in the original model (S1-S15) and the additional variables (S16-S20) were entered into a stepwise logistic regression model at a p=0.05 level. Five variables were significant at the p=0.05 level and were retained in the model (Table 20). Variables S5 and S6 were from the original food model, while variables S3, S17, and S20 were not. The five variables found significant at the p=0.05 level were entered into a logistic regression model at a p=0.01 level. Three of the five variables were significant at the p=0.01 level and were retained in the model (Table 20). All three variables were not in the original food model. The three variable model had a slightly better overall classification rate then the five variable model (75% vs 72% respectively). In the three

Table 19 Original (Buckmaster et al. 1995) elk HSI model for the life requisite of hiding cover.

Model	Function	n[a]	Used mean	Used SE	Available mean	Available SE
Original	S10 x S11 x S13 x S14	96	0.8	0.05	0.78	0.05

a = number of pairs

Table 20 Variables and classification results for the life requisite of food.

			Classification	Results	(% correct)
Variable[a]	Coefficient	SE	Group	No. Correct	% Correct
		Entry	Level = 0.05		
S5	0.0002	0.0001	Used	69	72
S6	0.0368	0.0180	Available	68	72
S20	-0.3600	0.1070	Overall	137	72
S3	-0.1091	0.0272			
S17	-0.0058	0.0017			
Constant[b]	1.2563	0.4827			
		Entry	Level = 0.01		
S20	-0.2526	0.0868	Used	73	76
S3	-0.0911	0.0247	Available	71	74
S17	-0.0059	0.0016	Overall	144	75
Constant[b]	2.1672	0.3829			

a = see Table 5 for variable labels
b = not an original variable but a variable produced by the model

variable model all of the variable coefficients were negative indicating that variables S3, S17, and S20 decreased with utilization.

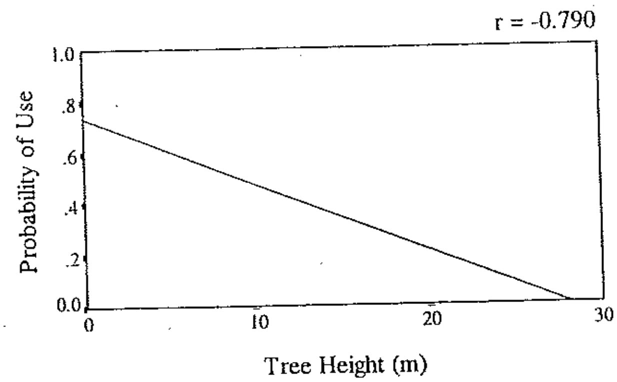
The relationship between the three predictor variables and the probability of use are givenin Figure 11. All variables produced first order models. None of the variables were in the original food model so no comparisons between the original theoretical HSI relationships and data-based HSI relationships were performed.

3.2.2.2 Thermal Cover Model Variables

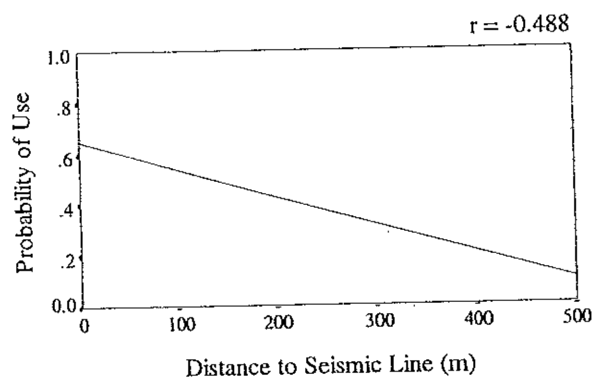
All of the variables contained in the original model (S1-S15) and the additional variables (S16-S20) were entered into a stepwise logistic regression at p=0.05 level. Only one variable, S20 (stem density) was significant at the p=0.05 level and was retained in the model (Table 21). Variable S20 was also significant at the p=0.01 level and retained in the model. The S20 variable had an overall classification rate of 65%. S20 had a negative coefficient indicating a decrease in stem density with utilization.

The relationship between stem density (S20) and the probability of use is given in Figure 12. The variable S20 produced a third order model. Stem density was not a variable in the original thermal cover model, so a comparison of the theoretical HSI relationship to the data-based HSI relationship was not performed.

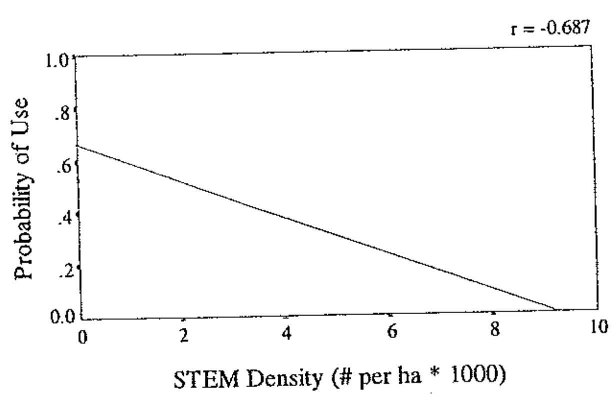
Figure 11 Relationships of the three predictor variables in the elk food model.



(a) variable S3: Tree Height



(b) variable S17: Distance to Seismic



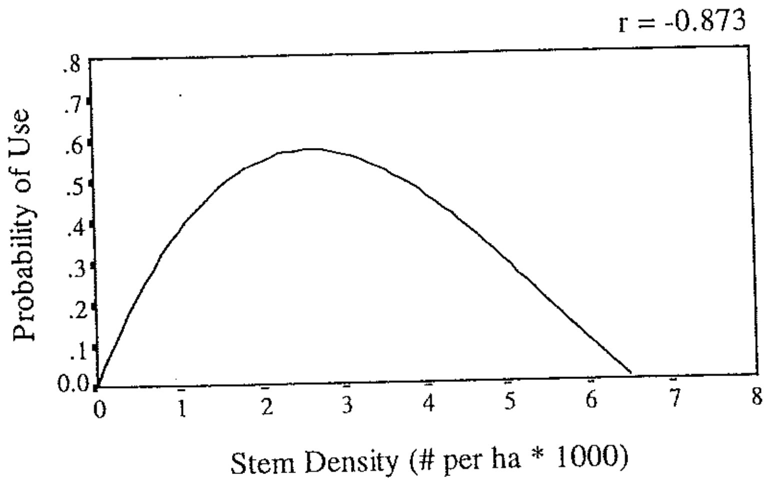
(c) variable S20: Stem Density

Table 21 Variable and classification results for the life requisite of thermal cover.

			Classification	Results	(% correct)
Variable[a]	Coefficient	SE	Group	No. Correct	% Correct
S20	-0.4017	0.1259	Used	46	74
Constant[b]	1.0126	0.3582	Available	34	55
			Overall	80	65

a = see Table 5 for variable label
b = not an original variable but a variable produced by the model

Figure 12 Relationship of predictor variable in the elk thermal cover model.



3.2.3 Alternative Model

All elk locations (96 feeding sites and 62 bedding sites) were pooled and compared to the pooled vegetation data (n=158) using stepwise logistic regression at a p=0.05 level. Three variables were found significant at the p=0.05 level and were retained in the model (Table 22). The three variable model had an overall classification rate of 66%. The logistic regression model takes the form:

$$W(Y) = \frac{\exp(1.52 + (-0.33 * S20) + (-0.04 * S3) + (-0.002 * S17))}{1 + \exp(1.52 + (-0.33 * S20) + (-0.04 * S3) + (-0.002 * S17))}$$

All three variables had a negative coefficient indicating that variables S3, S17, and S20 decreased with increased utilization.

4.0 Discussion

Variation in habitat exists at a variety of levels, allowing selection to occur at several scales (Dunning et al. 1992, Pedlar et al. 1997). Habitat selection may occur at multiple scales ranging from the landscape level to the selection of site attributes at feeding and bedding sites. The change in habitat attributes at each scale or level may change the criteria for selection, and researchers and managers must remember this when making inferences and decisions regarding habitat selection (Manly et al. 1993). Understanding how habitat selection by elk changes with spatial scale may allow for the long term management of elk at the local and broad scale.

Table 22 Variables and classification results for the alternative pooled elk stepwise logistic regression model.

			Classification	Results	(% correct)
Variable[a]	Coefficient	SE	Group	No. Correct	% Correct
S20	-0.3280	0.0722	Used	100	63
S3	-0.0405	0.0175	Available	109	69
S17	-0.0021	0.0009	Overall	209	66
Constant[b]	1.5176	0.2755			

a = see Table 5 for variable labels
b = not an original variable but a variable generated by the model

4.1 Habitat Selection

4.1.1 Landscape Level Selection

Black et al. (1976) proposed that optimal elk habitat consists of 40% of the land base as cover and 60% as food in the proper size and spatial arrangement. It has now become the standard definition of optimal elk habitat, but few studies have validated this definition. Irwin and Peek (1983) found elk home ranges consisted of 35% forage area, 24% thermal cover, and 40% hiding cover. Though the proportions found by Irwin and Peek (1983) were different than those given by Black et al. (1976), they still concluded that forage availability was the key function in the selection of a home range by elk. Elk home ranges during my study averaged 49% food, 1% class D2 thermal cover, 43% class C2 thermal cover, and 88% hiding cover. If the methods used by Black et al. (1976) are applied to my data, the ratio becomes 49% food: 51% cover. These values are similar to those given by Black et al. (1976).

Irwin and Peek (1983) concluded that forage density strongly influenced the size and location of elk home ranges. In dry shrub steppe environments, larger home ranges are believed to be a strategy utilized by elk to compensate for low forage availability (McCorquodale et al. 1989). I believe the proportion of the home range as forage to be the key factor in determining the location and size of the home ranges selected by elk. There was little variation in the proportion of each elk's home range classified as forage, but there was a large variation between individual elk's home range size. For example, elk F151.914 had a home range 2-4x larger than any other elk, but still only 45% of her home range was classified as forage. It appears that this animal had to cover a larger area in order to obtain sufficient forage. Other factors such as social interactions and population density may also contribute to differences in home range sizes but were not investigated during this study.

The avoidance of habitat within the vicinity of open roads by elk has been extensively documented (Lyon 1979, Rost and Bailey 1979, Wisdom et al. 1986, Thomas et al. 1988, Pope 1994). In a review of the effects of linear development on wildlife, Jalkotzy et al. (1997) stated that decline in habitat use by elk within the vicinity of roads was variable and depended on traffic volume, the type of traffic, topography, and the ratio of closed to open habitats. Most studies have established avoidances of roads in terms of a distance, but Lyon (1983) determined avoidance or loss of habitat in terms of road density. Habitat effectiveness decreases dramatically as the density of roads increases such that an area with a road density greater than 0.62 km/km^2 is reduced by 40% (Lyon 1983). Road densities in the elk home ranges were less than the 0.62 km/km^2 density given by Lyon (1983), suggesting that loss of habitat due to roads was minimal for the ranges selected by elk.

Elk home ranges had significantly higher seismic line densities than the available habitat buffers. Elk used the seismic lines and right of ways as forage areas. Jalkotzy et al. (1997) stated that linear developments, including seismic lines and right-of-ways, can have a positive effect for elk by increasing habitat diversity, but the level of utilization is governed by the level of human disturbance. Displacement of elk by construction activities of a pipeline right-of-way in west-central Alberta was noted by Morgantini and Olsen (1983). The displacement was short term, with elk returning shortly after construction stopped, with intensive use for grazing and travelling occuring the following summer and winter (Morgantini and Olsen 1983). Lees (1989) observed elk in west-central Alberta using pipeline right-of-ways as feeding areas year round, with only a dramatic decrease in use during periods of intense recreational activity. A shift in distribution by elk was also noted by Morgantini and Oslen (1983) during the fall hunting season. Avoidance of areas with high concentrations of seismic lines may occur during fall hunting seasons if hunters are using seismic lines as a means of accessing areas.

Patch density and mean patch size are simple statistics used to represent landscape configuration and can serve as a measure of habitat fragmentation or spatial heterogeneity (McGarigal and Marks 1995). Elk selected home ranges that had a greater mean patch density and smaller patch sizes than the available habitat. Being an ecotone species, the elk is adapted to take advantage of the diverse habitat found where plant communities join (Geist 1982, Robinson and Bolen 1989). Selecting heterogeneous areas for winter home ranges may have allowed elk the opportunity to feed in grass meadows while taking advantage of the adjacent areas for thermal and hiding cover.

4.1.2 Stand Level Selection

Selection of a habitat type at a population level may be negated because individual animals show differences in preference (White and Garrott 1990, Bradshaw 1994). White and Garrott (1990) recommend analyzing radio-telemetry habitat data at an individual level in order to maintain the variability in habitat selection exhibited by individuals. If few observations are taken on many animals, pooling the data may be appropriate (White and Garrott, 1990). In order to meet the requirement of the chi-square test that (1) there is at least one expected observation in each habitat category and (2) no more than 20% of all habitat categories contain less than 5 expected observations, I was forced to pool data for the 9 collared animals (Neu et al. 1974). Strong preferences for a habitat type exhibited amongst all individuals will actively benefit fitness at a population level (White and Garrott 1990). Selection that is cancelled by pooling data from all individuals may be of little benefit to fitness at a population level, but only serve the needs of the individual.

Availability is defined as the amount of a habitat type that is accessible to a species or individual (Neu et al. 1974, Johnson 1980, Wilson et al. in press). Most use-availability studies assume that all resources in a defined area are available for use by all animals. The selection of a study area boundary is critical because its area and location will determine the availability of each habitat type. The selection of an arbitrary study area boundary is inappropriate because it does not account for the area restricted or post dispersal movements made by an animal (Porter and Church 1987, Verbyla and Chang 1994, Wilson et al. in press). Using a herd or individual home range may be more appropriate as a boundary for determining availability, as long as the assumption that a selection process has likely occurred is stated (i.e. the selection of an area as a herd or individual home range). For my study, I measured the availability of habitat as the mean proportion of each type found within an individual's home range. By pooling the availability of each habitat from each individual's home range, I hoped to avoid including habitat that was not included in the individuals home ranges.

Habitat selection by elk at a stand level is governed by season, activity, climatic conditions, and availability. In Idaho, Irwin and Peek (1983) found elk to select grass-shrub and seral shrub successional stages for foraging, and pole-timber stands for bedding during the spring, while clear-cuts and seral shrub stands were utilized as foraging areas and pole-timber stands on ridges for bedding sites during the summer period. During the fall, habitat selection shifted to pole-timber stands on mesic slopes, with no apparent selection during winter (Irwin and Peek 1983). In Oregon, Witmer and deCalesta (1983) found female Roosevelt elk selected old-growth forests and hardwood stands, with mixed forests and sapling-pole stands being used less than expected. For foraging, elk utilized brush clear-cuts more than new clear-cuts (Witmer and deCalesta 1983). During dry years, elk in Montana, selected moist sites located at higher elevations while during wet years they preferred drier low elevation habitat types (Marcum and Scott 1985). During warm summers, elk selected closed canopy stands (Marcum and Scott 1985). Jenkins and Wright (1986) found elk in Montana preferred mature coniferous stands when snow depths exceeded 60 cm and open-canopied stands when snow depths averaged 40 cm. In Oregon, Pope (1994) found elk selected forb/grass habitats because of their high forage availability and avoided pole stands presumably because of limited forage availability.

Old growth stands were utilized by elk in proportion to their availability (Pope 1994).

During my study elk selected grass/meadows more than expected. The selection of grass/meadows by elk is not surprising because these areas contained high forage availability. Snow depths during my study were not restrictive to foraging or travel, so elk were able to utilize the open canopy areas. Morgantini (1988) also concluded that elk selected grasslands because these areas contained the highest quality of forage.

At a landscape level, I concluded that the proportion of an area comprised of food is important in the selection of a home range. The selection of grass/meadows by elk at a stand level justifies this conclusion. Though available to elk, all other habitat types were used in proportion to their availability. It appears that the use of all other habitat types was governed by their proximity to a grass/meadow stand.

4.1.3 Site Level Selection

Johnson's (1980) 4th order of selection entails the selection of food items from those available at the feeding site. Lofroth (1993) expanded the definition to include any habitat component that a species requires. I further refined the definition of fourth-order selection to include 3 levels: (1) the selection of habitat components by a species to satisfy the requirements of different life requisites, (2) the selection of habitat components by a species from the available habitat, and (3) the selection of habitat components at bedding sites by a species, in response to different climatic conditions. The above 3 levels allow for the examination of habitat selection at a site level based on behavioural requirements and availability of habitat.

4.1.3.1 Activity Dependent Habitat Selection

Landscapes are not homogeneous but are complexes of different vegetative and physical features. McFarland (1977) hypothesized that the decision making process of animals is tailored such that activity patterns would be optimally suited to current environments. McFarland's (1977) hypothesis centered around current environments or climatic conditions, but could be expanded to include different habitats. Natural selection would favor animals that were able to utilize the mosaic of habitat types in order to maximize energy intake (feeding) while minimizing energy loss (thermoregulation).

Elk within my study area showed activity-dependent habitat selection. In terms of the vegetative characteristics, elk selected open areas with high grass cover for feeding sites as compared to bedding locations. Elk prefer to graze on grasses when snow depths do not impede foraging (Nelson and Leege 1982, Nietfeld et al. 1985, Lees 1989). The open areas were selected for feeding sites because they tended to contain a higher forage biomass as compared to more closed areas. The selection of closed areas for bedding sites supports the findings reported in the literature. The closed areas offer elk both security and thermal cover as compared to more open areas (Beall 1976, Thomas et al. 1979, McCorquodale 1987, McCorquodale 1991).

In terms of the spatial characteristics, elk selected feeding sites that were closer to seismic lines than were bedding sites. Elk in my study area used seismic lines predominantly for feeding, but would also bed on them. The majority of bedding sites on seismic lines were discovered first thing in the morning, and therefore were presumably made during the previous night or early that morning. Seismic lines were the predominant way I accessed my study area, and elk may have habituated to my movements by moving into cover to bed during daylight hours.

4.1.3.2 Use Versus Availability

Numerous wildlife studies have focused on use versus availability at a variety of selection levels. In most cases, an arbitrary decision is made in regards to what is available and what is not available to the animal. At a site scale, availability has been determined using a number of different methods. Availability has been measured at random plots throughout the study area (Edge et al. 1987, Martin and Barrett 1991), at random plots within the same stand as the used site (Corn and Raphael 1992, Lofroth 1993), or at a plot located at a fixed distance from the used site (Brown 1994). Depending on the method used to assess habitat availability the results may vary. I used the fixed distance method because of time constraints.

4.1.3.2.1 Feeding Sites

Elk selected sites for feeding whose non-spatial and spatial characteristics were significantly different than the available habitat found within the vicinity of the feeding site. Elk selected feeding sites that were more open than the habitat in the immediate vicinity. Elk selected feeding sites which had significantly less canopy closure, with a lower proportion of the canopy consisting of conifer, lower mean tree height, and fewer stems per ha than the vegetation plots. The open habitat observed at elk feeding sites would allow for a greater amount of solar radiation to strike the ground, resulting in a better opportunity for grass growth (Beall 1976). This is supported by the fact that the feeding sites had a higher percent grass cover than the habitat within the immediate vicinity. These results support the general pattern found in the literature. Elk prefer to graze on grasses when both grasses and shrubs are available (Nelson and Leege 1982, Nietfeld et al. 1985, Lees 1989). Selecting areas of high forage concentration from the surrounding habitat would reduce energy expenditures associated with travel. Gates and Hudson (1983) stated that elk travelled further when feeding during periods of high forage quality and quantity. Since winter is the period where vegetation is at its lowest quality, elk should select areas containing a high quantity of forage.

In terms of spatial arrangements, only two of the six variables were significantly different. Elk selected feeding sites that were closer to seismic lines than the vegetation plots. This is probably due to the fact that elk used seismic lines for foraging. With the vegetation plot being located 300 m at a random angle from the feeding location, most vegetation plots were not found on seismic lines. In addition feeding locations may be biased towards feeding sites on seismic lines. Seismic lines were used as a means of travelling through the study area, and elk feeding sites on seismic lines were more readily detected than sites in less accessible areas.

Elk feeding locations were also found further from hiding cover than the vegetation plots. This is probably the result of two factors. The first is that elk used the large meadows of the Athabasca Ranch. Establishing the vegetation plot 300 m at a random angle from the feeding site usually placed the vegetation plot closer to hiding cover. The second factor is that elk were often observed feeding in groups (20 -221 elk/group, pers. obs). The added sense of security provided by a group enabled elk to venture further out into the open. Elk were not harassed on a regular basis while feeding in the meadows of the Athabasca Ranch, so there was a sense of security to venture further out into the meadow.

4.1.3.2.2 Bedding Sites

Elk select cover to reduce thermoregulatory costs, to take advantage of reduced snow depths, and for security (Peek et al. 1982, Skovlin 1982, Peek and Scott 1985, Campbell 1995). Thermal cover primarily provides protection against extreme temperatures and helps reduce thermoregulatory costs while hiding cover provides a sense of security from predators and human disturbance (Wisdom et al. 1986, Merrill 1991). In western Alberta, Morgantini and Hudson (1979), concluded that habitat selection by elk in winter was not a response to the thermal environment but governed by human disturbance. Elk selected bedding sites whose non-spatial characteristics were significantly different from the immediately available habitat. Elk bedding sites had less conifer content in the canopy (SPF and SPFR) and fewer stems per ha than the immediately available habitat. Based on these results the habitat within the vicinity of the bedding site was of higher quality thermal cover habitat. Therefore elk may have selecting bedding sites not in terms of thermal cover but for security cover. This is supported by the fact that elk were observed bedded in open meadows and along seismic lines, and would move into treed cover when disturbed.

4.1.3.3 Selection of Bedding Sites Based on Temperature

Elk are homeotherms maintaining a relatively high constant body temperature, by balancing heat gains and heat losses (Beall 1976, Merrill 1991). During extreme environmental conditions this balance is upset and elk must compensate for the imbalance by either modifying their behaviour and/or modifying their habitat (Beall 1976, Gates and Hudson 1979, Merrill 1991). The relative value of different habitat types may change with changing environmental conditions such that thermoregulatory costs may influence habitat selection. The modification of habitat selection to balance thermoregulatory costs may be apparent when site characteristics at bedding locations made during different winter temperatures are examined.

The selection of habitat characteristics to compensate for extreme weather conditions should occur when the critical temperature for a species is reached. At this point the loss of energy required to forage in open areas is significant enough to cause a shift in habitat selection to reduce these thermoregulatory costs. The lower critical temperature for elk has been estimated to be -18^{0}C, with this temperature being raised with varying wind than sites in less accessible areas.

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4.2 Elk Habitat Suitability Model

4.2.1 HSI Model Validation

Habitat Suitability Index (HSI) models have been developed as tools to assess habitat quality (USDI 1981, Schamberger and O'Neil 1986, Thomasma et al. 1991). HSI models are designed as planning tools for situations where habitat conditions are expected to change. HSI models are a means of assessing the changes in habitat quality and quantity for selected wildlife species (Schamberger and O'Neil 1986, Morrison et al. 1992). HSI models are hypothetical in nature, as they are derived from quantitative accounts and expert opinion regarding a species' habitat preferences (Bart et al. 1984, Brennan et al. 1986, Morrison et al. 1992).

Few HSI models have been field tested or validated. Some models that have been tested have resulted in model invalidation or modification (Lancia et al. 1982, Cole and Smith

1983, Bart et al. 1984, Cook and Irwin 1985, Thomasma et al. 1991). Schamberger and O'Neil (1986) stated that model testing serves two purposes : (1) it determines model performance and reliability in specific situations, and (2) it allows for insight for model improvement. Thomasma et al. (1991) supported Schamberger and O'Neil's (1986) reasons for testing models, stating that testing an HSI model determines if the model truly reflects habitat quality from an animal's perspective. To place any confidence in the elk winter model its assumptions and performance were tested.

4.2.2 HSI Model Assumptions

4.2.2.1 Critical Period

A central assumption to the elk model is that winter is the critical period, and that spring to fall habitat is not limiting (Buckmaster et al. 1995). With only one field season, during which atypical snow levels occurred, I was not able to test this assumption.

4.2.2.2 Life Requisites

The elk model assumes that the life requisites of food, thermal cover, and hiding cover are limited and therefore are expressed as separate model components (Buckmaster et al. 1995). The HSI models for the life requisites of food, thermal cover, and hiding cover were not validated by this study. In all cases there was no correlation between HSI class and performance index. If elk had shown a preference for particular habitats associated with each life requisite, then it would have been reflected in the PI index. For the life requisites of food and thermal cover the correlation between the PI index and the HSI value class, though not significant, was negative. This suggests that elk were using lower quality habitats relative to what is available. The paired t-tests supported the above findings. For the life requisite of food and hiding cover, elk used areas of equal habitat quality relative to what was available. In the case of thermal cover, the elk used sites of lower quality relative to what was available. Therefore, either the three life requisites are not limited or the model's for each life requisite are incorrect.

Modifying the variables and the equation for each life requisite produced mixed results. For the food model, changing variable S5 resulted in an increased performance of the model over the original model. It also resulted in a significant separation of mean HSI scores for the used sites and the available sites. I would argue that the life requisite of food is limited based on the model with the modified variable S5. Based on the habitat selection results and personal observations, I believe that the life requisite of food is limited.

The life requisites of thermal cover and hiding cover are not limited. Modifying the variables and the equation for thermal cover did not result in an increase in model performance. The life requisite of thermal cover is not limiting but its use is governed by its distance from food and level of disturbance. Elk bedded in open meadows and along seismic lines when not harassed, but would move to nearby stands to bed if disturbed. The life requisite of hiding cover is not limited in a forested environment, where there is an abundance of stands with trees $\geq$ 3m. If disturbance levels become critical, the need for cover my take precedence over forage requirements (Morgantini 1988). During these periods, cover may be limited.

4.2.2.3 Model Variables

For each life requisite it is assumed that the variables and relationships in each model are the habitat characteristics required to meet the needs of that life requisite (USDI 1981, Farr 1995). Variables contained in HSI models are either easily measured or can be included in a habitat supply model (Farr 1995). The significance of each variable in the model should be tested. Farr (1995) believed that deleting one or more variables would be unlikely given the intercorrelation of habitat variables, but would be justified if it could be clearly shown not to be correlated with animal abundance or productivity. He argued that adding variables was more appropriate because the abundance or productivity of a species is definitely governed by more than three or four variables (Farr 1995).

Multivariate analysis has become a popular method for testing HSI models, in particular the performance or significance of model variables (Cook and Irwin 1985, Brennan et al. 1986, Capen et al. 1986, Thomasma et al. 1991, Pauley et al. 1993). Two common methods for testing variable performance are stepwise logistical regression and discriminant function analysis. Capen et al. (1986) stated that stepwise logistical regression can be used as an alternative method to/or for cross validating models determined using discriminant function analysis. It was also suggested that logistic regression may be more appropriate for data sets consisting of continuous and discreet variables (Capen et al. 1986). Brennan et al. (1986) found that logistic regression analysis produced a better fit and group separation for their data than discriminant function analysis. Logistic regression tends to be more robust for dealing with deviations from multivariate normality and equal covariance than discriminant analysis, and accounts for some of the nonlinearity associated with predictor and response variables (Brennan et al. 1986, Morrison et al. 1992).

Stepwise logistic regression was applied to the feeding site data to test the assumption that the variables in the food model satisfied the life requisite of food. Based on my results this is an invalid assumption. The three variables significant at the P=0.01 level were not part of the original food model. All three variables had a negative r value indicating a decrease in utilization with an increase in the variable. Variables tree height (S3) and stem density (S20) are a measure of openness. With a decrease in tree height and a lower stem density, more solar radiation strikes the ground, resulting in better grass growth (Beall 1976). The same relationship of a decrease in utilization with an increase in variable occurred with the distance to seismic variable. Seismic lines tend to have more open canopy and better grass growth than the surrounding habitat and were utilized for feeding and travelling (per obs.). The variable percent grass cover (S2) was not significant at the P=0.01 level. Elk are known to prefer grasses over shrubs and herbs when all are readily available (Nelson and Leege 1982, Nietfield et al. 1985, Lees 1989). Diet selection was not determined as part of my study, but based on visual observations of feeding elk and elk feeding sites it appeared that elk selected grasses. Consequently, I would recommend leaving percent grass cover in the model.

I also tested the assumption that the variables in the thermal cover model were those required to meet the need of the life requisite of thermal cover. The results of the stepwise logistic regression analysis invalidated this assumption. Stem density (S20) was the only significant variable that differentiated between the used bedding sites and the available sites. Stem density was not a variable in the original thermal cover model, but originated as a variable to represent hiding cover in an early draft of the elk model (Todd et al. 1994). The relationship between stem density and utilization was not the same as for the food model. Stem density increased with utilization until approximately 2.5 stems per ha (*1000) upon which utilization decreased. The relationship of utilization to stem density may be related to visual detection of approaching predators. In areas where stem density is greater than 2.5 stems/ha (*1000), elk may be unable to visually detect approaching predators with enough time to flee (Campbell 1995). Therefore elk may select cover that provides some concealment from predators, but still allows for a clear advantage point for early detection of approaching predators. Based on the results of the logistic regression analysis and the bedding site selection analysis, I believe that thermal cover and hiding cover could be combined into one life requisite of cover, represented by the variable stem density.

4.2.2.4 Carrying Capacity

All HSI models estimate habitat quality with the assumption that the model output is correlated with carrying capacity or population levels (Bart et al. 1984, Brennan et al. 1986, Schamberger and O'Neil 1986, Farr 1995). In the elk winter model it was stated that model performance would be potential carrying capacity (# elk per ha) (Buckmaster et al. 1995). The assumption that the HSI model output is correlated with carrying capacity is suspect because not all factors that determine population levels are included in the model (Lancia et al. 1982, Schamberger and O'Neil 1986). The HSI index value is a measure of the capability of the vegetative structure to provide the needs of a species, but whether the habitat is utilized is also governed by predation, disturbance, disease, intraspecific competition and weather (Chalk 1986, Schamberger and O'Neil 1986). Population estimates were not performed due to time constraints and difficulties associated with the surveying of elk in a densely covered environment. The testing of the model was based on habitat selection and was not correlated to animal density. It should be made clear that the model represents "potential" carrying capacity and will not be an accurate predictor of population levels (Schamberger and O'Neil 1986).

4.2.3 Model Limitations

The results and conclusions made in the above sections are based on one years' habitat selection data. Model testing should be done with a minimum of two years of data, and thousands of observations, collected from a number of different sites (Cole and Smith 1983, Bunnell 1989). The fact that the model is tested with only one years' data is compounded by the fact that the winter of data collection was mild in terms of snow fall. To have any confidence in the model and to accept the proposed revisions further testing should be performed during different temperature and snow conditions. Caution should be used when implementing any model. Short-term studies may reflect recent past habitat use but may inadequately reflect long-term use (Schamberger and O'Neil 1986). My testing of the model should be considered a part of a regular routine of testing and revising of the model (Morrison et al. 1992). Models tested and revised based on long-term studies will provide confidence in the model during application. Correlating habitat maps produced using the HSI model with actual habitat selection by elk over a minimum of two years may allow for the confident application of the model at a planning level.

The design of my study involved comparing HSI values for used sites versus available sites under the assumption that the available sites were unused. The available sites were determined by measuring the spatial and non-spatial variables at a plot located 300m from the used site. The problem with this method is that it is highly likely that some of the available sites were in fact used. If time had permitted actually determining areas where elk use did not occur or sampling available habitat throughout the entire study area may have allowed for a stronger evaluation of the model.

The original elk model is very complex, consisting of three sub-models and 15 variables. The complexity of the original model is due to the fact that it takes into account the use of different habitat types for different behaviours (e.g. feeding, bedding, and hiding). In the previous sections I proposed simplifying the model by eliminating the thermal and hiding cover models and/or by reducing the number of variables in each sub-model. An alternative would be to implement the alternative multivariate model. The alternative model is based on use versus availability and does not take into account different habitat use based on behaviours.

The advantage of using the multivariate model over the HSI model is that, after initial model development, the calculations required to classify habitats into used or available, can be done on a standard calculator with a natural antilogarithm function (Brennan et al. 1986). This becomes less of an advantage now that GIS systems have been developed where calculations and habitat maps can be produced (Donovan et al. 1987, Clark et al. 1993). A second advantage of multivariate model is that it is one model not three. The three variables in the multivariate model are the same three found to be significant for the food model. If the food HSI model is changed to contain the three variables found to be significant, and the thermal cover and hiding cover models are dropped, then the advantage of the multivariate model may be negated.

Though the elk winter model did not perform well it should not be discarded. Knowledge into the system and information gaps were identified. There should not be any reluctance to implement the model based on the modifications suggested, as long as we as managers continue to test and refine the model. Simplifying the model would allow for easier implementation and interpretation of results by forest managers, and will improve communication between trained wildlife professionals and forest managers, so that wildlife requirements can be incorporated into forest management (Salwasser 1985, Chalk 1986). The model is not the ultimate solution, it is the cooperation and team work of resource managers and decision makers that will decide the ultimate future of elk and other species in a multiple-use environment.

5.0 Synthesis and Recommendations

5.1 Behavioural Adaptive Strategies

Elk are considered generalists because of their ability to adjust to and successfully colonize a wide range of habitats. They are distributed from the boreal forest of the Yukon (Florkiewicz 1994), to the dry shrub-steppe of Washington (McCorquodale 1987), to the montane regions of Alberta (Morgantini 1979). Morgantini (1988) concluded that the elk's ability to be flexible was the major behavioural adaptation that facilitated its successful colonization of North America. Adaptive strategies allow groups and individuals to respond to the micro-environment in order to maximize forage intake while minimizing the chance of being fed upon (Morgantini 1988). Morgantini (1988) believed that the elk along the eastern slopes of Alberta did not exhibit any unique adaptations in their selection of habitats, but instead showed adaptive strategies for dealing with local vegetational structure, forage availability and quality, and the availability of hiding cover.

Similar behavioural adaptive strategies were noted for elk inhabiting the lower foothills of west-central Alberta. On a landscape level elk selected a winter range that contained a consistant proportion of forage. The shift in range observed during the fall was to areas that contained high concentrations of grasses. Winter diets of elk are adapted to maximize digestible energy intake by switching to a predominantly grass diet, when possible (Morgantini and Hudson 1985). The switch to a high grass diet was verified at a stand level, where elk selected grass/meadow habitats in greater proportion than their availability. At a site scale elk selected open areas for feeding sites that contained a greater proportion of grass cover than the available habitat. In conclusion, the selection of habitat types at the three scales examined appears to be governed by the local availability and quality of forage. The selection of habitat types may change with changing levels of disturbance.

Group size is a function of forage availability and distibution, with large group occuring in open grasslands and small groups occurring in patchy environments (Franklin and Lieb 1979, Morgantini 1981). The large open meadows of the Ya Ha Tinda Ranch allowed large nursery groups (50-400 animals) to congregate during the winter season (Morgantini 1988). In west-central Alberta, Morgantini (1981) reported small herd sizes during the winter (1.9 - 3.1 elk/group) and stated that this was a reflection of the closed forest cover of the study area. Elk in the lower foothills subregion of west-central Alberta occurred in small groups. On one occasion a group of 224 elk were observed in the same meadow, but the majority of the time winter herds consisted of 12-30 animals. During the spring and summer periods the average herd size was further reduced to 2-7 individuals. The adaptation to small herds is a response to the local vegetational environment. Though not directly measured I believe the forage in the lower foothills is aggregated in small and widely distributed clumps. By adapting small groups, elk are able to maximize forage intake by dispersing across the landscape. In addition the small and dispersed groups may also offer protection from predators. Further investigation in to the adaptation of small herd sizes is required.

5.2 Management Implications

Modelling has been adopted by land managers to aid them in making important decisions. Models are tools that give insight into how a system is governed or the driving force behind it (Starfield 1997). HSI models are simple, single species models that describe the habitat requirements of a species in terms of vegetative and spatial variables. A winter HSI model for elk was developed to assist Weldwood of Canada Inc, Hinton Division land managers in their management plans. As part of my study I tested the model. As with previous studies, my testing of the model produced mixed results. Each component of the model performed differently, with some parts fitting well while others had a poor fit. Mixed results should not simply lead to model invalidation, but to a further understanding of the issues at hand. HSI models aim to predict habitat potential over the long term, and testing them with short term studies is unlikely to capture the range of variation in habitat selection. The true validation of a model should be conducted over the long term, with numerous observations over a range of climatic conditions, until a climax in habitat selection has occurred. Only then will we have better insight into the processes driving the system.

HSI models are only one approach used to help land managers make decisions regarding habitat management. HSI models should only be used on a local basis and as a means of assessing potential habitat. Factors such as predation, disease, inter and intra-competition are not accounted for and may change the way a species utilizes its environment. An ecosystem based approach may be able to address these other factors, but can become more complicated. Using either approach to managing wildlife is a step in the right direction. The true test of a model may not be how accurately the data fits but whether the managers will make better "informed" decisions with the model than without it (Starfield 1997).

5.3 Recommendations

Based on the conclusion of my study and 16 months of field experience, I offer the following recommendations. Though presented separately, all recommendations are inter-related.

(1) Because my results are based on only one field season, I recommend that an additional 3-5 years of study into the habitat use by elk be conducted. A long term study into the habitat use patterns by elk would serve two primary functions: (a) it would allow further testing and refinement of the HSI model or the proposed alternatives and (b) examine the influence of weather on the use of habitat types by elk (i.e. during periods of extreme cold and deep snow).

(2) I was unable to estimate a population density for my study area. Smith (1985)

recommended a population of 400 elk within Wildlife Management Unit #344, within which my study area falls. I believe this management goal has been achieved but this needs to be verified. A combination of track surveys and mark-recapture aerial surveys could be used to verify the population level.

(3) Based on the movements of collared and non-collared elk observed, it appears that the meadows of the Athabasca Ranch are critical winter range for elk within my study area. Elk depredation of both pasture land and stacked feed needs to be addressed to ensure the long term management of elk. Methods to rectify the problem may include financial retribution for lost feed, or fencing the land with either page wire or electric fencing, both of which would be costly. If fencing is installed, the effects of preventing access to the forage offered by the ranch area should be examined. Alternative foraging areas may be needed to maintain the population levels existing today.

(4) By supporting elk during the critical winter period, I believe the ranch winter population acts as a source for other elk herds within the local area. For example, elk 151.904 wintered in the ranch area during the winter of 1994-1995, but disappeared in the spring of 1995. Her collar was recovered from a carcass down stream of the confluents of the Big and Little Berland Rivers in the spring of 1996. The significance and number of elk dispersing from the ranch area should be examined.

(5) The importance of conifer trees as thermal cover should be examined in detail.

The small sample sizes used in the analysis of bedding site selection in response to temperature may have resulted in the insignificant difference. Until adequate sample sizes are obtained, my results should be considered inconclusive. During extended periods of extreme cold and increased snow depths thermal cover may become a key component to the survival of elk.

(6) I did not examine the importance of riparian habitats to elk. I believe that elk use the riparian habitat as migration corridors during both the fall and the spring migrations. The riparian habitat may also serve as critical calving areas for elk. Further examination of the importance of riparian habitats is required before any land use occurs within these areas.

(7) I did not examine the effect timber harvesting has on the selection of habitat types by elk. The effects on habitat selection within the direct area of timber harvesting should be examined over both short and long term periods. The effects of timber harvesting on the selection of habitat by elk should be incorporated into both short-term and long term management plans (i.e. into any model used to predict habitat availability).

6.0 Literature Cited

Baker, B. W., B. S. Cade, W. L. Mangus, and J. L. McMillen. 1995. Spatial analysis of sandhill crane nesting habitat. J. Wildl. Manage. 59(4):752-758.

Bart, J., D. R. Petit, and G. Linscombe. 1984. Field evaluation of two models developed following the habitat evaluation procedures. Trans. North Am. Wildl. Nat. Res. Conf. 49:489-499.

Beall, R. C. 1976. Elk habitat selection in relation to thermal radiation. pp. 97-100 in: S. R. Hieb (ed.). Proceedings of the Elk-Logging-Roads Symposium. University of Idaho, Moscow, Idaho. 142 pp.

Beck, J. A., and B. H. Beck. 1995. Integration of timber and wildlife habitat supply. Forestry Canada and Alberta Forest Service. 110 pp.

Beckingham, J. D., I. G. Corns, and J. H. Archibald. 1996. Field guide to ecosites of west-central Alberta. Nat. Resour. Can., Can. For. Serv., Northwest Reg., Edmonton, Alberta. Rep. no. 9. 630 pp.

Berry, K. H. 1986. Introduction: development, testing, and application of wildlife-habitat models. pp. 3-10 in: Verner, J., M. L. Morrison, and C. J. Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. 470 pp.

Bessie, W. 1995. Habitat structure sampling manual for wildlife habitat suitability index projects: interm report. Foothills Model Forest. 34 pp.

Black, H., R. Scherzinger, and J. W. Thomas. 1976. Relationships of Rocky Mountain elk and Rocky Mountain mule deer habitat to timber management in the Blue Mountains of Oregon and Washington. pp. 11-31 in: S. R. Hieb (ed.). Proceedings of the Elk-Logging-Roads Symposium. University of Idaho, Moscow, Idaho. 142 pp.

Bonar, R., R. Quinlan, T. Sikora, D. Walker, and J. Beck. 1990. Integrated management of timber and wildlife resources on the Weldwood Hinton Forest Management Agreement Area. Integ. Res. Manag. Steer. Comm. Weldwood of Canada Ltd and Alberta Forestry, Lands and Wildlife, Hinton, AB.

Bradshaw, C. J. 1994. Woodland caribou habitat selection. M. Sc. Thesis, University of Alberta, Alberta. 121 pp.

Brennan, L. A., W. M. Block, and R. J. Gutierrez. 1986. The use of multivariate statistics for developing habitat suitability index models. pp. 177-182 in: Verner, J., M. L. Morrison, and C. J. Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. 470 pp.

Brown, R. L. 1994. Effects of timber management practices on elk. Arizona Game and Fish Dept. Tech. Rep. No. 10. 70 pp.

Buckmaster, G., M. Todd, K. Smith, R. Bonar, B. Beck, J. Beck, and R. Quinlan. 1995. Elk (Cervus elaphus) winter range habitat suitability index (HSI) model. pp. 51-62 in: Beck, B., J. Beck, W. Bessie, R. Bonar, D. Farr, K. Smith, G. Stenhouse, and M. Todd (eds.). Habitat suitability index models for 35 wildlife species in the boreal foothills of West-Central Alberta. Foothills Model Forest, Hinton, AB.

Bunnell, F. L. 1989. Alchemy and uncertainty: what good are models? USDA Forest Service, Pacific Northwest Research Station Gen. Tech. Rep. PNW-GTR-232. 27 pp.

Campbell, K. L. 1995. Testing habitat suitability models for Roosevelt elk. M. Sc. University of British Columbia, British Columbia. 60 pp.

Capen, D. E., J. W. Fenwick, D. B. Inkley, and A. C. Boynton. 1986. Multivariate models of songbird habitat in New England Forests. pp. 171-175 in: Verner, J., M. L. Morrison, and C. J. Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. 470 pp.

Chalk, D. E. 1986. Summary: development, testing, and application of wildlife-habitat models - the researcher's viewpoint. pp. 155-156 in: Verner, J., M. L. Morrison, and C. J. Ralph (ed.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison WI. 470 pp.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. J. Wildl. Manage. 57(3):519-526.

Cole, C. A., and R. L. Smith. 1983. Habitat suitability indices for monitoring wildlife populations - an evaluation. Trans. North Am. Wildl. Nat. Res. Conf. 48:367-375.

Cook, J. G., and L. L. Irwin. 1985. Validation and modification of a habitat suitability model for pronghorns. Wildl. Soc. Bull. 13(4):440-448.

Corn, J. G., and M. G. Raphael. 1992. Habitat characteristics at marten subnivean access sites. J. Wildl. Manage. 56(3):442-448.

Donovan, M. L., D. L. Rabe, and C. E. Olson. 1987. Use of geographic information systems to develop habitat suitability models. Wildl. Soc. Bull. 15(4):574-579.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65(1):169-175.

Edge, W. D., C. L. Marcum , and S. L. Olson-Edge. 1987. Summer habitat selection by elk in western Montana: a multivariate approach. J. Wildl. Manage. 51(4):844-851.

Farr, D. R. 1995. Forest birds and ecosystem conservation in the Rocky Mountain Foothills of Alberta. Ph. D. Thesis. University of Alberta, Alberta. 81 pp.

Florkiewicz, R. F. 1994. Nutritional ecology of wapiti and carrying capacity of late winter and spring range in the Yukon. M. Sc. Thesis, University of Alberta, Alberta. 74 pp.

Franklin, W. L., and J. W. Lieb. 1979. The social organization of a sedentary population of North American elk: a model for understanding other populations. pp. 185-198 in: M. S. Boyce and L. D. Hayden-Wing (eds.). North American elk: ecology, behaviour, and management. University of Wyoming, Larmine, Wyoming. 294 pp.

Gates, C. C., and R. J. Hudson. 1979. Effects of posture and activity on metabolic responses of wapiti to cold. J. Wildl. Manage. 43(2):564-567.

Gates, C. C., and R. J. Hudson. 1983. Foraging behaviour of wapiti in a boreal forest enclosure. Nat. Can. 110:197-206.

Geist, V. 1982. Adaptive behavioral strategies. pp. 219-277 in: Thomas, J. W. and D. E. Toweill (eds.). Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa. 698 pp.

Houlthansen, R. S., M. J. Wisdom, J. Pierce, D. K. Edwards, and M. M. Rowland. 1994. Using expert opinion to evaluate a habitat effectiveness model for elk in western Oregon and Washington. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, OR. Res. Pap. PNW-RP-479. 16 pp.

Irwin, L. L. and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. J. Wildl. Manage. 47(3):664-672.

Jalkotzy, M.G., P. I. Ross, and M. D. Nasserden. 1997. The effects of linear developments on wildlife: A review of selected scientific literature. Report prepared for: Canadian Association of Petroleum Producers, Calgary, AB. 115 pp.

Jenkins, K. J. and R. G. Wright. 1986. Influence of snow on winter habitat use by elk in the North Fork of the Flathead Valley, Montana. pp. 307-308 in: D. L. Eastman (ed.). Proceedings of the 1986 Western States and Provinces Elk Workshop. Coos Bay, Oregon. 316 pp.

Johnson D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1):65-71.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. Calhome: a program for estimating animal home ranges. Wildl. Soc. Bull. 24(2):342-344.

Kotliar, N. B. and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos. 59(2):253-260.

Lancia, R. A., S. D. Miller, D. A. Adams, and D. W. Hazel. 1982. Validating habitat quality assessment: an example. Trans. North Am. Wildl. Nat. Res. Conf. 47:96-100.

Lees, R. T. 1989. The effect of recreational activity on elk use and distribution along a pipeline right-of-way. pp. 133-143 in: Proceedings IV: Issues and technology in the management of inpacted wildlife. Thorne Ecological Institution.

Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. J. Wildl. Manage. 50(1):110-117.

Lofroth, E. C. 1993. Scale dependent analysis of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone, British Columbia. M. Sc. Thesis. Simon Fraser University, British Columbia. 109 pp.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. J. For. 77(1):658-660.

Lyon, L. J. 1983. Road density models describing habitat effectiveness for elk. J. For. 81(9):592-595.

Lyon, L. J., and C. E. Jensen. 1980. Management implications of elk and deer use of clear-cuts in Montana. J. Wildl. Manage. 44(2):352-362.

Manly, B., L. McDonald , and D. Thomas. 1993. Resource selection by animals. Chapman & Hall, London. 177 pp.

Marcum, C. L. and M. D. Scott. 1985. Influences of weather on elk use of spring-summer habitat. J. Wildl. Manage. 49(1):73-76.

Martin, S. K., and R. H. Barrett. 1991. Resting site selection by marten at Sagehen Creek, California. Northwestern Nat. 72:37-42.

McCorquodale, S. M. 1987. Fall-winter habitat use by elk in the shrub-steppe of Washington. Northwest Sci. 61(3):171-173.

McCorquodale, S. M. 1991. Energetic considerations and habitat quality for elk in arid grasslands and coniferous forests. J. Wildl. Manage. 55(2):237-242.

McCorquodale, S. M., K. J. Raedeke, and R. D. Taber. 1989. Home ranges of elk in an arid environment. Northwest Sci. 63(1):29-34.

McFarland, D. J. 1977. Decision-making in animals. Nature 269:15-21.

McGarigal, K. and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U. S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. Gen. Tech. Rep. PNW-GTR-351. 122 pp.

McNay, R. S., J. A. Morgan, and F. L. Bunnell. 1994. Characterizing independence of observations in movements of columbian black-tailed deer. J. Wildl. Manage. 58(3):422-429.

Merrill, E. H. 1991. Thermal constraints on use of cover types and activity time by elk. Appl. Anim. Behav. Sci. 29:251-267.

Morgantini, L. E. 1979. Habitat selection and resource division among bighorn sheep, elk and mule deer in western Alberta. M. Sc. Thesis, University of Alberta, Alberta. 187 pp.

Morgantini, L. E. 1981. Pipeline construction and wildlife; results of a monitoring program along the Edson mainline loop 1st winter. prepared for Nova, an Alberta Corporation (Calgary). 107 pp.

Morgantini, L. E. 1988. Behavioural adaptive strategies of wapiti (Cervus elaphus) in the Canadian Rocky Mountains. PhD Thesis, University of Alberta, Alberta. 193 pp.

Morgantini, L. E., and R. J. Hudson. 1979. Human disturbance and habitat selection by elk. pp. 132-139 in: M. S. Boyce and L. D. Hayden-Wing (eds.). North American elk: ecology, behaviour, and management. University of Wyoming, Larmine, Wyoming. 294 pp.

Morgantini, L. E., and C. O. Olsen. 1983. Pipeline construction and wild ungulates; results of a two year monitoring study along the Edson mainline loop Final report. prepared for Nova, An Alberta Corporation (Calgary).

Morgantini, L. E., and R. J. Hudson. 1985. Changes in diet of wapiti during a hunting season. J. Range Manage. 38(1): 77-79.

Morgantini, L. E., P. M. Woodard, and D. Eslinger. 1994. Logging and elk in the Bighorn Creek Valley in Western Alberta: the response of elk and important forage plants to forest harvesting (1988-1991). Univ. of Alberta, Edmonton, Alberta. 57 pp.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat relationships: concepts and applications. The University of Wisconsin Press, Madison, Wisconsin. 343 pp.

Nelson, J. R., and T. A. Leege. 1982. Nutritional requirements and food habits. pp. 323-367 in: Thomas, J. W. and D. E. Toweill (eds.). Elk of North America: ecology and management. Stackploe Books, Harrisburg, Pa. 698 pp.

Neu, C. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. J. Wildl. Manage. 38(3):541-545.

Nietfeld, M., J. Wilk, K. Woolnough, and B. Holskin. 1985. Wildlife habitat requirement summaries for selected wildlife species in Alberta. Alberta Forestry, Lands, and Wildlife; Fish and Wildlife Division. ENR Tech. Rep. No. T/73. 260 pp.

Pauley, G. R., J. M. Peek, and P. Zager. 1993. Predicting white-tailed deer habitat use in Northern Idaho. J. Wildl. Manage. 57(4):904-913.

Pedlar, J. H., L. Fahrig, and H. G. Merriam. 1997. Raccoon habitat use at 2 spatial scales. J. Wildl. Manage. 61(1):102-112.

Peek, J. M., and M. D. Scott. 1985. Elk and cover. pp. 75-82 in: G. W. Workman (ed.). Western Elk Management: a Symposium. Utah State University, Logan, Utah. 213 pp.

Peek, J. M, M. D. Scott, L. J. Nelson, D. J. Pierce, and L. L. Irwin. 1982. Role of cover in habitat management for big game in Northwestern United States. Trans. North Am. Wildl. Nat. Res. Conf. 47:363-373.

Pope, M. D. 1994. Roosevelt elk habitat use in the Oregon Coast Range. M. Sc. Thesis, Oregon State University, Oregon. 76 pp.

Porter, W. F., and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. J. Wildl. Manage. 3(51):681-685.

Quinlan, R. W., W. A. Hunt, K. Wilson, and J. Kerr. 1990. Habitat requirements of selected wildlife species in the Weldwood Forest Management Agreement Area. Rep. to Weldwood Forest Management Area Integ. Res. Manage. Steer. Comm. 189 pp.

Robinson, W. L., and E. G. Bolen. 1989. Wildlife ecology and management, second edition. Macmillan Publishing Company, New York. 574 pp.

Rost, G. R., and J. A. Bailey. 1979. Distribution of mule deer and elk in relation to roads. J. Wildl. Manage. 43(3):634-641.

Salwasser, H. 1985. Integrating wildlife into the managed forest. For. Chron. 61(2):146-149.

Schamberger, M. L., and L. J. O'Niel. 1986. Concepts and constraints of habitat-model testing. pp. 5-10 in: Verner, J., M. L. Morrison, and C. J. Ralph (eds.). Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI. 470 pp.

Skovlin, J. M. 1982. Habitat requirements and evaluations. pp. 369-414 in: J. W. Thomas and D. E. Toweill (eds.). Elk of North America: ecology and management. Stackpole Books, Harrisburg, Pa. 698 pp.

Smith, K. 1985. A preliminary elk (Cervus elaphus) management plan for the Edson wildlife management area. Alberta Fish and Wildlife, Edson, Alberta. 106 pp.

Starfield,A. M. 1997. A pragmatic approach to modeling for wildlife management. J. Wildl. Manage. 61(2):261-270.

Swihart, R. K., and N. A. Slade. 1985. Testing for independence of observations in animal movements. Ecology 66(4):1176-1184.

Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. J. Wildl. Manage. 54(2):322-330.

Thomas, J. W., H. Black, R. J. Scherzinger, and R. J. Pedersen. 1979. Deer and Elk. in: J. W Thomas (ed.). Wildlife habitats in managed forests; the Blue Mountains of Oregon and Washington. U. S. D. A. Forest Service Handbook No. 553, Washington, D.C.

Thomas, J. W., D. A. Leckenby , M. Henjum , R. J. Pedersen , and L. D. Bryant. 1988. Habitat-effectiveness index for elk on Blue Mountain winter ranges. U. S. Department of Agriculture, Forest Services, Pacific Northwest Research Station. Gen. Tech. Rep. PNW-GTR-218. 28 pp.

Thomasma, L. E., T. D. Drummer, and R. O. Peterson. 1991. Testing the habitat suitability index model for the fisher. Wildl. Soc. Bull. 19(3):291-297.

Thompson, M. J., R. E. Henderson, T. O. Lemke, and B. A. Sterling. 1989. Evaluation of a collapsible clover trap for elk. Wildl. Soc. Bull. 17(3):287-290.

Todd, M., K. Smith, B. Beck, J. Beck, and R. Quinlan. 1994. Habitat suitability index model: elk (Cervus elaphus) winter range. Foothills Model Forest. 19 pp.

Trimble Navigation, Ltd. 1992. Pathfinder system general reference. Trimble Navigation Ltd., Sunnyvale, California. 143 pp.

USDI. 1981. Standards for the development of suitability index models. U.S.D.I. Fish and Wildlife Service, Div. Ecol. Serv., Washington DC Ecological Services Manual 103. 150 pp.

Verbyla, D. L. and K. Chang. 1994. Potential problems in using GIS for wildlife habitat research. pp. 271-277 in: Eighth annual symposium on geographic information systems in forestry, environmental and natural resources management. Polaris Conferences, Inc, Vancouver, British Columbia. 750 pp.

White, G. C. and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, Inc., San Diego, California. 383 pp.

Wilson, S. F., D. M. Shackleton, and K. L. Campbell. Making use-availability analysis spatially explicit. in press.

Wisdom, M. J., L. R. Bright, C. G. Carey, W. W. Hines, R. J. Pedersen, D. A. Smithey, J. W. Thomas, G. W. Witmer, and R. J. Pedersen . 1986. A model to evaluate elk habitat in Western Oregon. USDA Forest Service, Pacific Northwest Region. No. R6-F&WL-216-1986. 36 pp.

Witmer, G. W., and D. S. deCalesta. 1983. Habitat use by female Roosevelt elk in the Oregon coast range. J. Wildl. Manage. 47(4):933-939.

Appendix A: Summary of the variables, relationships, and equations contained in the winter HSI model developed by Buckmaster, G., M. Todd, K. Smith, R. Bonar, B. Beck, J. Beck, and R. Quinlan. 1995. Elk (Cervus elaphus) winter range draft habitat suitability index (HSI) model. pp 51-62 in: Beck, B., J. Beck, W. Bessie, R. Bonar, D. Farr, K. Smith, G. Stenhouse, and M. Todd (eds). Habitat suitability index models for 35 wildlife species in the boreal foothills of west-central Alberta. Interm Report, Foothills Model Forest, Hinton, Alberta. (Permission to reproduce granter from J. Beck (University of Alberta), R. Bonar (Weldwood of Canada Inc., Hinton), and D. Farr (Foothills Model Forest)).

A.1 Life Requisite / Habitat Variable Descriptions:

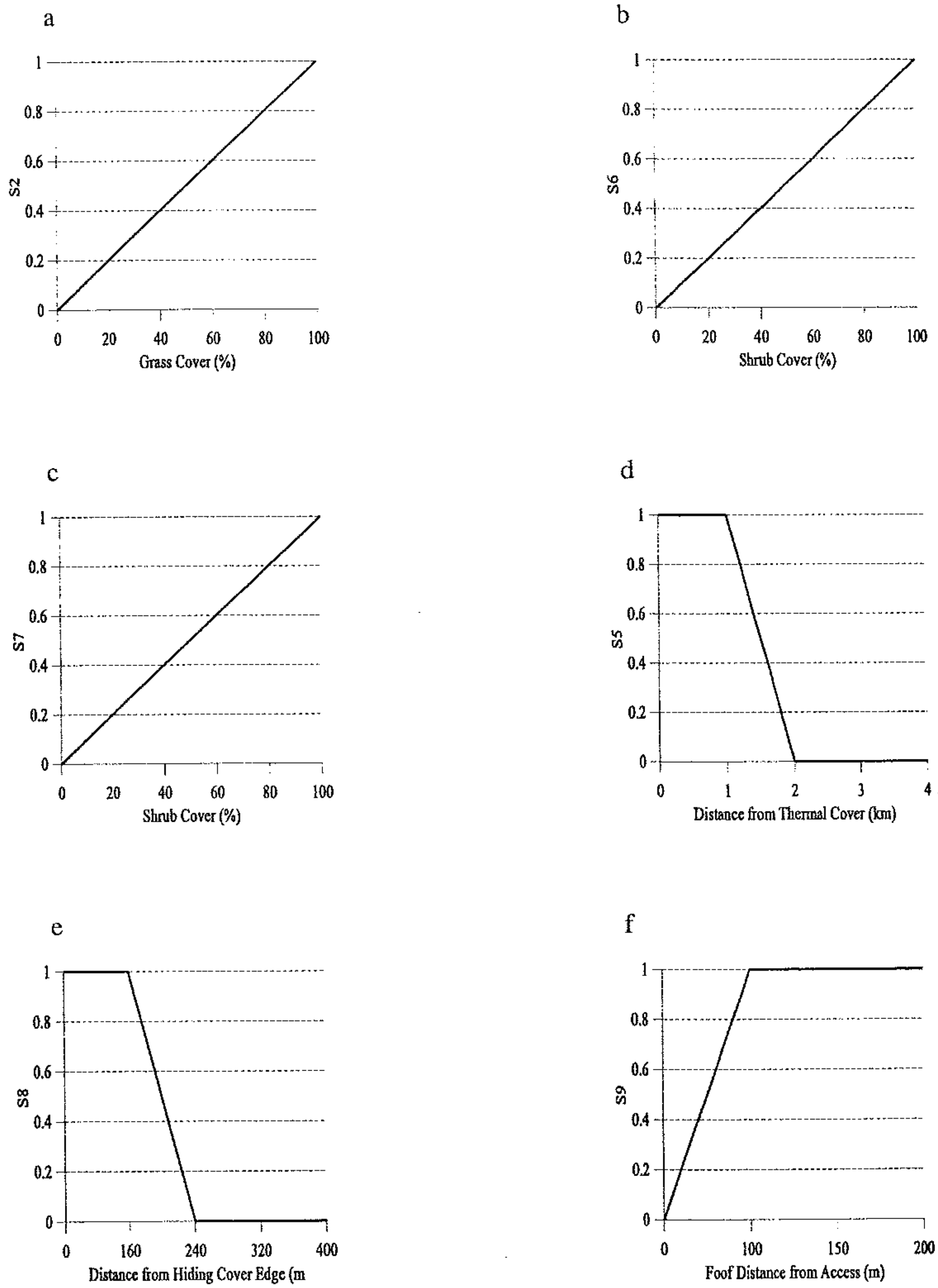
A.1.1 Food

The winter diet of elk consisted of grasses, herbs (forbs) and shrubs (browse). These components are represented by percentage grass cover (S2), percentage herbaceous cover (S6) and percentage shrub canopy closure (S7) (Figures A1a, A1b, A1c). Grass is assumed to be the most important food type, with herbs allotted half the value of grass and shrubs a quarter of the value of grass; e.g. (% grass cover + .5 % herbaceous cover + .25 % shrub canopy closure) max = 1.

Habitat polygons must be within 2 km of thermal cover (S5) in order to have any food HSI value (Figure A1d). S5 has an Suitability Index (SI) value of 1 at 1 km and 0 at 2 km. Movement over distances is assumed to increase survival costs in terms of energetics and predation risk. Therefore, food habitat farther than 1 km away from thermal cover is reduced in value. Habitat polygons must be within 220 m of hiding cover (S8) in order to have any food HSI value (Figure A1e). S8 has a SI value of 1 at 160 m and 0 at 240 m to provide confidence limits around the 200 m boundary. This assumes that 80% of elk foraging occurs within 200m of hiding cover.

Habitat within 100 m of permanent access will be reduced in food HSI value. This assumes that, in hunted situations, elk avoid foraging habitat up to 500 m from roads. Because road avoidance distances can vary, S9 has a SI value of 1 at 100m and 0 at 0 m (Figure A1f).

Figure A1 Variables and relationships for the food component of the winter HSI elk model.

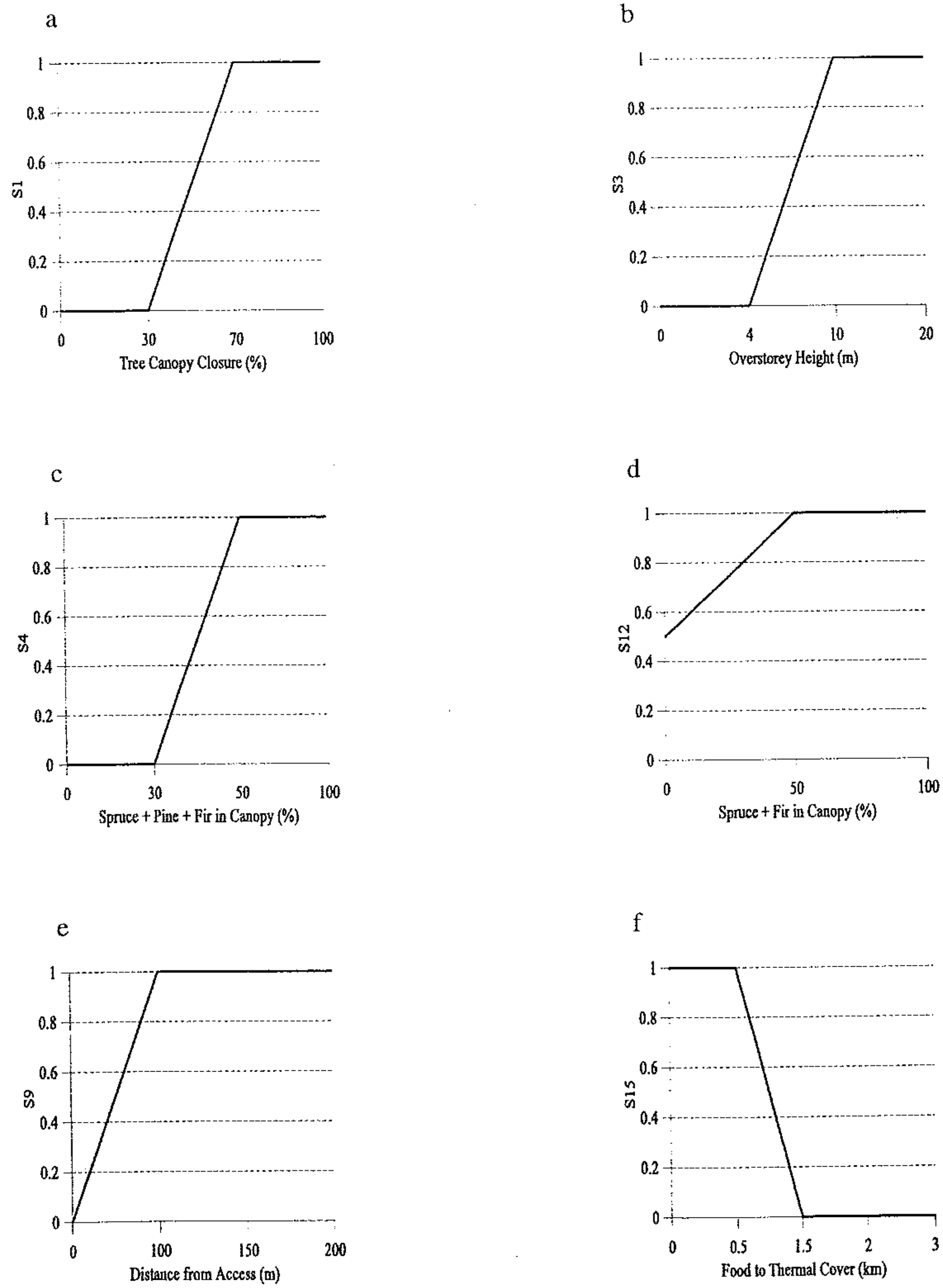


A.1.2 Thermal Cover

A percentage tree canopy closure (S1) of C density or better (>= 70%) is considered to provide optimum thermal cover (Figure A2a). Therefore S1 has a value of 1 at 50 and 0 at 30. A canopy closure of 30% or less (A density) has no value as thermal cover. Overstorey height (S3) must be 10 m or higher for a SI value of 1; anything less than 4 m has no value (Figure A2b). There must be over 30 percent conifer (spruce, pine and/or fir) (S4) in order for a polygon to have value as thermal cover (Figure A2c). Anything 50+ percent is considered optimum. Spruce and fir are considered to provide better thermal cover than pine and therefore increase the value of habitat as thermal cover as their percentage in the canopy increases (S12) (Figure A2d). However, stands with pine but no spruce or fir still have an SI value of 0.5.

Habitat within 100 m of permanent access will be reduced in thermal cover HSI value. This assumes that, in hunted situations, elk avoid habitat up to 500 m from roads. Because road avoidance distances can vary, S9 has a SI value of 1 at 100m and 0 at 0 m (Figure A2e). For thermal cover to be useful it must be within the required distance of food (S15) (Figure A2f).

Figure A2 Variables and relationships for the thermal cover component of the winter HSI elk model.



A.1.3 Hiding Cover

Hiding cover for elk is dependent upon four variables. Firstly, at least 30 percent canopy closer is required for an optimal S11 value (Figure A3a). Coniferous vegetation provides better cover than deciduous vegetation. Thus canopy closure is calculated by coniferous closure + 0.25 deciduous closure. Secondly, an average tree height of 3m or greater is needed for an optimal S13 value (Figure A3b). However, an average tree height of 2m provides good enough cover for a S13 value of 0.75. Any stand with an average height less than 2m has an S13 value of 0. Hiding cover distance from human access (S10) is important for hiding cover (Figure A3c). Any hiding cover 100m or further distance from access is considered optimal (S10=1). The S10 value will equal 0 when the hiding cover is immediately adjacent to access. Finally to be useful hiding cover must be within the appropriate distance of food S14 (Figure A3d).

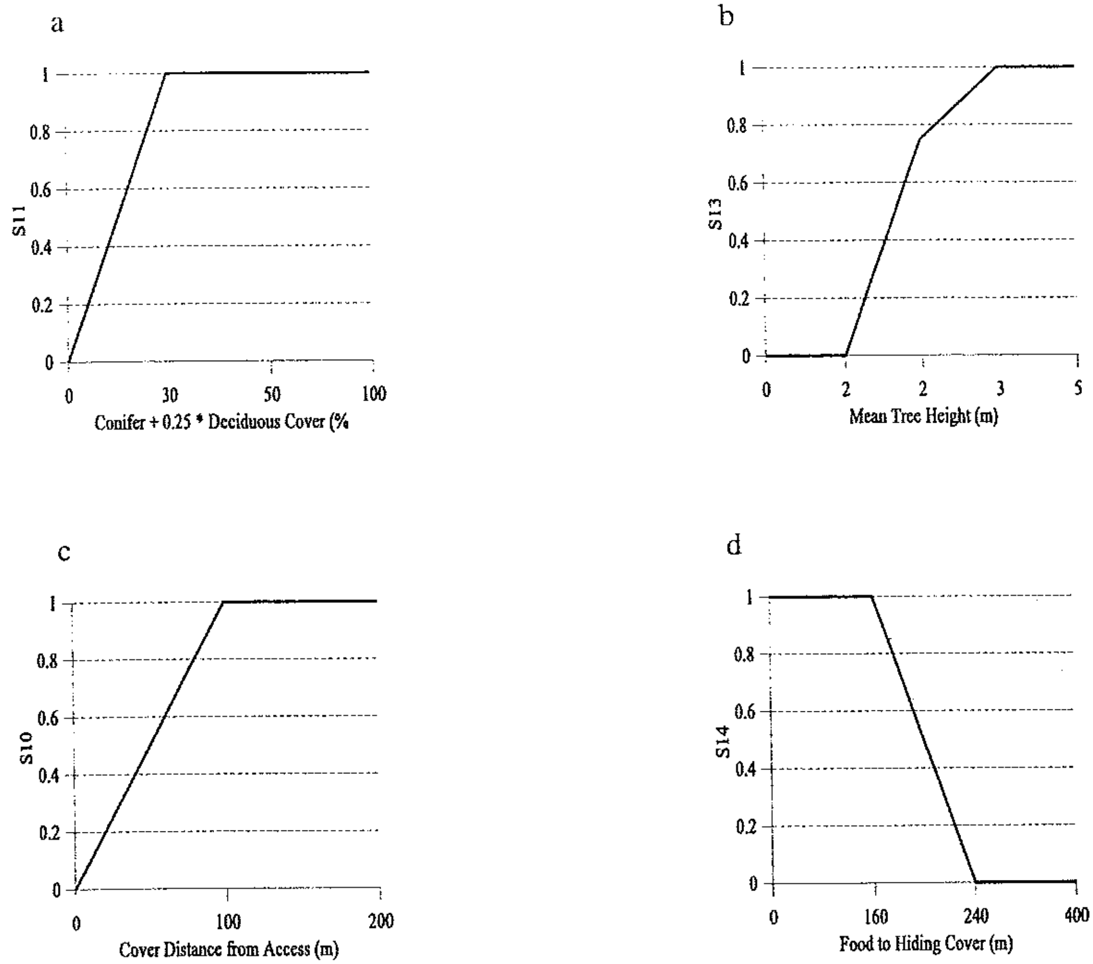
A.2 Equations

A.2.1 Food

$$HSI\ (Food) = (max = 1(S2 + .5S6 + .25S7)) \times S5 \times S8 \times S9$$

This equation assumes grass to be the most important food type, with herbs allotted half the value of grass and shrubs, a quarter of the value of grass. The sum total of these food types cannot equal more than 1. The "distance from" variables, S5, S8 and S9, are equal and non-compensatory.

Figure A3 Variables and relationships for the hiding cover component of the winter HSI elk model.



A.2.2 Thermal Cover

HSI (Thermal Cover) = S1 x S3 x S4 x S10 x S12 x S15

All the variables in this equation are equal and non-compensatory for thermal cover.

A.2.3 Hiding Cover

HSI (Hiding Cover) = S10 x S11 x S13 x S14

Variables S10, S11, S13 and S14 are equal and non-compensatory in providing hiding cover.

Appendix B: Distribution and home range sizes for elk in the lower foothills of west-central alberta.

B.1 Introduction

This appendix summarizes the distribution and home range sizes for elk within the study area. Distribution of elk were based on movements of the collared elk and their associates. The minimum convex polygon (MCP) (Hayne 1949) and the non-parametric adaptive kernel method (ADK) (Worton 1987) were used to estimate home range sizes. Core areas were defined as areas that included 50% adaptive kernal contours. Home range estimates and core activity areas at the 95%, 75%, and 50% contour levels were generated using the program CALHOME (Kie et al. 1996).

B.2 Distribution

There were 2 distinct herds whose ranges were spatially and temporally independent. Both herds wintered predominantly in the western half of the study area (Figure B1). The Obed herd was located on the south side of the Athabasca River and was based on the movements of one collared elk (F151.914) and associated group of non-collared elk. The Ranch herd was located on the north side of the Athabasca River and was based on the movements of nine collared elk (F151.805, F151.814, F151.823, F151.834, F151.844, F151.885, F151.904, F151.945, AND M151.975) and associated groups of non-collared elk.

The Ranch herd was comprised of 3 sub-groups that were spatially or temporally separated during the winter of 1994/95, but were known to occupy the same area during other periods (Figure B2). The sub-groups were based on the movements of collared elk

Figure B1 Location of the 2 herd home ranges (Ranch and Obed) within the lower foothills of west-central alberta.

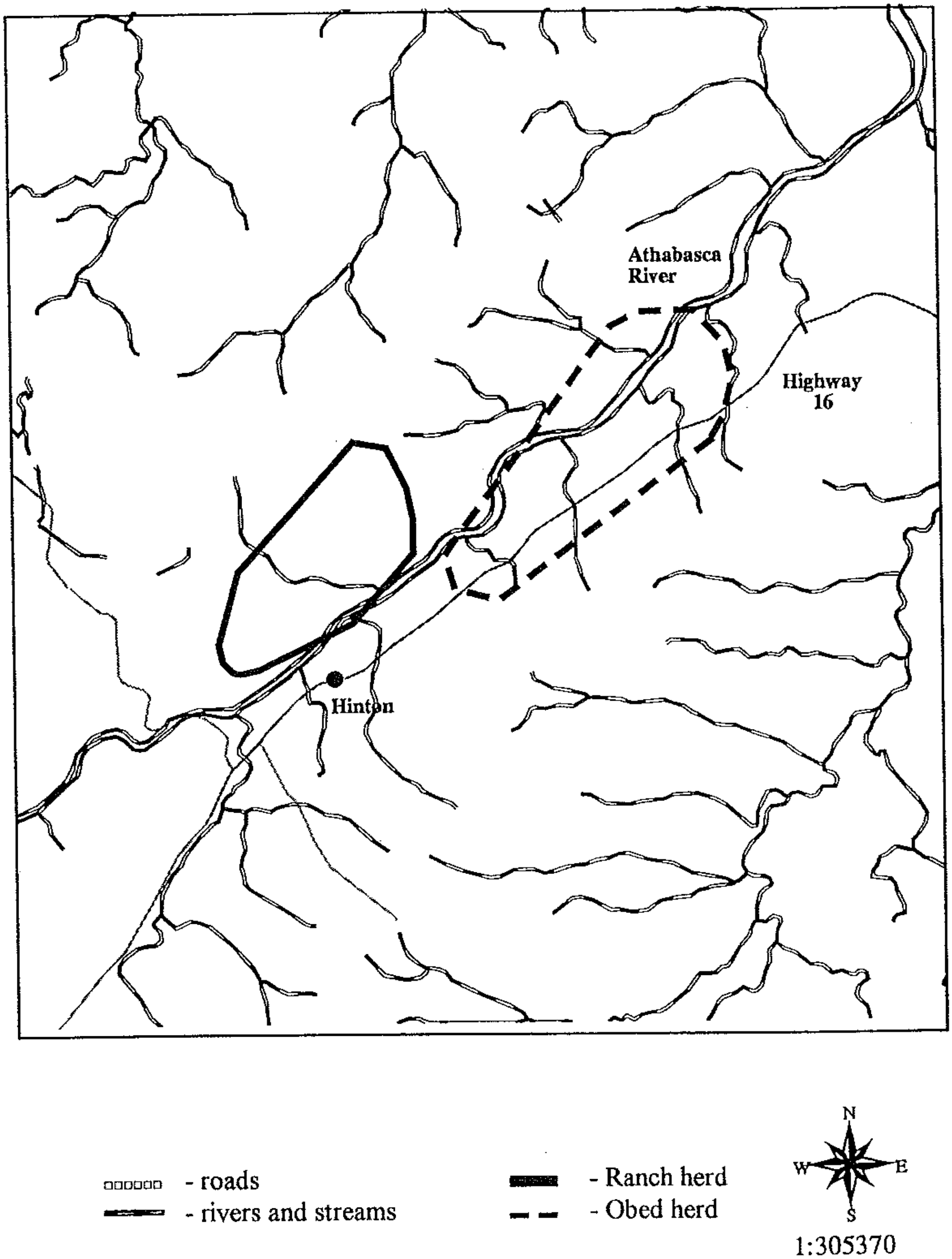
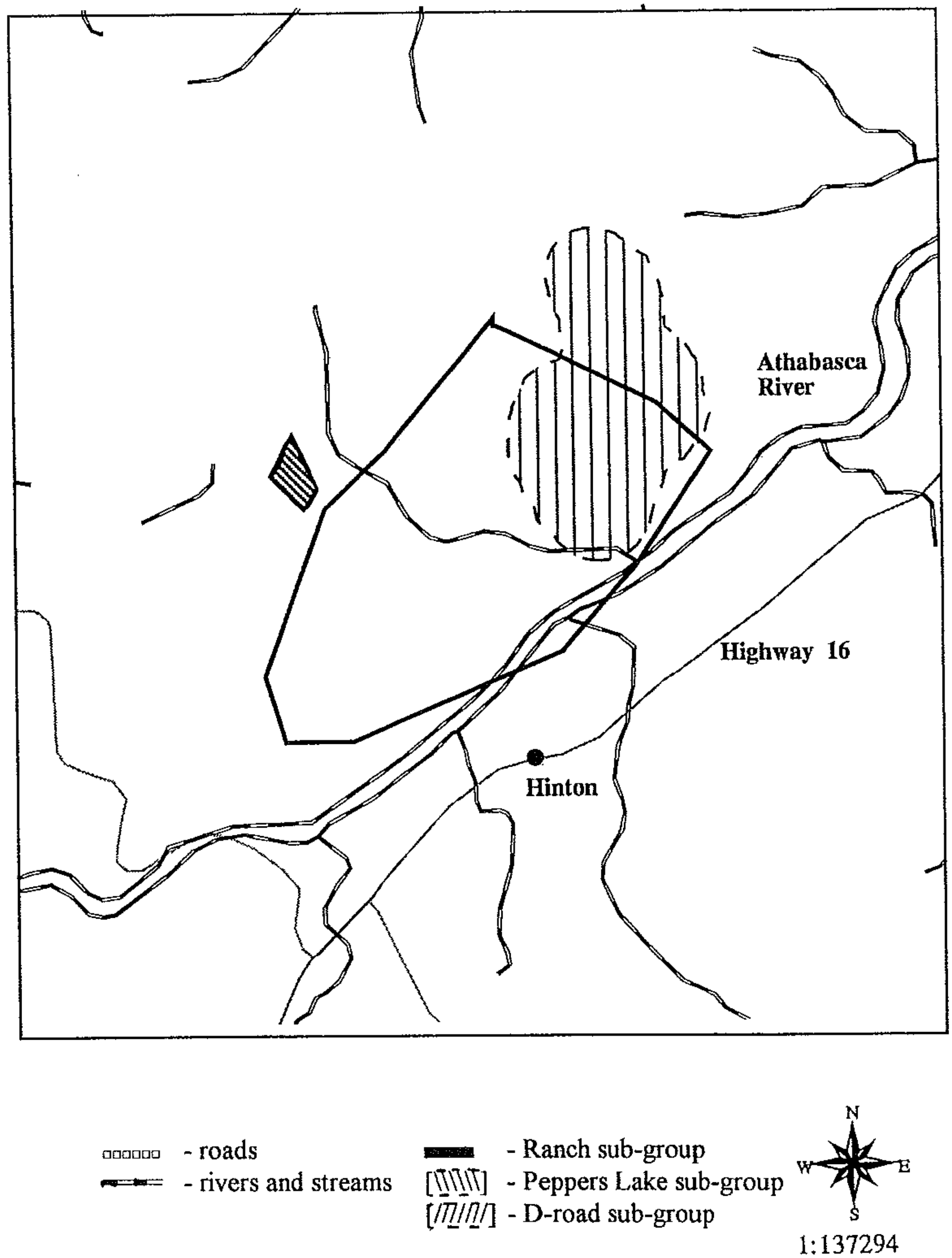


Figure B2 Location of the 3 sub-group home ranges (Ranch, D-road, and Peppers Lake) within the lower foothills of west-central alberta.



and their associated groups on non-collared animals. The D-road sub-group had one collared animal (F151.885), the Peppers Lake sub-group had one collared animal (F151.805), while the Ranch sub-group had seven collared animals (F151.814, F151.823, F151.834, F151.844, F151.904, F151.945 and M151.975). Locations of individual home ranges are given in Figures B3 - B7.

B.3 Home Range Size

The home range sizes for the 2 herds and the 3 sub-groups are summarized in Tables B1 and B2 respectively. The Ranch herd had a MCP home range that was approximately twice the size of the Obed herd at the 95% contour level. The ADK method at the 95% contour level resulted in approximately equal home range size for both herds (Obed = 5299 ha, Ranch = 5170 ha). The Ranch and D-road sub-groups of the Ranch herd had comparable home range sizes, which were dramatically larger than the Peppers Lake sub-group (Table B2). This is due to the Peppers Lake sub-group's home range consisting of locations from February 1995 to March 1995 instead of December 1994 to March 1995 as is the case with the other 2 sub-groups.

Home range size was estimated for 9 of the 12 collared elk during the winter 1994/95 (Table B3). The average number of locations for the 9 animals was 24 (range = 18-29). Minimum convex polygon estimate of home range size at the 95% contour level resulted in a mean home range size of 1125 ha (SE = 159) for the 9 elk. MCP estimates for individual elk ranged from 745 ha to 2295 ha. Using 95% contours, the ADK method

Figure B3 Home range location for elk F151.805 and F151.814 within the lower foothills of west-central alberta.

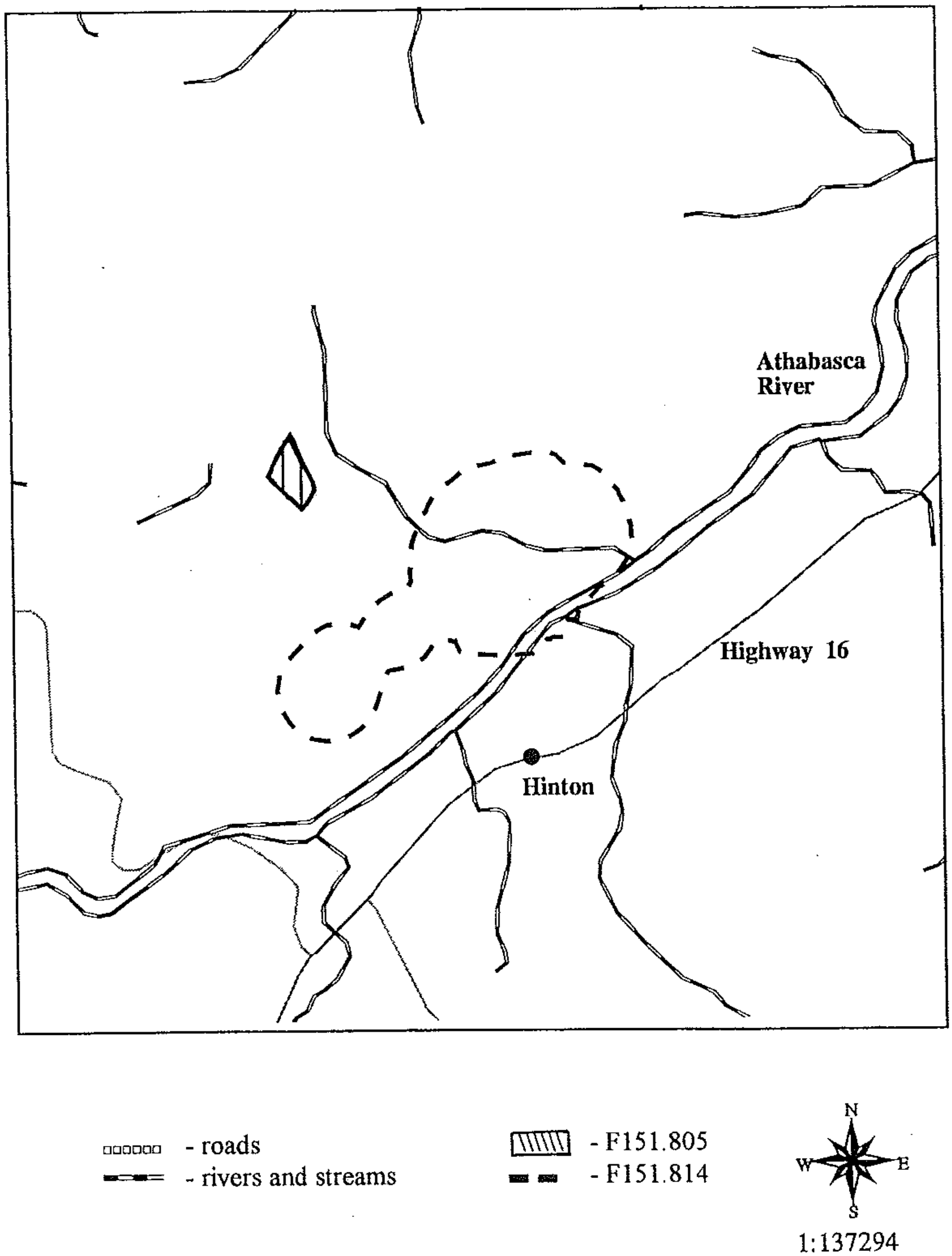


Figure B4 Home range location for elk F151.823 and F151.834 within the lower foothills of west-central alberta.

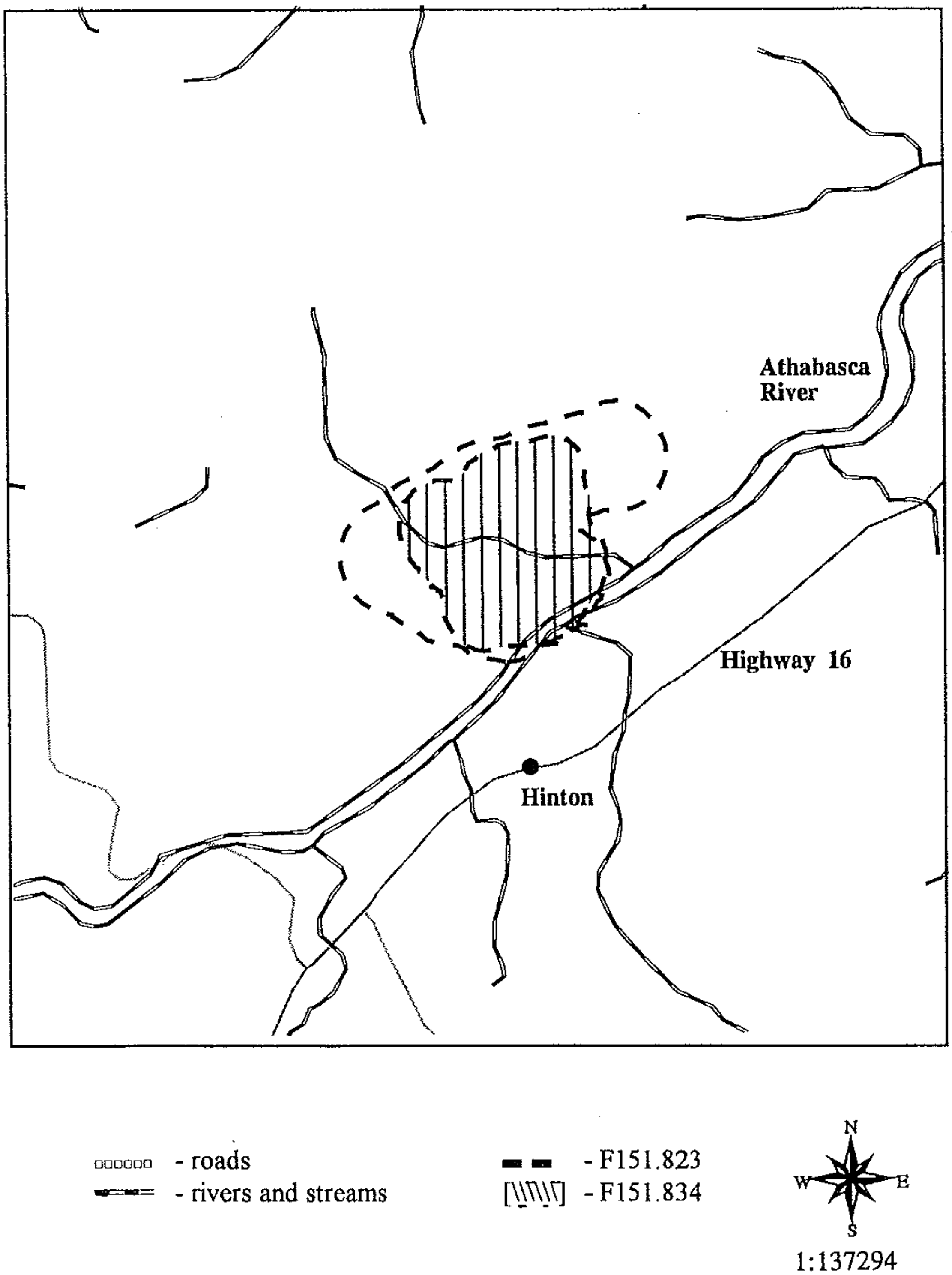


Figure B5 Home range location for elk F151.844 and F151.885 within the lower foothills of west-central alberta.

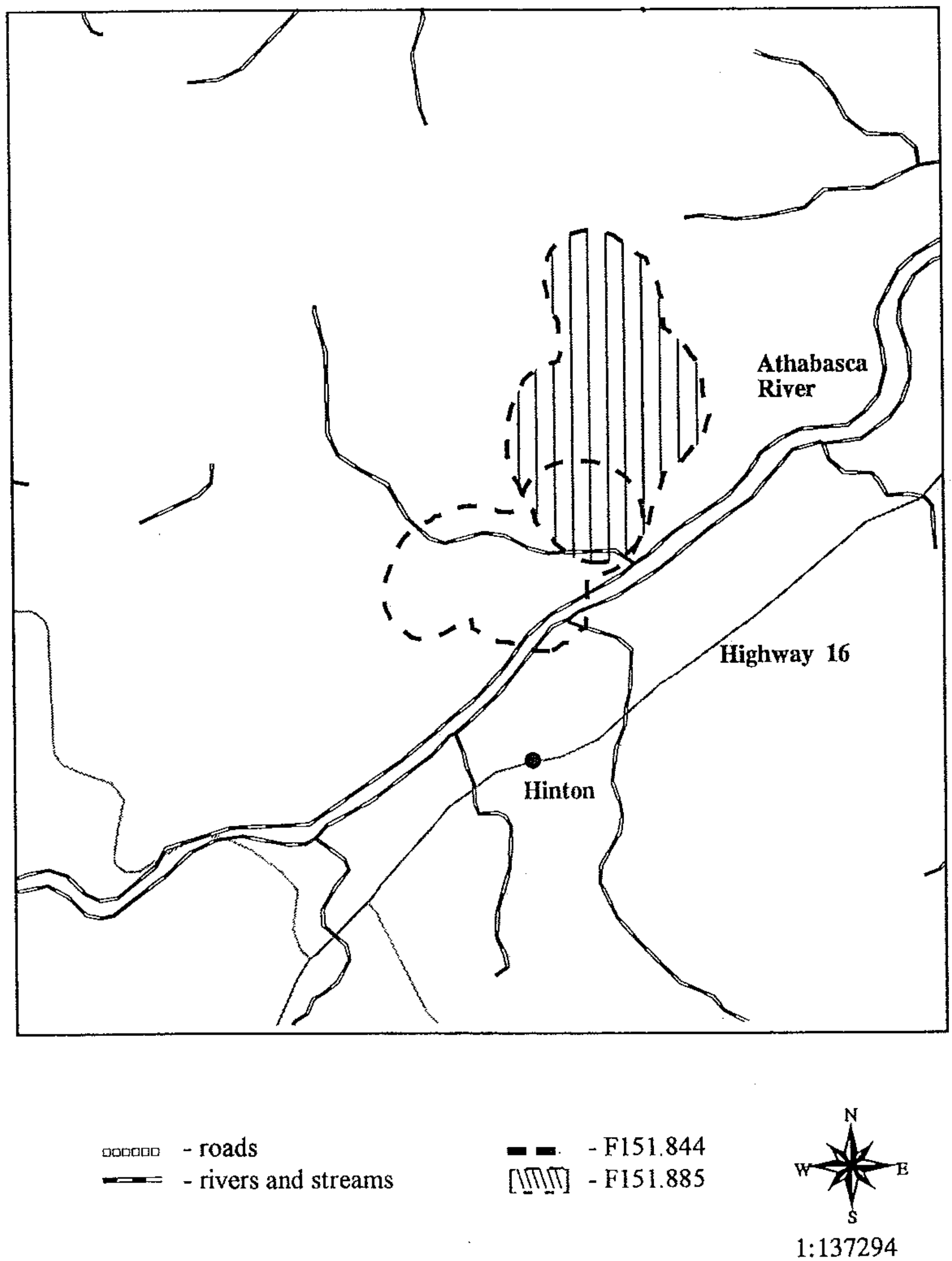


Figure B6 Home range location for elk F151.904 and F151.914 within the lower foothills of west-central alberta.

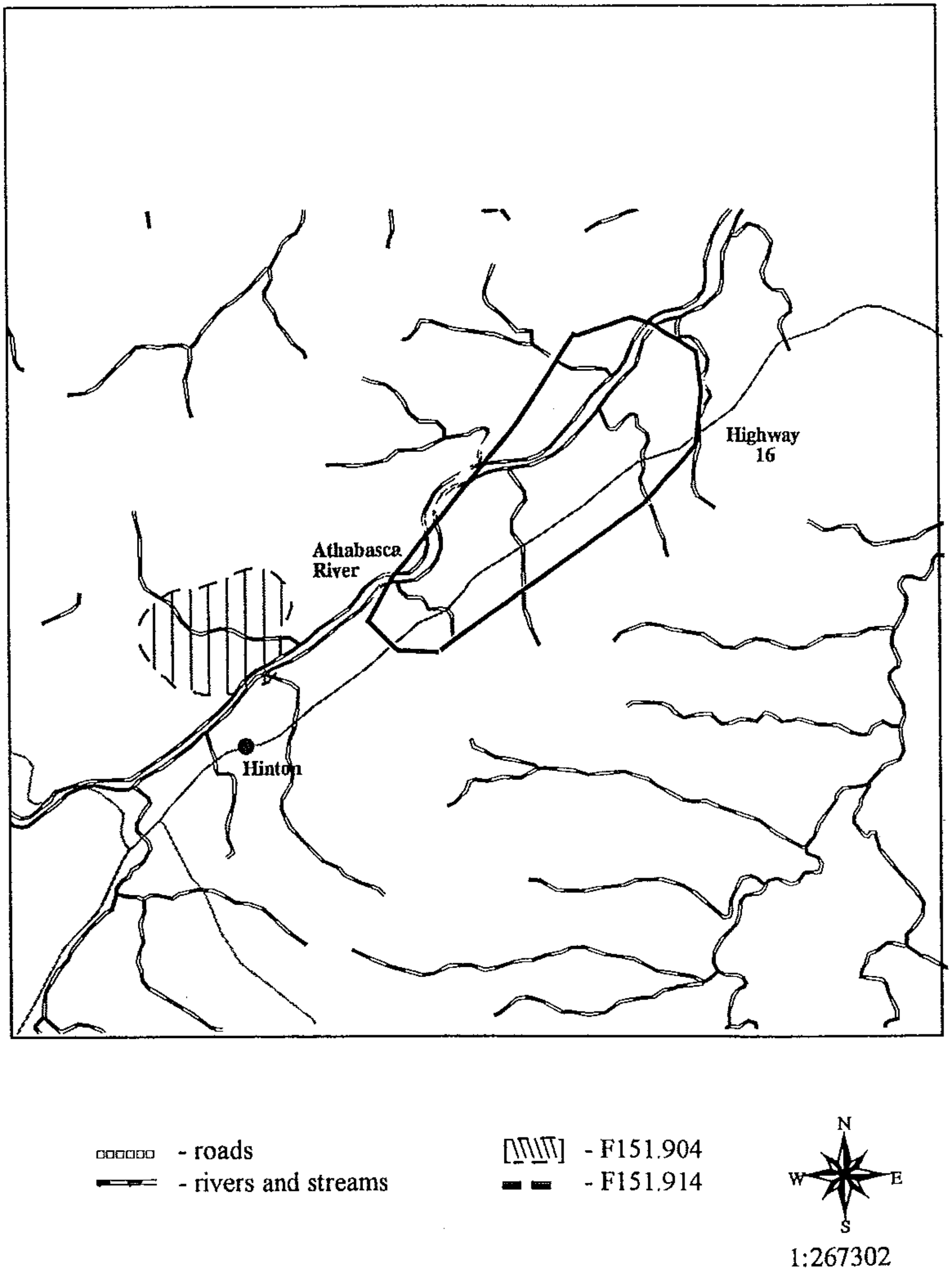


Figure B7 Home range location for elk F151.945 and M151.975 within the lower foothills of west-central alberta.

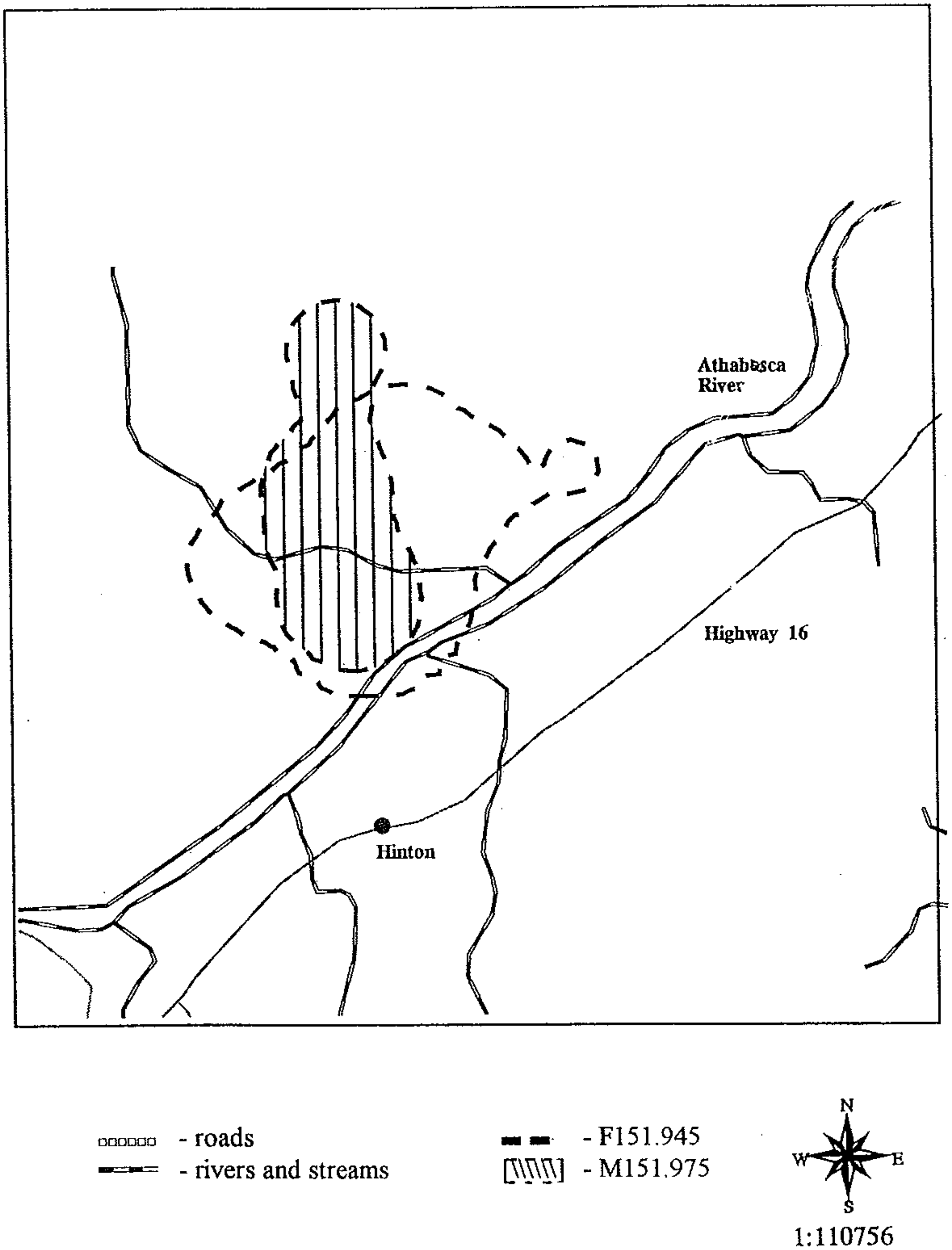


Table B1 Minimum Convex Polygon (MCP) and Adaptive Kernal (ADK) home range estimates (ha) at 95%, 75%, and 50% contour levels for the 2 herds in the study area for the winter of 1994-1995.

Sub-population	# of Collared elk	MCP 95	MCP 75	MCP 50	ADK 95	ADK 75	ADK 50
Obed	1	2295	1464	1075	5299	3225	630
Ranch	9	4307	1535	517	5170	1690	575
Mean		3301	1500	796	5235	2458	603
SE		1006	36	279	65	768	28

Table B2 Minimum Convex Polygon (MCP) and Adaptive Kernal (ADK) home range estimates (ha) at 95%, 75%, and 50% contour levels for the 3 sub-groups of the Ranch herd.

Sub-group	# of Collared elk	MCP 95	MCP 75	MCP 50	ADK 95	ADK 75	ADK 50
D-road	1	1194	551	254	2040	835	485
Peppers Lake*	1	64	37	10	123	78	222
Ranch	7	2192	863	269	3291	1028	285
Mean		1155	484	178	1821	647	272
SE		611	241	84	922	290	127

* home range size based on locations from February 1, 1995 to March 21, 1995.

Table B3 Minimum convex polygon (MCP) and Adaptive Kernel (ADK) home range estimates (ha) at 95%, 75%, and 50% contour levels for individual elk during the winter of 1994 - 1995.

Animal	MCP 95	MCP 75	MCP 50	ADK 95	ADK 75	ADK 50
F1814	915	501	178	2193	1002	222
F1823	1049	337	87	2388	831	172
F1834	770	344	153	1458	603	170
F1844	745	330	53	1490	815	124
F1885	1194	551	254	2040	835	485
F1904	1215	429	109	2442	1005	215
F1914	2295	1464	1075	5299	3225	630
F1945	1158	636	358	2190	1219	529
M1975	784	395	109	1224	707	389
Mean	1125	554	264	2304	1138	326
SE	159	119	106	402	268	62

resulted in a mean home range size of 2304 ha (SE = 402) which was larger than the MCP method. Individual home range sizes varied from 1224 ha to 5299 ha. Animal 151.914 produced the largest estimated home range using both methods. Core area was defined as the area containing 50% adaptive kernal contours. The mean core area for elk in this

study was 326 ha (SE = 62) (Table B3)

B.4 Literature Cited

Hayne, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1-18.

Kie, J. G., J. A. Baldwin, and C. J. Evans. 1996. Calhome: a program for estimating animal home ranges. Wildl. Soc. Bull. 24(2):342-344.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecol. Modelling. 38:277-298.