University of Alberta

Assessing suitable and critical habitat for Wood Bison (*Bison bison athabascae*) using Remote Sensing and Geographic Information Systems

by

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requirements for the degree of Master of Science

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Dedication

For Alison, who has supported me through this process including the long nights, occasional frustration, field work and classes. You motivated me, inspired me and pushed me to complete this project.

Abstract

Wood bison (*Bison bison athabascae*) are listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as threatened. The Species at Risk Act (SARA) requires that listed species have their critical habitat identified in a recovery or action plan. Defining critical habitat requires that the species-habitat relationship for wood bison be clearly understood at several spatial scales that would be applicable to the management and conservation of this species. To create the most accurate picture of critical habitat a very accurate map of land cover was created. I explored a technique of image segmentation using ecological regions as a means of explaining the spectral variance in remote sensing imagery to increase classification. Results show a significant increase in classification accuracy ($\alpha = 0.05$, one-tailed) over two-stage approaches ($Z = 2.49$, $Z_{crit} = 1.65$ $p=0.0063$). Resource use was assessed by examining a series of models established *a priori* using logistic regression. The resultant models were compared by assessing the Aikake Information Criteria (AIC) scores and the final models was assessed by using k-fold cross validation and out-of sample validation with data for a separate study area. I found that a good model of resource use could be created using predictors of use that included measures of habitat type as well as several measures of landscape physiognomy, Contrast Weighted Edge Density (CWED), Patch Density (PD), and Contagion.

Acknowledgements

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Chapter 1

Background, context and objectives

1.0 Purpose and objectives

The most recent National Recovery Plan for the Wood Bison (Gates et al. 2001) precipitated the need for an objective habitat-assessment tool that is expected to flow from the completion of this thesis. Further, the Species at Risk Act (SARA) explicitly requires that suitable and critical habitat be defined in both the recovery and action plan for wood bison (and all species at risk). Finally, the Research Advisory Committee for the Bison Research and Containment Program (2001) suggested that a habitat map created using GIS and remote sensing is a high priority for the program. Therefore the specific objectives of this thesis are:

> Objective 1: Evaluate how a hierarchal unsupervised classification technique using image segmentation based on ecological regions and a classification scheme based on an ecosystems approach, can be used to characterize land cover types in boreal environments.

The product of this investigation will be a very accurate digital land cover map. Accuracy in a classification can be increased by image segmentation. Thematic accuracy will be expressed in an error matrix, and as normalized accuracy, Kappa and Tau statistics (Congalton 1991, Ma and Redmond 1995). Image segmentation will be based on eco-climactic regions or ecoregions. Accuracy improvements are predicted to be marginal in images that span two or more similar ecological regions and greatest in images that span two or more dissimilar ecological regions. Similarity will be assessed based on the null hypothesis (H_o = no difference in thematic accuracy) at α=0.05 using a pair-wise test of significance (Cohen 1960) from the Kappa statistics from both classifications.

> Objective 2: Using an information-theoretic approach, assess a set of resource selection models for wood bison using location data obtained from aerial surveys, air and ground radio-telemetry in conjunction with classified satellite imagery and characterize habitat use at the site, home range and landscape scales.

The result of this analysis will be a resource selection or probability-of-use function that describes habitat use at multiple spatial scales by wood bison. Habitat selection is disproportionate to its availability. Resource selection is scale dependent, it differs from sward to site to landscape. Rather then test a single null hypothesis a set of biologically plausible resource selection models will be identified from a review of the relevant literature and an examination of the available data. Resource selection data from aerial survey and telemetry Design I, II and III sample data (Manly et al. 2002) will be used to test the models. Deviations from the fit of the model will be used to calculate Aikake Information Criteria (AIC) values and select the best models from the set of candidate models. The models will be logistic in form and will be further assessed by their ability to predict the location of animals. Model validation based on predictive success will use data withheld for this purpose from a k-fold partition of the original samples (Fielding and Bell 1997, Boyce et al. 2002).

Through this process, I aim to improve our current understanding of the multi-scale habitat requirements of wood bison, and consider how a definition of "critical habitat" can be developed and applied to management and conservation of wood bison habitat. From an applied perspective, this research is important because of the legislative requirement under SARA to define and protect "critical habitat" for listed species in Canada. My results may also assist managers in developing and evaluating potential reintroduction projects for wood bison.

2.0 Background

Wood bison (*Bison bison athabascae*) are the largest grazing ungulate in North America and a keystone species in the boreal forest (Gates et al. 2001). Wood bison were never considered to be as numerous as the plains bison (*Bison bison bison*) in their evolutionary history, and prior to 1800, wood bison were estimated to have numbered approximately 168,000 animals (Soper 1941). Concurrent with the demise of plains bison, wood bison decreased to an estimated low of 250 animals. Protection efforts in the early 20th century, including the establishment of Wood Buffalo National Park (WBNP), coincided with an increase of wood bison to an estimated 1500 animals. However, the initial recovery of wood bison was irrevocably affected by the Government of Canada's decision to move 6673 plains bison to WBNP during the period 1925 to 1928 (Fuller 2002). The translocation introduced plains bison genes, and the cattle diseases: bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*) to the native wood bison population. Introgression of plains bison genes was widespread (Wilson & Strobeck 1999) and the WBNP bison population remains enzootic with the two cattle diseases (Joly & Messier 2004). In 1957 a remnant herd of bison whose morphology were felt to most closely resemble wood bison was discovered in the Nyarling River area, a remote corner of WBNP. Conservation efforts that followed the capture of this remnant herd resulted in the establishment of the Mackenzie Bison Sanctuary (MBS) and the Elk Island National Park (EINP) wood bison herds, both of which are now considered free of bovine tuberculosis and brucellosis (Nishi et al. 2002).

Wood bison are currently listed as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and a recovery team has been established. The principal goal contained in the National Wood Bison Recovery Plan is "*to foster the recovery of wood bison in other parts of their original range and in suitable habitat elsewhere, thereby ensuring their long term survival.*" A specific objective is to establish a minimum of four free-roaming, disease-free herds of at least 400 animals (Gates et al. 2001). Not only is a definition of critical habitat in the context of wood bison inseparable from these population goals but SARA requires "*an identification of the species' critical habitat, to the extent possible, based on the best available information and consistent with the recovery strategy, and examples of activities that are likely to result in its destruction*". These must be included in the recovery strategy and the action plan.

2.1 History and distribution of wood bison

Wood bison are gregarious and their distribution is clumped with concentrations centred on expanses of suitable forage. Historically, wood bison occurred throughout much of the boreal plains: from the southern edge of the boreal forest and aspen parkland in what is now Alberta and Saskatchewan northwards, bounded to the east by the Canadian Shield, and to the north by the Beaufort Sea near the Mackenzie Delta. The western edge of the distribution of wood bison follows the eastern slopes of the Rocky Mountains into the Yukon and Alaska (Stephenson et al. 2001 - Figure 1.1).

Continental populations of wood bison decreased to an estimated low of less than 250 animals by 1896 (Soper 1941). A Buffalo Protection Act was passed in 1877 and enforcement of this act began in 1897 when the Northwest Mounted Police (NWMP) were given responsibility to enforce the act. Not until 1907 was a police outpost created at Fort Fitzgerald, close to the remaining herds of wood bison. After a few years of formal patrols by NWMP, populations of wood bison were estimated in 1914 to have reached 500 animals (Banfield and Novakowski 1960). Wood Buffalo National Park, Canada's largest national park was established in 1922 to protect the 1500 bison estimated to live within its boundaries at the time.

By 1934 the population of wood bison in WBNP had reached 12 000 animals. This dramatic increase was due in large part to the introduction of 6673 plains bison to WBNP from Buffalo National Park located at Wainright, Alberta, during the period from 1925 to 1928. These introduced plains bison hybridized the resident population of wood bison and introduced the cattle diseases: bovine tuberculosis (*Mycobacterium bovis*) and brucellosis (*Brucella abortus*) to the native wood bison population. Population numbers were maintained until the 1960's through wolf control in WBNP. The capture of a remnant herd of

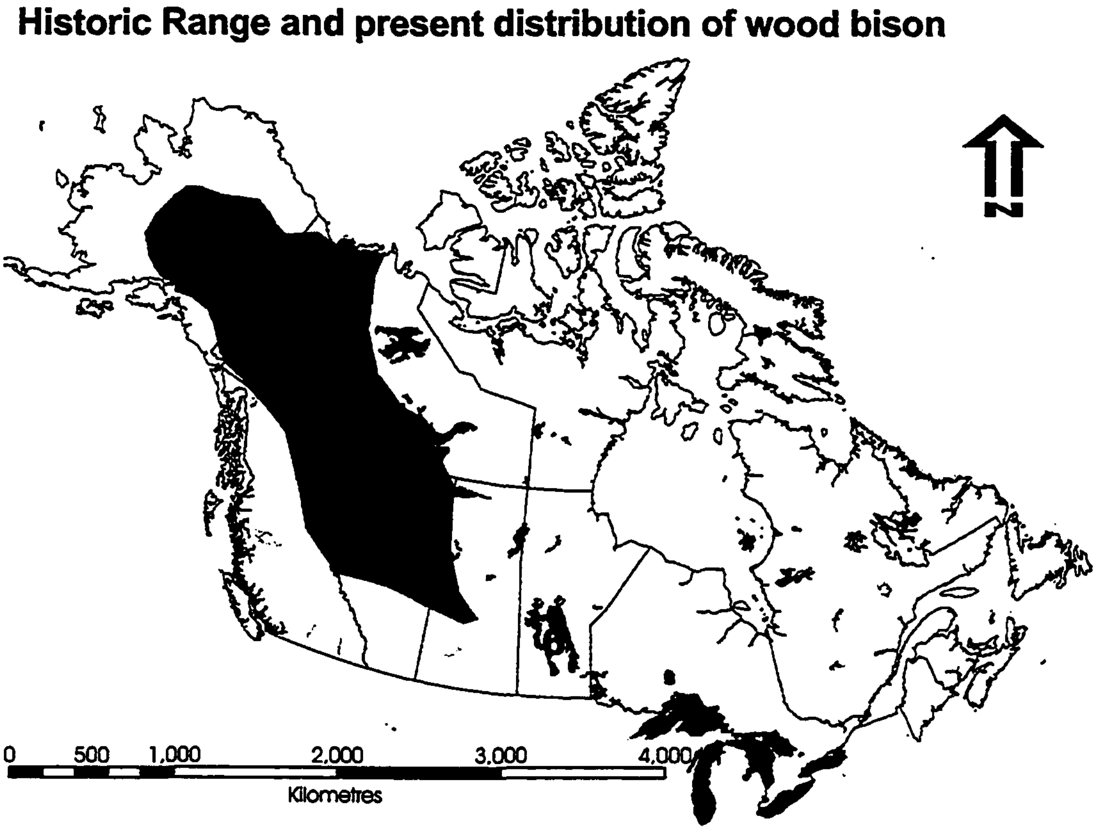

Figure 1.1 Historic and present distribution of wild, free-roaming wood bison in Canada (adapted from Stephenson et al. 2001). Present day populations are numbered as follows: 1, Mackenzie Bison Sanctuary; 2, Aishihik herd; 3, Hay-Zama Lakes; 4, Nahanni; 5, Nordquist; 6, Chitek Lake; 7, Slave River Lowlands; 8, Wood Buffalo National Park; 9, Caribou Mountains (Wentzel and Wabasca).

morphologically representative wood bison in the remote Nyarling River range in WBNP in 1959 was the start of wood bison recovery efforts. A number of capture, disease-testing and breeding programs were initiated and today, wild, free-ranging and disease-free herds of wood bison can be found in the Mackenzie Bison Sanctuary (NWT), Aishihik River herd (Yukon), Chitek Lake (Manitoba), Hay-Zama (Alberta), Nahanni (NWT), and Nordquist (British Columbia). A number of captive breeding and private herds also exist (Table and Figure 1.1).

Table 1.1 Total numbers of wood bison in public and private, captive and wild, diseased and disease-free herds (Gates et al. 2001).

Location	Status			Population
Mackenzie Bison Sanctuary	Public	Wild	Disease-Free	1908
Yukon Flats	Public	Wild	Disease-Free	500
Hay-Zama	Public	Wild	Disease-Free	130
Nahanni / Etthithun	Public	Wild	Disease-Free	200
Nordquist	Public	Wild	Disease-Free	50
Chitek Lake	Public	Wild	Disease-Free	70
Total wild, disease-free wood bison				**2818**
Slave River Lowlands	Public	Wild	TB, Brucellosis	600
Wood Buffalo NP	Public	Wild	TB, Brucellosis	2178
Wentzel	Public	Wild	TB, Brucellosis	110
Wabasca	Public	Wild	TB, Brucellosis	51
Total wild, diseased wood bison				**2939**
Elk Island	Public	Captive	Disease-Free	350
Hook Lake	Public	Captive	Disease-Free	65
Etthithun	Public	Captive	Disease-Free	43
Syncrude Canada	Private	Captive	Disease-Free	150
LaPrairie Ranch	Private	Captive	Disease-Free	50
Waterhen Ranch	Private	Captive	Disease-Free	185
Total captive, disease-free wood bison				**843**
Misc. Private Ranches	Private	Captive	Disease-Free	500
LaPrairie Ranch	Private	Captive	Disease-Free	50
Misc. Zoos	Private	Captive	Disease-Free	50
Total, other				**550**

At present time, two populations of wood bison meet the recovery requirements of the Wood Bison Recovery Plan, those in the Mackenzie Bison Sanctuary and Yukon Flats. Further recovery efforts are hampered by an incomplete understanding of the habitat requirements of wood bison, as they relate to landscape use and population expansion, and, the continued presence of disease in and around WBNP (Gates et al. 2001). This study is intended to shed some light on the former.

2.2 Ecology of wood bison

2.2.1 Habitat

Bison utilize a variety of habitats where forage resources containing high amounts of crude protein can be found. In the Mackenzie bison population, Larter and Gates (1991) found that, in the spring and summer, this habitat type was predominately meadow systems dominated by slough sedge (*Carex atherodes)* containing patchily distributed willow (*Salix* spp.) which they termed "*willow-savannah*". Wet meadows are used more in the winter when soils are frozen and these meadows become more accessible (Reynolds et al. 1978, Larter and Gates 1991). Grass and sedge meadows are used throughout the year and in the fall bison have been observed by Larter and Gates (1991) foraging on arboreal lichen in forests dominated by jack pine (*Pinus banksiana*). Additionally, bison use deciduous forests for resting and ruminating and in the winter bison appear to select smaller meadows than in summer (Reynolds et al. 1978).

In general, bison appear to avoid coniferous forests, except jack-pine dominated forests in the fall. Historically bison appear to have ranged south from Lake Athabasca south to the Clearwater River on a sandy plain dominated by jack-pine forest (John Richardson, 1851 cited in Gates et al. 1992). Additionally, European bison studied in Bialowieża, Poland forage exclusively in deciduous forests (Krasińska et al. 1987). Forest habitats, which contain forage that surround meadow complexes, can also be important in winter when snow crusting makes meadows unavailable for foraging.

2.2.2 *Competition and complementation*

Since bison are primarily grazers and not browsers they are generally not in direct competition for forage with elk (*Cervus canadensis*), mule and white-tailed deer (*Odocoileus hemionus*, *O. virginianus*), caribou (*Rangifer tarandus*) or moose (*Alces alces*) (Reynolds et al. 1982, Gates et al. 2001). Where free-ranging cattle (*Bos taurus*) are present, direct competition for forage is possible although bison demonstrate better forage digestibility rates and are better adapted to habitats that would be considered marginal for cattle (Reynolds et al. 1982).

Wood bison provide food for a large number of scavengers including coyotes, ravens and crows and their behaviour, including wallowing creates habitat for arthropods. Bison are considered to be a keystone species on the boreal plains (Gates et al. 2001). Their role as grazers utilises an ecological niche that is otherwise not exploited in boreal environments.

3.0 Geographic Information Systems and Remote Sensing

Remote sensing and geographic information systems have greatly expanded the ecologist's ability to produce land cover (or "habitat") maps of large areas. These digital land cover maps are increasingly used in ecological resource-use studies, for example for predictive distribution of muskoxen (Danks & Klein 2002), multi-scale selection by moose (Erickson et al. 1998), critical habitat for elk (Huber 1992), and assess potential reintroduction sites for lynx (Schadt et al. 2002). Classification of remotely-sensed imagery requires a careful understanding of the geographic entities under investigation as well as careful construction of a classification scheme and recognition of the limitations of the sensor (spectral, spatial and radiometric) and thus the resultant maps (Adams 1999, Marceau & Hay 1999, Joseph 2000). Further, GIS have greatly increased the ecologist's ability to characterize the environment using patch and landscape metrics. The correlation between these metrics and species distribution can be significant but needs to be better understood.

Careful consideration of the classification scheme and a definition of the geographic entities under investigation is an important first step to image classification. (Adams 1999, Marceau & Hay 1999). Image classification and plant community classification are two very different approaches to land cover mapping. Classification here is defined as a logical method of ordering elements or objects while image interpretation or image classification is a method of agglomerating and then labelling groups of similar spectral values. Classification is done using induction, elements or objects are ordered or grouped using, for example in a traditional taxonomic Braun-Blanquet classification; field data of understorey, overstorey composition, soil type, geomorphology and site moisture (Hakes 1994, Matveyeva 1994, Ponomarenko & Alvo 2001). Classification can be performed using logical taxonomic methods like the Braun-Blanquet or numerically using clustering and ordination procedures such as two-way indicator species analysis (TWINSPAN).

Classification of vegetation is governed by logical rules. However, this is complicated by the fact that like the continuous data in a remotely-sensed image ecological variables vary continuously at almost every scale. Classification is a simplification of a complex reality (Adams 1999), classification systems "*are not truths that can be discovered but rather are methods of organising information and ideas in ways that seem logical and useful*" (Soil Classification Working Group, 1998). According to Adams (1999), optimal classification schemes have the following characteristics: they rely on the structural and physiognomic characteristics of vegetation; the limits between vegetation types are carefully defined; the characteristic factors are easy to map in the field; there are enough but not too many categories, and; guidelines are provided for mapping across mosaics. The Braun-Blanquet method is taxonomic in approach to its ecological elements and relies on species composition, soil chemistry and elevation data to guide the construction of phytosociological tables and is one of the most important schools of element-based classification (Hakes 1994, Matveyeva 1994, Ponomarenko & Alvo 2001). Associations, or ecological communities in traditional classification are the objects under study. These are the smallest unit of the biosphere and the unit to be studied; they have been defined as "*a plant community of definite floristic composition, uniform habitat condition and uniform physiognomy*" (Ponomarenko & Alvo 2001).

The object under investigation in image classification is directly related to the spectral, spatial and radiometric properties of the sensor. Spectral reflectance is measured in steridians, a cone of electromagnetic energy that is received by the sensor. By convention these steridians of electromagnetic energy are converted into a raster grid of digital numbers with a nominal spatial resolution of 28.5

metres. This value is highly variable and constrained by the raster format (Landsat Science Data Users Handbook). We can consider then that raster data of this type is point data with some spatial extent and the boundaries of these pixels is fuzzy (Edwards et al. 1998). Further, considering the spatial inaccuracies inherent in the data the minimum mappable unit approximates plot size, an object greater than 0.4 hectares in size (4174m^2 or 64.61 x 64.61 metres).

A hierarchal element-based classification is developed for the study area (Beckingham & Archibald 1996). This hierarchal element-based phytotopological classification entitled A Guide to the Ecosites of Northern Alberta is based on the premise that the vegetation growing at a particular site is a product of the local climate, geomorphology, and soil conditions. This concept closely approximates that of Holdridge who held that the "*natural vegetation in an area could be objectively determined by local climate*" (Monserud & Leemans, 1992).

Remote sensing offers tremendous potential to mapping large and relatively unknown areas (Roughgarden et al. 1991). As discussed, there are some inherent limitations to remote sensing that are a product of the Instantaneous Field of View and the radiometric resolution of the sensor. Classification systems need to be developed in consideration of these limitations. Nilsen et al. (1999) determined that Landsat TM5 resolution was not fine enough to map vegetation to the level of plant association. Mapping sedge meadows and forests is possible only to the broadest level of definition.

GIS allows for habitat use to be evaluated at several spatial scales simultaneously and allows for the assessment of many habitat and non-habitat variables. Habitat variables analysed within a GIS produce spatially-informed metrics of landscape pattern. With GIS analysis we can move past the limitations of resource selection studies based only on habitat. The size and physical layout of landscape patches, the landscape physiognomy, has been shown to be a strong predictor of habitat use in studies of bison (Fortin et al. 2003) and butterflies (Ricketts 2001), for example.

4.0 Political and management context

Wood bison were first listed in 1978 by COSEWIC as an endangered species. Following recovery efforts coordinated by the WBRT the species was down-listed to a threatened species in 1988, which means, "*a species likely to become endangered if limiting factors are not reversed*" (COSEWIC 2004). The WBRT has four broad goals (Gates et al. 2001):

1. "*To re-establish at least four discrete, free-ranging, disease-free, and viable populations of 400 or more wood bison in Canada* [.]"
2. "*To foster the restoration of wood bison in other parts of their original range and in suitable habitat elsewhere* [.]"
3. "*To ensure the genetic integrity of wood bison is maintained without further loss as a consequence of human intervention.*"
4. "*To restore disease-free wood bison herds, thereby contributing to the aesthetic, cultural, economic, and social well-being of local communities and society in general.*"

Only the Mackenzie and Yukon Flats wood bison herds meet the criteria outlined in goal number one (Table 1.1). The re-establishment of free-roaming wood bison herds necessitates a landscape-scale understanding of the habitat requirements of the species. Management and conservation within the context of an industrial landscape, where oil and gas exploration, mining and forestry activities are prevalent or proposed requires that an objective tool be created to map habitat and model population expansion. Finally, what is meant by the term "suitable" and "critical" habitat needs clarification and definition by scientific study.

COSEWIC is a scientific body charged with evaluating the status of species proposed for inclusion on the list of endangered species now within the context of SARA. Listed species are accorded protection within the legislative and regulatory framework of the province in which the species is found. Provinces and territories with wood bison can place restrictions on the taking of individual wood bison. Voluntary actions of the provinces and territories, coordinated by the recovery team ensured a coordinated approach to managing wild herds of wood bison. The Convention on the International Trade in Endangered Species (CITES) listed wood bison in 1977 thereby limiting international trade in the animal, parts or derivatives (Reynolds and Gates, 1991). Not until 2003 when bill C5, the Canadian Species at Risk Act (SARA) was established was any legislative mechanism available to protect species at risk. SARA requires the recovery and action plan must include: "*an identification of the species' critical habitat, to the extent possible, based on the best available information and consistent with the recovery strategy, and examples of activities that are likely to result in its destruction.*" This project is intended to augment the best information available and develop an objective, multi-scale and ecological definition of suitable and critical habitat to facilitate conservation of wild wood bison.

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Chapter 2

Satellite-derived ecosystems classification: Image segmentation by ecological region for improved classification accuracy, a boreal case study

1.0 Introduction

Image segmentation to explain spectral variance and increase classification accuracy is not a new concept for image classification (Mason et al. 1988, De Bruin & Gorte 2000). However, in general image segmentation has been performed based on spatial attributes such as elevation derived from a digital elevation model (Franklin et al. 2001). Segmentation has also been performed based on digital map products of a very large-scale, for example 1:5000 (Cross et al. 1988, Mason et al. 1988). Two problems exist with using this approach for boreal environments; large-scale data are often not available to guide the segmentation process and the assumption that the data used to segment the image are accurate or better than the imagery itself is untested. Digital elevation data are often on too small (1:50 000 or less) a scale to be useful in explaining the variance in spectral response. However, these works have fostered the concept that spatial attributes such as elevation influence spectral response across a scene. Spatial attributes can be used to segment an image to partition the variance in spectral response. Marceau and Hay (1999), in an analysis of the Modifiable Aerial Unit Problem (MAUP) concluded that the careful selection of any zoning system, such as ecological regions, is paramount since spatial data *"are not independent of the aerial units used to collect them"*.

Despite an increasing body of literature, there is little consensus within the remote sensing community on classification algorithms, techniques, accuracy assessment or even the underlying classification schemes (Cihlar 2000). However, these should be expected to vary with the purpose of the project and the intended application of the land cover map. The accuracy and categorical resolution of many land cover maps often limit their utility. For boreal regions, classification schemes vary in their categorical resolution from broad land cover classes (forested, non-forested) to marginally more precise (deciduous, coniferous) and very precise (ie, black-spruce/sphagnum), and have in some cases, incorporated structural properties of vegetation (Treitz & Howarth 1996, Zarco-Tejeda 1999). The classification scheme developed for a particular classification exercise is always a compromise between what is desirable given the research question, and what is possible given the spatial, spectral and radiometric properties of the sensor.

Image segmentation using ecological regions is defined as image masking using small-scale (i.e., continental) data on ecological or geo-climactic regions to partition imagery into ecologically and spectrally unified segments. Spectral outliers are first removed and the image is classified again. These two-stage classifications then are expected to produce better results since the placement of cluster seeds in a k-means algorithm is more precise (Miguel-Ayanz & Biging 1996, Brook & Kenkel 2002). This two-stage approach to classification is essentially a way of removing a portion of the spectral variance in an image.

Partitioning the variance in an image by explaining its source is a way of improving the performance of a k-means clustering algorithm like ISOCLUS.

Using ecological regions to explain spectral variation across a scene is one method of improving image classification results for boreal environments. Ensuring that categories in the classification scheme are mutually exclusive is another (Adams 1999). Marceau and Hay (1999) advocated the careful definition of the geographic entities under investigation prior to analysis. To define these entities it is necessary to understand how they are created through the classification of remote sensing imagery and how these land cover entities are structured in a classification scheme.

The objects under investigation in a land cover classification exercise are often poorly described. In fact, forests, ecosystems, communities of plants *etc.*; rather than existing as discrete objects form nebulous groups that vary in a continuous fashion at nearly every spatial scale (Townshend 1992). This is a challenge to remote sensing that has been described as the Modifiable Aerial Unit Problem (Marceau & Hay 1999). The spatial context of these objects contrasts with the need for land cover maps to be necessarily categorical, therefore demanding that an objective definition of the objects in the context of pre-defined land cover categories. The Instantaneous Field of View (IFOV) of the sensor places a limitation on the minimum mappable unit and, therefore, in effect, predetermines the objects that may be measured and categorized in a landscape.

In the context of developing land cover classifications, aimed to support conservation biology initiatives, these relationships are even more relevant given that in many cases the main outcome of such maps are related to policy development. Conservation, management and planning for resource-use are challenges related to scale. The partitioning of a continuous spectral space into discrete categories is an additional challenge since trees, stands of trees or plant associations are being measured indirectly, from an ecological point of view, based on their electromagnetic properties. These electromagnetic responses are affected by the floristic and physiognomic properties of the objects and also local temperature, moisture, soil conditions, substrate, productivity and biomass at the site (Kalliola & Syrjanen 1991, Brook & Kenkel 2002).

In this paper, we evaluate the role of using ecological regions to segment Landsat imagery as part of a two-stage land cover classification in northern Alberta, Canada. We endeavour to demonstrate the importance of careful consideration of the classification scheme, that it be based on ecological criteria whenever possible. The large spectral variance associated with land cover classes is presented, and multivariate analysis is used to demonstrate that a good portion of this variance can be explained by their spatial relationship with ecological regions (Lunetta et al. 2002).

2.0 Study Area

The study area straddles the Alberta and Northwest Territories border along the 60th parallel. Image segmentation was tested on a subset of a larger classification project using Landsat image path and row 43-19 (Figure 2.1). The image covers a large portion of boreal forest characterised by coniferous and deciduous forest in a spatially heterogeneous complex of bogs, fens, marshes, lakes and other wetlands (Beckingham & Archibald 1996). The centre of the scene is dominated by Lake Claire, the largest lake by surface area in the province of Alberta, Canada (1436km^2) and North America's largest inland delta, the Peace-Athabasca Delta. Much of the region is within Wood Buffalo National Park (WBNP), Canada's largest national park (44 000km^2) and is almost uninhabited. Roads, cutlines and other anthropogenic disturbances are largely absent from the region. Natural disturbances, primarily fire and flooding are the dominant ecological disturbance processes on the landscape. The study area was chosen because of its spatial heterogeneity and reasonable availability of training data.

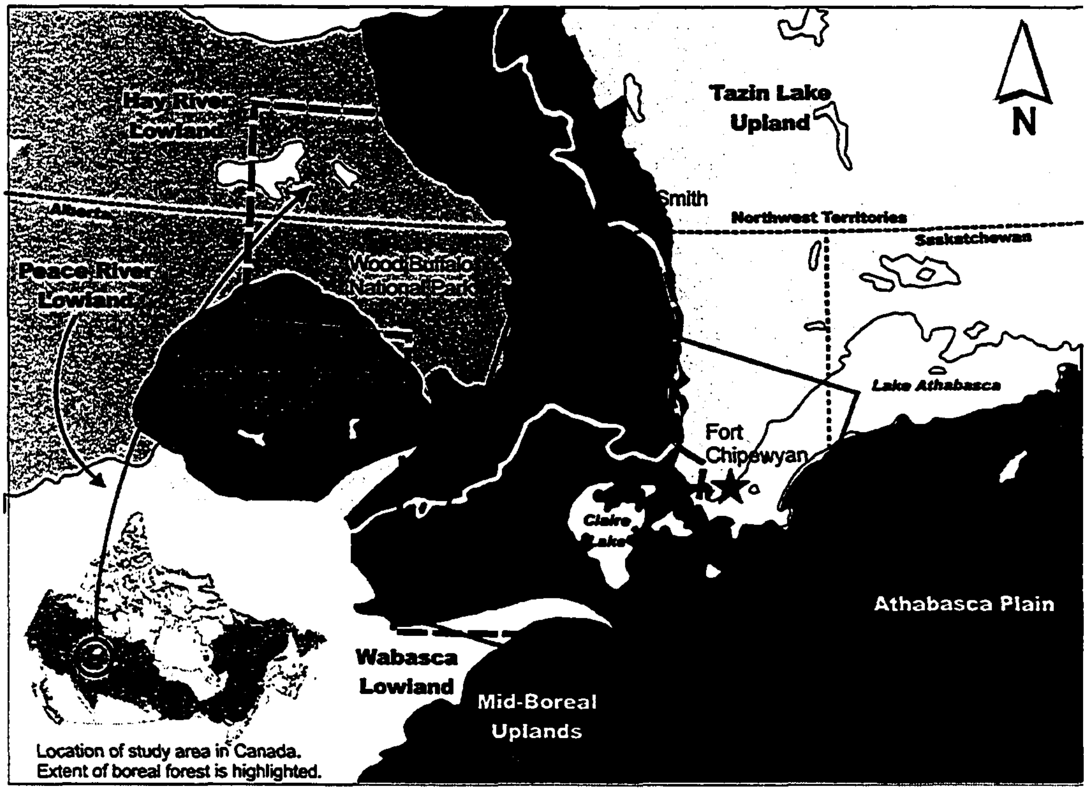

Figure 2.1 Study area and ecological regions. Landsat scene 43-19 is highlighted with a dark boundary.

Ecoregions were spatially defined using data obtain from Natural Resources Canada. The data set was created as a result of the work of the Canadian Committee on Ecological Land Classification (CCELC). Ecoregions are "*characterized by distinctive large order landforms or assemblages of regional landforms, small order macro or meso-climates, vegetation, soils, water and regional human activity patterns/uses.*" (http://geogratis.cgdi.gc.ca). Ecological regions, then, are geographically large areas of similar climate and geomorphology. Climate, the average weather conditions of a particular region includes such variables as temperature, precipitation, evapo-transpiration (Table 2.1).

3.0 Methodology

3.1 Image Correction

A Landsat 7 TM imagery collected on August 17th 1999 was used in this study. Geo-rectification of the imagery was performed using 1:50,000 scale National Topographic Series (NTS) data and a second order polynomial was used to rectify the imagery and place it in the Universal Transverse Mercator (UTM) projection, Zone 12 North American Datum (NAD) 1983. The RMS error after georectification is 18.05 metres (0.63 pixels). Given the relatively flat nature of the terrain orthorectification was not performed. Atmospheric correction was performed using the ATCOR module in ERDAS Imagine (v8.6). This process was performed to convert the digital number values to physical quantities, still normalized to the eight bit data format of Landsat.

Table 2.1 Physical and environmental statistics describing key variables for ecoregions in the study area (Landsat path 43 and row 19). Statistics are taken from metadata and attributes of the dataset "Ecozones of Canada" (Environment Canada, 2003: http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/1-1.cfm). Slave River and Wabasca Lowland have multiple listings due to the presence of several segments of these ecoregions in the study area. Claire Lake is a subset of the Slave River Lowland ecoregion.

Eco-Region	Elevation				Evapo-	Precipitation			Growing	
	Min	Max	Mean	Difference	Transpiration	Total	Snow	Rain	Degree Days	Surficial Material
Slave River Lowland	206.0	377.0	263.6	171.0	489.5	346.8	156.4	217.3	1893.9	Alluvial
Slave River Lowland	210.0	274.0	242.8	64.0	509.0	363.9	147.0	239.0	1957.0	Glacio-Fluvial Plain
Slave River Lowland	213.0	368.0	274.3	155.0	532.3	411.6	154.8	276.1	2143.2	Alluvial
Claire Lake	205.0	277.0	218.1	72.0	492.1	376.3	146.3	242.0	1983.1	Eolian
Wabasca Lowland	236.0	720.0	446.9	485.0	558.5	404.9	123.2	286.5	2089.7	Till Blanket
Mid-Boreal Uplands	256.0	870.0	706.2	614.0	519.4	449.4	134.8	326.7	2027.9	Till Blanket
Mid-Boreal Uplands	460.0	836.0	683.4	376.0	449.1	420.8	132.4	293.3	1754.1	Glacio-Lacustrine
Athabasca Plain	212.0	605.0	357.4	393.0	507.6	372.7	176.2	234.4	2039.5	Till Blanket
Tazin Lake Upland	156.0	626.0	318.2	470.0	480.7	369.1	159.8	231.1	1837.3	Colluvial Rubble

Nominal Landsat bands 1,2,3,4,5 and 7 were included in the classification and a seventh band was created using the Modified Simple Ratio (MSR) technique proposed by Chen (1996). The MSR band has proven useful at extracting biophysical properties from imagery obtained over the boreal forest. Although correlation between bands is anticipated, we thought that additional spectral information contained in the bands would add value to the classification and correlation tests were not performed.

3.2 Classification Scheme

A hierarchal classification scheme was developed (Table 2.2) based on an analysis of an element-based phytotopological classification developed for the study area (Beckingham & Archibald 1996), a structural dominance classification being used in the province of Alberta (Alberta Lands Forestry and Wildlife 1991), and the recently published guidelines on the establishment of a Canadian vegetation classification (Ponomarenko & Alvo 2001). Plant associations were

Table 2.2 Ecological land-cover classification scheme. Ecosite phase and plant community type presented on the right side of the table are taken from Beckingham & Archibald (1996) and the alpha-numeric codes in that column can be cross-referenced to the guide. Ecosite class combines community types into classes that are ecologically similar and the column 'Land Cover Class' represents an agglomeration of ecosite classes based on functional and physiognomic similarity.

Land Cover Class		Ecosite Class	Ecosite Phase and Plant Community Type		
1	Jack Pine Dominated	Jack Pine Dominated	a1	Pj lichen	
			c1	Pj-Sb	
			b1	Pj-Aw blueberry	
		Jack Pine Regenerating			
2	Other Conifer	Black Spruce Dominated	g1	Sb-Pj hygric	
		White Spruce	d3	Cranberry Sw	
			e3	Dogwood Sw	
			f3	Horsetail Sw	
		Conifer	b4	Sw-Pj	
3	Deciduous	Deciduous	b2	Aw(Bw) submesic	
			d1	Aw cranberry	
			e1	Pb-Aw dogwood	
			f1	Pb-Aw horsetail	
		Deciduous Dominated	b3	Aw-Sw blueberry	
			d2	Aw-Sw cranberry	
			e2	Pb-Sw dogwood	
			f2	Pb-Sw horsetail	
4	Bog	Tamarack	k1	Treed rich fen	
		Open Black Spruce	j1	Treed Poor Fen	
		Shrubby Bog	i2	Shrubby Bog	
		Treed Bog	i1	Treed Bog	
		Shrubby Poor Fen	j2	Shrubby Poor Fen	
5	Shrub Fen	Shrubby Rich Fen	k2	k2.1	Dwarf Birch, Sedge, Willow
			k2	k2.2	Willow, Sedge
			k2	k2.3	Willow, Calamagrostis
6	Grass Fen	Graminoid Fen	k3	k3.1	Sedge Fen
			k3	k3.2	Marsh Reed Grass Fen
		Grasslands			
7	Wetlands	Wetland	l1	l1.1	Cattail Wetland
			l1	l1.2	Reed Grass Wetland
			l1	l1.3	Bullrush Wetland
8	Not Vegetated	Mud			
		Sand			
		Rock			
9	Water	Water			
10	Anthropogenic	Urban Residential			
		Urban Commercial			
		Access Major			
		Access Minor			
		Agricultural Cropland			
		Agricultural Pastureland			
		Cut Block			
11	No Data	NA			
12	Burn	Burn			

organised into ecological and physiognomically similar ecosite classes. Land cover classes were created from an agglomeration of these ecosite classes based on their physiognomic and ecological properties.

3.3 Field Data Collection

Several image classification projects had been undertaken in the study area prior to this study. Field data collected for the purposes of classifying a 1989 Landsat MSS image, (Ow et al. 1993) was entered into a database. Field data including oblique air photos collected during a classification exercise (WBNP unpublished data) were entered into the same database. Oblique air photos were used as an ancillary data source to reconcile conflicting class labels during class labelling. Training sites from the Alberta Ground Cover Characterization project (AGCC), a province-wide LandSat classification project (Sánchez-Azofeifa et al. 2003), which included low-level oblique aerial photos, were also included in the database for this study. Additional field sites were visited in 2002 by fixed and rotary wing aircraft, vehicle and canoe

Sampling sites visited in 2002 were selected by performing an unsupervised classification of the imagery using 70 classes per image (enough to capture the expected variation) as a cluster seed with the ISOCLUS algorithm in ERDAS Imagine (v8.6). A minimum of two sites were selected from each of these spectral groups. The image was assessed to find sites that were contiguous, spectrally similar and larger than one hectare. The plot size for plant community assessment was considered in relation to the various sources of spatial error, these included: georectification error (RMS error), and global positioning system error.

Considering the geometric accuracy of the imagery and the spatial resolution of the sensor, the area to be sampled was calculated using $A = (P(1+2G))^2$ (Justice and Townsend 1981, Brogaard & Olafsdottir 1997). Where A is the area to be sampled, P is the pixel size of the sensor (28.5m) and G is the geometric accuracy of the image in number of pixels (RMS error = 0.63). Using this formula, plots in the order of 0.4ha (4,174 m^2) were selected. Approximate proportions of each identifiable plant were noted for each stratum and a digital photo was taken at the site, just above the canopy. Data sheets were later examined and the plot was assigned to one plant association type based on Beckingham and Archibald's (1996) guide. Within image 43-19, 125 field sites were visited and a further 177 were integrated from existing data sources for a total of 302 field sites.

3.4 Image Segmentation by Ecological Region

The image was segmented using public data obtained from Natural Resources Canada. Bitmap masks were created from these data and the imagery was separated into ecoregions. Aside from its anticipated usefulness as an explanatory variable, it is also possible that ecological regions could be used as a sampling stratification variable. In boreal regions where regional variation is very much influenced by recent geological and climatological events (Pielou 1991) image segmentation may be a useful approach to land cover classification.

3.5 Image Classification

Cihlar (2000) recommended that when the distribution of land cover classes is not know *a priori*, which is almost always the case with boreal environments, that unsupervised classifications would yield superior results. Unsupervised classifications often utilize the Iterative Self-Optimizing Clustering (ISOCLUS) or *k*-means clustering algorithm implemented in a single or two-stage classification (Ertap et al. 1992). Two-stage approaches first use an unsupervised classification to isolate spectral outlier clusters (such as water, clouds, ice or rock), these outliers are removed from the image using a bitmap mask and the remaining image is classified again, the resulting clusters labelled and the results assessed (Miguel-Ayanz & Biging 1996). The ISOCLUS algorithm seeds a specified number of cluster means into the data along the vector determined by the means and standard deviation of the data. The Euclidean distance to each pixel is calculated from the means. The means are adjusted iteratively until a specified convergence threshold is achieved. From this preliminary classification spectral outliers; water, rock, sand, mud classes were isolated and removed from the input imagery using a bitmap mask. A second ISOCLUS classification was performed on the masked imagery. For a comparison between classification techniques, the ecoregion (image segmentation) approach images were segmented by ecological regions as specified above. An image classification was performed in each image segment. The pixels in a two by two window around a ground-control point were labelled with the class label. Pixels adjacent to the classified pixels that had similar spectral values were given a temporary label to describe their possible association with the information class. After labelling, spectral classes with more than one information class were labelled based on a simple class membership majority rule.

3.6 Error Assessment

Statistically valid reporting of error rates in classified satellite imagery requires the collection of a large number of test sites (Ginevan 1979). Since data collection in remote areas is time consuming and costly, a balance must be found between what is practicably attainable and what is statistically sound (Congalton 1991). *K*-fold cross validation was selected as the accuracy assessment method for image 43-19 (Schaffer 1993). Using this technique the data are divided into *k* partitions. Field sites were selected so a minimum of two field sites would overlap each spectral class obtained from preliminary unsupervised classifications and in consideration of broad, obvious classes like water and after considering logistical and financial constraints on sampling. The number of *k* partitions selected is based on the number of predictors: the number of bands in the case of image data, in this case six image bands (nominal Landsat bands 1,2,3,4,5, and 7) and one ratio band, the Modified Simple Ratio (Chen 1996). Other predictors such as ancillary data should not be included; their use as predictors often includes much subjectivity (Vogelman et al. 1998, Franklin et al. 2001). The ratio of test to training data can be calculated as $[1 + (p-1)^{1/2}]^{-1}$,where p is the number of predictors – in this case seven bands and a resultant ratio of 0.25. This approximates a rule-of-thumb that was developed from this formula suggesting that 25 to 35% of the data be used for testing (Huberty 1994). From the *k* partitions a training set *T* is created that contains all the data except those in the k^{th} group. The training algorithm is tested with the k^{th} group. This is repeated for each *k* group. The mean error and pooled variance for all test sets is reported.

The method used in this study is considered less wasteful of training data although, depending on the number of *k* partitions selected, is more process-intensive. Usual approaches to separating training and testing data is to simply split this dataset in half. The k-fold approach with seven predictors provides 25% more data with which to create the classification. Results are expected to be more accurate because of the larger number of training sites and there is no loss of accuracy in assessment using the mean error and pooled variance.

Any two classification methods can be compared using a pair-wise test of significance with a *Z* distribution as proposed by Cohen (1960), assuming that the results of the classification are normally distributed. This method has been used to compare the Kappa statistics for several pairs of classifications (Miguel-Ayanz & Biging 1996). The *Kappa* statistic was derived to assess overall accuracy while considering intra-class accuracy and inter-class agreement. Ma and Redmond (1995) proposed the *Tau* coefficient as a better measure of classification accuracy. They argued that *Kappa* can provide an underestimate of classification accuracy and variance is more difficult to calculate than with the *Tau* coefficient. A comparison of the *Tau* coefficients derived from independent classifications can be evaluated for significance, then, using a *Z* distribution assuming correctly that the percentage agreement, and therefore *Tau* are normally distributed (Ma & Redmond 1995, Steel et al. 1997). Tau coefficients (Ma & Redmond, 1995) and their variance are compared using a one-tailed Z-test of significance with a pre-set alpha level of 0.05. The null hypothesis is that classification accuracies, expressed as *Tau* coefficients will not be significantly different (α =0.05) between a simple two-stage classification and a classification employing image segmentation by ecological region. The alternative hypothesis is that classification using ecoregion segmentation will result in significantly better (α =0.05) accuracies than a two-stage classification alone.

For each testing data set a class label and *x, y* locations were output to a text file. The centre value and a buffer of pixels were extracted from the image. The buffer was a 3x3 window around the centre pixel. Median, mode and count values were calculated for each testing site. The resulting spread sheet was assessed using the following rule for class assignment: *if the testing class-value is equal to the centre value and there are more than five cells in the buffer with the same value make the centre value the reference value if not return the modal value from the buffer array*. Oblique and vertical air photos were used to resolve any outstanding conflicts.

3.7 Multi-Group Discriminant Analysis (MDA)

Multi-group discriminant analysis was used to test for significant differences between ecoregion-groups of ecosites. MDA is a multivariate analysis technique that allows spectral data in multiple bands to be compared simultaneously; data are presented graphically, modelled in *n* dimensions. The technique allows spectral data to be assessed for spectral outliers and class distinctiveness. Data for the MDA test were collected from the atmospherically corrected imagery. A 3x3 window was placed over all the points in the Jack Pine (*Pinus banksiana*) class (number one in the matrix). Jack Pine plant associations were selected for MDA analysis because of the large number of field site data available, the expected variance within these communities and their wide spatial distribution. Spectral values were extracted for each point in each band in this window. The spectral values per point were classed by ecological region and assessed using the multivariate analysis software SYN-TAX 2000 (Podani 2001).

3.8 Landscape Structure Analysis

To assess the effect of classification using image segmentation on landscape structure, landscape metrics were calculated using the program FRAGSTATS (McGarigal et al. 2002). To avoid redundant analysis a subset of scene 43-19, classified using a two-stage and image-segmentation approach was imported into FRAGSTATS for analysis. Class and landscape metrics were calculated for each subset and the results assessed.

4.0 Results and Discussion

4.1 Segmentation by Ecological Regions

Landsat scene 43-19 is dominated by the Slave River Lowlands ecoregion, an undulating landscape derived from glacio-fluvial materials and alluvium (Figure and Table 2.1). Other physically and ecologically disparate ecoregions form part of the scene 43-19, these include; the Athabasca plain, a dry region dominated by sandy soils including active dune complexes; the Mid-Boreal Uplands (Birch Mountains) characterised by a cool and wet climate and the Tazin Lake Upland, a rugged landscape dominated by pre-Cambrian rock (Canadian Shield). The large area covered by a Landsat scene, approximately 32,400km^2, contains landforms and natural regions that are geologically and ecologically disparate. The physical and environmental traits of these regions, evapo-transpiration, precipitation, growing degree days and surficial geology determine, in large part, the ecological communities that will evolve and persist (Holdridge et al. 1971, Guisan & Zimmermann 2000).

Spectral response recorded at the Landsat sensor is a product of the physical and biological properties of materials in the scene. Figure 2.2 shows at-ground reflectance (in digital number) for three spectral bands (Landsat band 3, red: 0.63 – 0.69µ; Landsat band 4, near infrared: 0.76 – 0.90 µ; Landsat band 7, infrared: 2.08 – 2.35 µ) for all the ecoregions represented in scene 43-19.

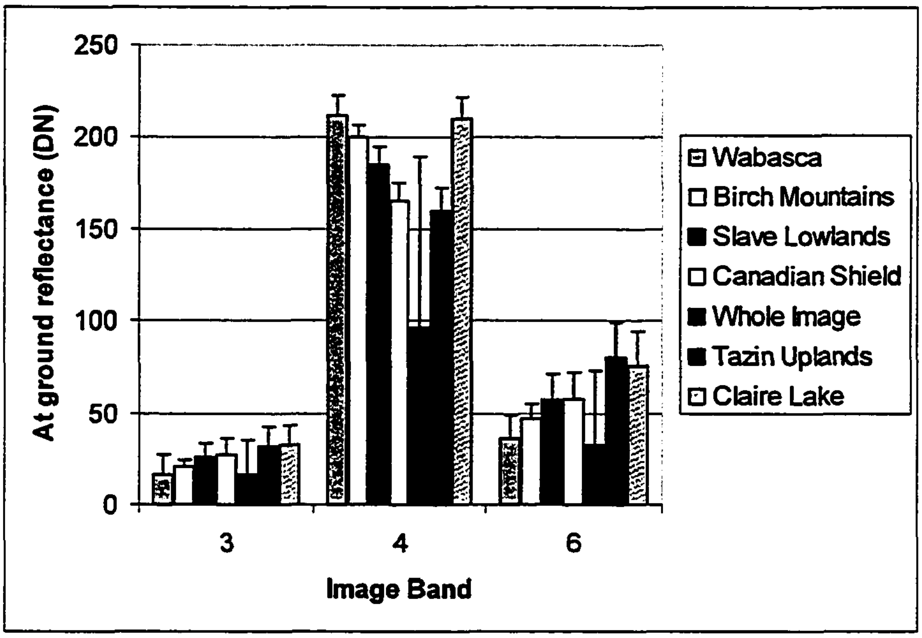

Figure 2.2 Digital number means for the population of pixels in ecological regions in the study area. Selected bands 3,4 and 6 are represented here, which correspond to Landsat bands 3,4 and 7 respectively. One standard deviation is indicated by the line-bars over each column. Greater variation in spectral response across the entire scene than in any single ecological region can be deduced from the figure.

4.2 Classification and Error Assessment

Clustering algorithms that divide spectral space are an objective means of grouping data. Cluster labelling and conflict resolution in labelling is essentially a series of structured subjective decisions (Brook & Kenkel 2002). Foody (1999) stressed *"that classification is a subjective process"*. Repeatability of results however requires that as much as possible these subjective decisions be replaced by objective, automated procedures. Cihlar (2000) was careful to point out that the continued use of discrete-category classifications would require a certain degree of subjectivity by the analyst in an image classification. Cluster labelling was done as much as possible to ensure objective labelling of spectral classes. Although the procedure used in this study could conceivably be fully automated some subjective control over resolution of conflicting class assignments was used in the classification process.

Tau coefficients and pooled variance were used to test the null hypothesis. A one-tailed test using a *Z* distribution found that the ecoregion image sub-setting method significantly improves the accuracy of the classification ($\alpha = .05$) compared to a standard two-stage classification approach (Table 2.3). The test is appropriate since the errors are themselves presumed to be normally distributed when drawn from samples close to 100 (Ma & Redmond, 1995). The mean of the *Tau* coefficients is 0.722 ($\sigma^2 = 1.92 \times 10^{-3}$) and 0.556 ($\sigma^2 = 2.47 \times 10^{-3}$) for ecoregion and two-stage tests respectively (Tables 2.3 and 2.4). To test for effects of the segmentation method all other factors were held constant or not included in the classification algorithm. These additional factors included classification refinement using ancillary data, textural classifiers, and image data used for training. Variance for both means was calculated as pooled variance (Table 2.3).

Table 2.3 Accuracy assessment results from a k-fold cross validation test. P_0 is percentage agreement and σ^2 its variance; Tau coefficient and its variance is listed with P_r, the random agreement. Upper and lower 95% confidence limits are also given for the Tau coefficients.

Method	P_0	$P_0\,\sigma^2$	*Tau*	P_r	*Tau* σ^2	*Upper CL*	*Lower CL*	*n*
Ecoregion 1	0.857	0.002	0.833	0.125	0.002	0.914	0.753	56
Ecoregion 2	0.758	0.002	0.718	0.077	0.002	0.799	0.637	91
Ecoregion 3	0.738	0.002	0.701	0.075	0.002	0.778	0.624	107
Ecoregion 4	0.696	0.005	0.635	0.130	0.003	0.750	0.519	46
Two Stage 1	0.643	0.004	0.571	0.107	0.003	0.683	0.459	56
Two Stage 2	0.731	0.002	0.686	0.075	0.002	0.770	0.603	93
Two Stage 3	0.607	0.002	0.542	0.065	0.002	0.629	0.456	107
Two Stage 4	0.522	0.005	0.426	0.130	0.004	0.552	0.301	46

Using the normal *Z* distribution the critical value was determined to be 1.65 for a one-tailed test. The value of *Z* was obtained using the equation 2 provided by Ma and Redmond (1995). This value of $Z = 2.49$ is greater than Z_{crit} (1.65). Image classification using a two-stage approach and image segmentation by ecological region is therefore significantly better ($\alpha = .05$) than a two-stage image classification approach alone. The results of each separate *k*-fold classification, represented by percentage agreement, variance, *Tau* coefficients, its variance and its confidence limits are presented in Table 2.3. Pooled results from analysis are presented along with Z scores in Table 2.4. Classification results are consistently better for ecoregions compared to two-stage classifications for each *k*-fold partition. However, results of the classification vary from partition to partition presumably as a result of the type and quality of available training data in each partition. Classification results, in the form of error matrices, are presented in

Table 2.5. Results from the segmentation by ecological region are presented in the four matrices on the left side of Table 2.5; these are paired with results from the two-stage classification contained in the four matrices on the right side of Table 2.5. The statistical test of these results is outlined above; however, results can be qualitatively assessed by visually comparing the dispersal of misclassifications from the diagonals in each error matrix, which represent correctly classified data. Note especially the differences between the two side of Table 2.5 in class 1, Jack Pine, from the ecoregion segmentation approach (matrices on the left) and the two-stage approach (matrices on the right).

Table 2.4 Results from a test of the differences between the Tau coefficients for two image classification techniques using a *Z* distribution. Variance is calculated as pooled variance.

	Ecoregion	*Two-Stage*
Mean	0.722	0.556
Known Variance	1.92×10^{-3}	2.47×10^{-3}
Z	2.49	
P(Z<=z) one-tail	0.0063	
z Critical one-tail	1.65	

An assumption is often made that vegetation classes will have unique spectral responses; that discrete ecological classes have some direct relationship to spectral response (Miguel-Ayanz & Biging 1996). Ecological phenomena vary continuously in time and space and at almost every spatial scale. This variability combined with the restrictions of the sensor and platform (pixel size, spectral and radiometric resolution) make obtaining unique spectral signatures a challenge (Kalliola & Syrjanen 1991, Brook & Kenkel 2002). Since we deduce the ecological attributes we are measuring from spectral response measured at the sensor we have an indirect and therefore imperfect measure of ecological attributes (Kyriakidis & Dungan 2001). Floristic diversity combined with the spatial heterogeneity of ecological communities makes mapping of vegetation types especially complex (Nilsen et al. 1999). Further to the problems of signature extension (Cihlar 2000), and spectral mixing (Brook & Kenkel 2002) we have also to face the confounding effects of spectral similarity. Not only will similar ecological communities have different spectral responses due to their unique combination of soil, structure and vegetation but very different ecological communities can have nearly identical spectral responses (Brook & Kenkel 2002). In image 43-19 for example, rock (informational class 8, shield rock) can be spectrally similar to informational class 6 (sedge and reed-grass meadows) especially when these sedge meadows contain a high proportion of cured grass. The spectral similarity is due in part to the high reflectance of lichen in the former and dry grass (lacking chlorophyll) in the later. It is highly improbable that any lichen-covered rock outcrops will be found in the ecoregion containing large extents of sedge meadows. By constraining both the classification algorithm and the labelling process, errors in class confusion are reduced. Further proof of this is provided by multi-group discriminant analysis (MDA) (Figure 2.3).

Table 2.5 Error matrices of image classification results from independent classifications of land cover types. Observed values are presented along the x axis and reference data along the y axis.

Ecoregion Test 1

	1	2	3	4	5	6	7	8	9	10	11	12	
1	17			1									18
2		1											1
3			9	1			1		1				12
4		1		3									4
5			1		6	1							8
6						6							6
7							2						2
8													
9			1						4				5
10													
11													
12													
	17	2	11	5	6	7	3		5				56

Two-Stage Test 1

	1	2	3	4	5	6	7	8	9	10	11	12	
1	11	1		2					1				15
2	3	1					2						6
3	2		10	1									13
4					2								2
5				1	4	1							6
6	1			1		6							8
7													
8													
9			1				1		4				6
10													
11													
12													
	17	2	11	5	6	7	3		5				56

Ecoregion Test 2

	1	2	3	4	5	6	7	8	9	10	11	12	
1	18	2			1								21
2	3	10	1										14
3			15										15
4				3									3
5	1	2	1	4	6	1							15
6				3	1	14							18
7													
8								1					1
9							1		2				3
10													
11													
12	1												1
	23	14	17	10	8	15	1	1	2				91

Two-Stage Test 2

	1	2	3	4	5	6	7	8	9	10	11	12	
1	19	2		2	1	1							25
2	3	11	1	1	1								17
3			16		1								17
4				2									2
5		1		2	3								6
6				5	1	14	1						21
7													
8								1					1
9							1		2				3
10													
11													
12	1												1
	23	14	17	12	7	15	2	1	2				93

Ecoregion Test 3

	1	2	3	4	5	6	7	8	9	10	11	12	
1	16			3									19
2		17	1	6		1							25
3	2		19	2	1		1						25
4	1	1		3									5
5				1	5	1							7
6			1	1	1	13							16
7							2						2
8								2					2
9		1							2				3
10													
11													
12	2					1							3
	21	19	21	16	7	16	3	2	2				107

Two-Stage Test 3

	1	2	3	4	5	6	7	8	9	10	11	12	
1	16	3		8	2	1							30
2	1	12	2	3									18
3	2	2	17	1	1		2						25
4				1									1
5	1			1	2								4
6		1	2	2	2	13	2						22
7													
8								2					2
9		1							2				3
10													
11													
12	1					1							2
	21	19	21	16	7	15	4	2	2				107

Ecoregion Test 4

	1	2	3	4	5	6	7	8	9	10	11	12	
1	5				2								7
2	1	9	1										11
3			9		1	1							11
4				4	1								5
5			1	1		1							3
6				1		2							3
7													
8													
9									3				3
10													
11													
12				1		2							3
	6	9	11	7	4	6			3				46

Two-Stage Test 4

	1	2	3	4	5	6	7	8	9	10	11	12	
1	5	1	1	2	2								11
2		4	1										5
3		1	8		1								10
4	2												2
5			1	2	1								4
6				2		4							6
7													
8													
9		1				1			2				4
10													
11													
12		1		1		2							4
	7	8	11	7	4	7			2				46

4.3 Landscape Structure

Qualitative and quantitative measures of the landscape are sensitive to the remote sensing algorithm used to create a land-cover map. The ecoregion-segmented classification produced a landscape that, in general, is less patchy, containing more core areas and has less of a "salt-and-pepper" appearance than the two-stage classification (Figure 2.3 and Tables 2.6 and 2.7). In four land-cover categories, classes 3 (Deciduous), 5 (Shrub Fen) and 6 (Grass Fen), representing

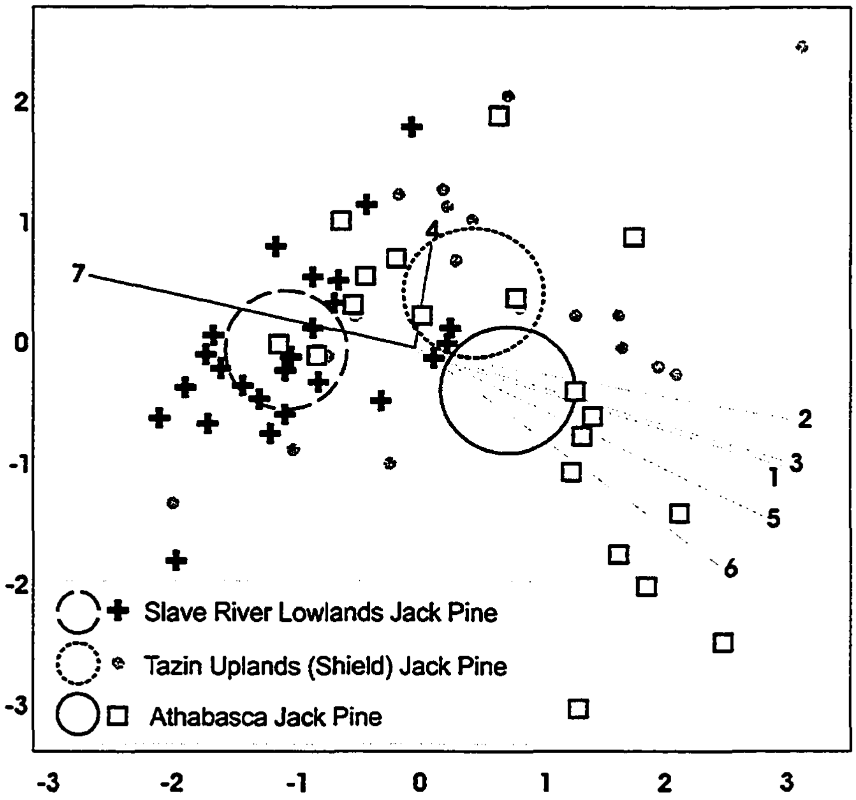

Figure 2.3 Multi-group Discriminant Analysis (MDA) of mean spectral data at Jack Pine (*Pinus banksiana*) associations in different ecological regions in Landsat scene 43-19. Confidence ellipsoids of 95% around group centroids are shown on the graph. Long-dashed circle on the left and crosses are Slave River Lowlands Jack Pine plant associations, solid circle on the right with squares is the Athabasca Jack Pine plant associations and short-dashed circle and solid grey circles is the Tazin Uplands (Canadian Shield) Jack Pine plant associations.

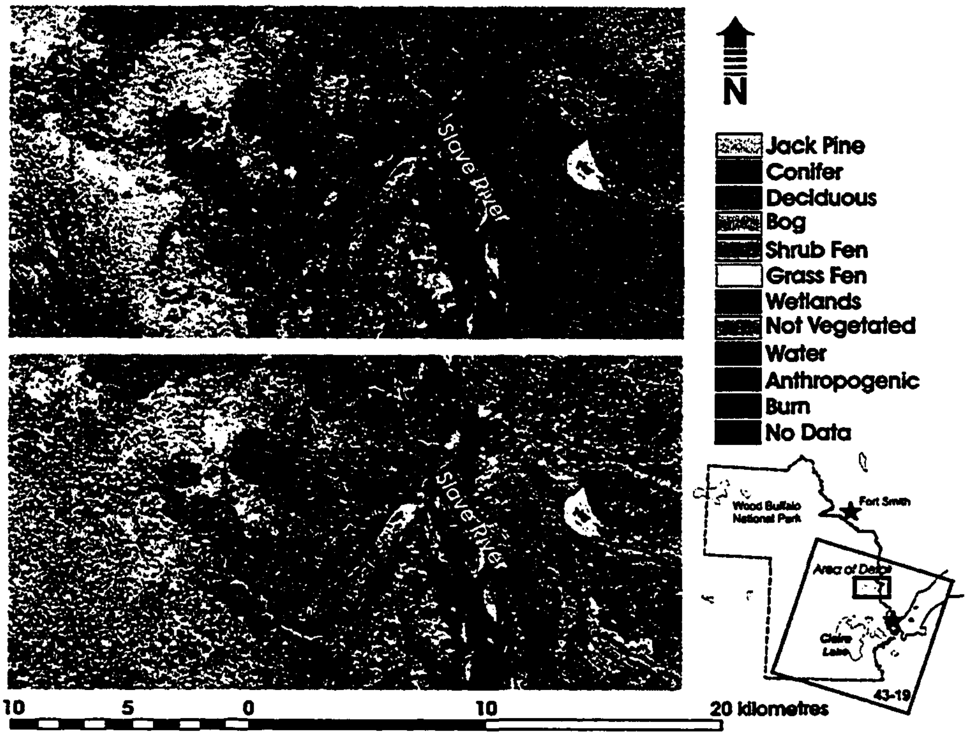

Figure 2.4 Subset of classified image 43-19. Results from ecoregion segmentation classification process is shown on top; results from two-stage classification are shown on the bottom.

59.2% of the eco-region landscape, patches are larger, there are less of them and they have a larger core-area index (Table 2.6). A special note is class 6 (Grass Fen), where total class area is reduced but Total Core Area Index (TCAI) is much larger. This likely resulted from the confusion, in the two-stage landscape, between grass and rock. Pre-Cambrian (Canadian Shield) rock was found only of the east side of the landscape (Figure 2.4), to the east of the Slave River. Class confusion results from the two-stage algorithm allowing graminoid fens to appear in an area where they are unlikely, thus, there is a larger class area of graminoid fen but they were smaller and more widely dispersed; supplanting the rock (class 8) where it should have appeared. There was a trend towards increased landscape heterogeneity (salt-and-pepper appearance) in an increased number of patches but reduced Mean Patch Size (MPS); Largest Patch Index (LPI) was also much reduced in the two-stage classification (Table 2.7).

4.4 Multi-Group Discriminant Analysis

Following multi-group discriminant analysis the results were assessed visually in a bi-plot in which the centroids and 95% confidence ellipsoids for each group of objects are presented (Figure 2.4). Object groups in this case are spectral means of each ecosite grouped by ecological region. Spectral data from Jack Pine (*Pinus banksiana*) plant associations, grouped by ecological region was found to differ significantly (Figure 2.4).

Table 2.6 Class metrics derived from subset landscape, Landsat scene 43-19 (Figure 6), minimum mapping unit is 4 hectares. Selected metrics include: CA, Class Area; NP, Number of Patches; LPI, Largest Patch Index; MSI, Mean Shape Index; TCAI, Total Core-Area Index; MCAI, Mean Core-Area Index.

Classification	Class	CA	NP	LPI	MSI	TCAI	MCAI
Two-stage	8 – No Veg.	11.86	1	0.046	1.730	0.000	0.000
Ecoregion	8 – No Veg.	171.72	4	0.576	1.980	8.386	2.467
Two-stage	9 – Water	1159.32	7	4.169	2.411	22.956	3.599
Ecoregion	9 – Water	1228.78	7	4.499	2.436	28.266	4.256
Two-stage	1 – Jack Pine	7069.57	59	14.610	2.243	30.511	4.454
Ecoregion	1 – Jack Pine	3031.08	43	3.260	2.222	20.906	5.097
Two-stage	2 – Conifer	2784.96	48	1.819	2.371	9.826	2.580
Ecoregion	2 – Conifer	1952.57	48	1.647	2.203	6.659	1.532
Two-stage	3 – Deciduous	10727.38	98	15.673	2.350	28.372	2.755
Ecoregion	3 – Deciduous	13267.45	49	25.366	2.633	41.678	2.072
Two-stage	5 – Shrub Fen	2302.82	25	2.653	2.662	12.944	3.440
Ecoregion	5 – Shrub Fen	4221.02	25	9.530	2.421	33.118	4.232
Two-stage	6 – Grass Fen	1663.87	43	1.184	2.198	9.081	2.052
Ecoregion	6 – Grass Fen	1421.32	21	3.234	2.428	17.410	2.282
Two-stage	4 – Bog	97.95	4	0.272	2.053	6.406	2.720
Ecoregion	4 – Bog	116.48	5	0.124	2.003	0.000	0.000

Table 2.7 Landscape metrics derived from subset landscape, Landsat scene 43-19 (Figure 6), minimum mapping unit is 4 hectares. Selected metrics include: NP, Number of Patches; LPI, Largest Patch Index; MPS, Mean Patch Size; MPFD, Mean Patch Fractal Dimension; SIDI, Simpson's Diversity Index; CASD1, Core-Area Standard Deviation.

Classification	NP	LPI	MPS	MPFD	SIDI	CASD1
Ecoregion	202	25.366	125.450	1.332	0.809	270.229
Two-stage	287	15.673	90.307	1.332	0.811	141.423

The results from MDA are presented in an ordination diagram with variables represented by vectors leading away from their origin; the ability of each variable to explain variation in the analysis is represented by the distance between them, similar to the diagrammatic output of principle components analysis. Jack pine was selected because of its relatively large ecological amplitude. Data, in this case spectral data from ecosites, are grouped *a priori* by ecoregion. Jack pine data from three ecoregions that held a large enough sample size to warrant analysis are presented here. The ordination diagram displays the 95% confidence ellipsoids around each group; significant differences exist when the ellipsoids do not overlap. There were significant ($\alpha = 0.05$) spectral differences between Jack Pine communities in the Slave River Lowlands and those in the Tazin Uplands and the Athabasca Plain (Figure 2.4). Further, although there appear to be differences between plant communities in the Tazin Uplands and the Athabasca Plain, these differences were not significant ($\alpha = 0.05$) as the 95% confidence ellipsoids overlap in Figure 2.4. Intra-class spectral variation in this plant association can then be at least partly explained by some ecological regions. Since this approach is used to assess the real differences among groups we can say that, although some ecological regions exhibit high variance and a number of outliers, there are statistically significant differences between some similar plant associations in different ecoregions. Jack Pine has the ability to grow in a wide range of environmental conditions; they have a large ecological amplitude (Beckingham & Archibald 1996). Jack Pine will form an open or closed canopy with a wide range of possible understorey conditions. This amplitude means that although these plant associations or species-structural groups might fit in to one or two informational classes, there will be tremendous variance (in terms of plant community composition and spectral response) in each class. The MDA demonstrates that some of this intra-class variance can be explained by ecoregion.

5.0 Conclusions

Image segmentation using ecological regions and two-stage classification can be effectively used to improve the results of land cover classification. A classification scheme based on ecological units, ecosites or vegetation communities can be used to created informational classes for a land cover map that are meaningful and broadly applicable. Ecological regions are a means of explaining the spectral variance within informational classes and predicting their occurrence within a scene. Species with a large ecological amplitude such as Jack Pine (*Pinus banksiana*) or Black Spruce (*Picea glauca*) are examples of species within informational classes that contain a large amount of spectral variation. Understanding the environmental conditions in which these species are likely to be found is a key to predicting and mapping their distribution. The two-stage approach to unsupervised classification seems a reasonable technique for improving the results of classification in boreal environments. Ecological regions can also be used to stratify data collection during field sampling. Collection of this type would be more spatially distributed. Conceivable it could require at worst no more training sites than usual collect. The prime advantage to this approach is that the training data would be more spectrally representative and exhaustive. Finally, given the spatial, spectral and radiometric properties of the Landsat sensor the ecosite can be conceived as the minimum mappable unit. A clearer definition of the minimum mappable unit can help the remote sensing community to better define the object under investigation. Further, using the ecosite as the MMU can clarify the relationship between remote sensing classification and traditional ground-based vegetation classification.

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Chapter 3

Landscape scale resource selection by wood bison (*Bison bison athabascae*)

1.0 Introduction

Conservation and management of wildlife requires a quantitative understanding of the link between species and environment. Generalized Linear Models (GLM), Geographic Information Systems (GIS), remote sensing and model assessment using Akaike Information Criteria (AIC) are tools through which ecologists come to understand the relationship between the distribution of species and their environment (Rushton et al. 2004). The use of information-theoretic approaches comprise a paradigm shift by which ecologists develop the conceptual framework of these species-environment linkages and test the most parsimonious models. A quantitative linkage describing the species-habitat relationship underlies our understanding of the ecological requirements of a species. An understanding of the functional species-habitat relationship is required to ensure that key habitat attributes can be managed so as to protect them from the consequences of human land-use activities. This is especially true in the case of rare or endangered species.

The development of predictive models of habitat use is dependent upon the use of biologically relevant correlates of resource selection and proper determination of the spatial and temporal scale at which resource selection occurs. The multi-scale structure of resource selection has been identified as an important consideration in ecological investigations (Wiens 1989). Hierarchy theory provides the context in which we understand that higher spatial or temporal scales in ecology in some way regulate the behaviours of systems and organisms at lower levels (Allen & Starr 1982). Johnson (1980) provides a rough approximation of the species-specific cut-offs for the levels of the hierarchy in the ecological context: first-order being the geographical range of a species; second, the home-range; third, habitat components and finally; fourth, the food items consumed. At each level in this hierarchy choices are made based on different criteria. Significant predictor variables at lower levels will not likely prove effective at predicting resource use or distribution at higher levels.

Classical foraging theory and energy maximization principles are often useful tools for predicting resource use by ungulates at fine spatial scales (<1ha). However, at larger spatial scales Fortin et al. (2003) found that landscape physiognomy – the size and physical layout of landscape patches was a stronger predictor of meadow use by plains bison (*B. b. bison*) in the aspen parkland and boreal forest of Saskatchewan. Landscape physiognomy includes measures of contagion, composition and complementation (Dunning et al. 1992). With respect to foraging behaviour, wood bison were found to use different foraging strategies at different temporal scales, acting as energy maximizers at the shortest scale and time minimizers over the longest temporal scales (Bergman et al. 2001). In a study of moose in Alaska, Erickson et al. (1998) determined that resource selection for moose is more than a function of forage availability. Parker (2003) suggested that the linkage between the lower and upper scales of selection is not simply a linear combination of lower scale selection processes. These linkages were moderated by tradeoffs between a large number of ecological factors. Johnson et al. (2001) revealed an incongruity between selection for all ungulates studied at the feeding site, where biomass and snow depth determined selection, and at the patch scale where the same factors could not explain a significant proportion of the observed variation. Boyce et al. (2003) demonstrated with elk in Yellowstone NP that there are different determinants of selection at different spatial scales. At the largest spatial scales abiotic factors such as Site Severity Index and elevation are greater predictors of use than simple forage availability. In a similar study Pearson et al. (1995) found that while habitat type was a good predictor of distribution at the finest spatial scale (1ha), abiotic factors such as burn status and topography were better predictors of use at larger scales (225ha).

Resource selection functions are a useful statistical modelling tool since they can incorporate variables from a number of spatial scales (Boyce et al. 2003). The former studies indicate that resource selection can be measured at any spatial or temporal scale. However, a model of resource selection that is to be useful for management and conservation must consider selection at the lowest scales, the landscape features that constrain the use and selection of resources, as well as the management and policy context at the highest spatial scales. The interplay of these scale-effects, both ecological, political and administrative will determine the usefulness of any model developed for conservation and management.

Wood bison (*Bison bison athabascae*), are a large grazing ungulate that are listed as a threatened species in Canada (COSEWIC 2004). Bison select resources within a hierarchy of spatial scales (Johnson 1980). At the smallest spatial scale, fourth-order selection, bison select slough sedge (*Carex atherodes*), and seasonally select northern reed-grass (*Calamagrostis canadensis*) to satisfy their daily energetic requirements, and they select meadows dominated by these plants (Reynolds et al. 1978, Larter & Gates 1991, Fortin et al. 2002). Meadow selection comprises third-order selection and includes selection of other plant communities including deciduous forest, which are used for resting, ruminating and avoiding biting flies (Reynolds et al. 1978). Second-order selection, the selection of the home range is influenced by the cumulative contributions of such factors as distance to water (Fortin et al. 2003), patch size (Reynolds et al. 1978), and the type of plant community found proximate to a patch of forage habitat. Finally, first-order selection includes the selection of specific landforms that are conducive to the production of forage habitat. In the study area, this landform is the lake-bed of glacial lake McConnell whose poorly-drained alluvium create the proper growing conditions for sedges and grasses (Carbyn et al. 1993).

In this paper we endeavour to create a predictive model of habitat use by analysing distribution data obtained in WBNP and by testing the model in the Mackenzie bison range. We aim to assess resource selection at multiple spatial scales and demonstrate that measures of landscape physiognomy can be useful predictors of resource use. We will develop a conceptual model of habitat use from a review of the literature relevant to bison. This conceptual model will guide the selection and development of resource variables and covariates obtained from an unsupervised classification of Landsat Thematic Mapper satellite images and subsequent analysis of this classification using landscape pattern analysis. Models will be assessed using AIC and the final model will be first assessed using k-fold cross validation and further evaluated using out-of-sample validation.

Our assessment of resource selection is significant for conservation of the species because we assess selection at multiple ecological, political and administrative scales simultaneously to create a model of habitat use at the landscape scale. Since conservation decisions related to reintroduction and restrictions on resource extraction are made at this scale a model of selection applicable at the landscape will enable managers to make rational and informed decisions.

2.0 Study Area

The study area encompasses the remnant distribution of wood bison since the early 1900's (Figure 3.1). Wood bison are though to have at one time been patchily distributed across the boreal forest. By the turn of the 19th century hunting had reduced continental populations of both plains and wood bison to less than a few hundred animals. What wood bison remained where found north of Claire Lake in what is now Wood Buffalo National Park and south of Great Slave Lake, primarily in the Slave River Lowlands. The study area is dominated by WBNP straddling the Alberta and Northwest Territories border and the Mackenzie bison range in the Northwest Territories. The large region (>60 000km^2) is nearly uninhabited, fire and flooding are the dominant processes on the landscape. Geographically, the study area is a broad plain broken by glacial features such as kames and eskers and bounded by the Caribou and Birch mountains to the west and south, the Athabasca Plain and Kazan Uplands, regions of Canadian Shield to the east, and Great Slave Lake, the Peace-Athabasca and Slave River Deltas. Ecologically, the study area represents a large and intact portion of the Boreal Mixedwood forest and includes portions of Boreal Highlands in the Birch and Caribou Mountains, Canadian Shield and Subarctic forest to the east and north (Beckingham & Archibald 1996).

The unifying geological feature of bison range within the study area is the bed of glacial lake McConnell, a deep layer of alluvium overlying glacial till (Rowe 1972). The soil conditions and hydrology have created the proper growing conditions for sedge meadows which form the core of winter habitat for wood bison (Raup 1935; Carbyn et al.

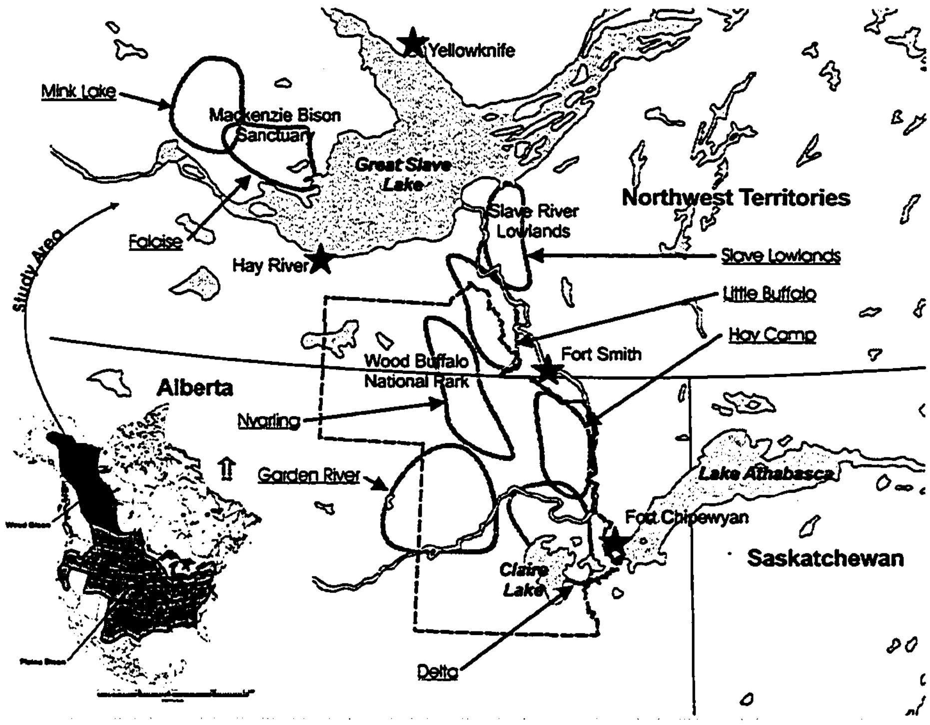

Figure 3.1 The study area including approximate boundaries of bison populations mentioned in the text and the historical range and distribution of plains and wood bison (Gates et al. 2001).

1993). Periodic flooding and changes in sub-surface water levels help maintain the grass communities with the assistance of frequent fires (Quinlan et al. 2003). Historically, bison roamed the boreal forest utilizing sedge and grass meadows. After the introduction of more than 6000 plains bison from Buffalo National Park (now Canadian Forces Base, Wainright) during the period from 1923 to 1928 bison were also found in the Peace-Athabasca Delta (Fuller 2002, Carbyn et al. 1993). Fur post and explorer records up to this time had never recorded bison in the Delta and their utilization of the large expanses of sedge and grass meadows is a recent phenomenon. Bison occur in a diversity of habitats in this study area including jack pine (*Pinus banksiana*) forests in the central part of the range; grass dominated fens and meadows throughout but especially in the Mackenzie Bison Sanctuary and the expansive alluvial Peace Athabasca Delta.

3.0 Methods

We modelled habitat selection using logistic regression in a used/available design (Manly et al. 2002) using positional data obtained from aerial survey and telemetry relocation data and random locations generated in a Geographical Information System (GIS). Through an unsupervised classification of Landsat imagery using training data we created a digital land cover map (Jensen & Sánchez-Azofeifa, submitted). We created a digital elevation model, terrain ruggedness index, distance to water grid, and digitized soils maps for inclusion as covariates in the analysis. Landscape metrics generated from the resources grid using FRAGSTATS include distance, density, class area, contagion and interspersion metrics (McGarigal et al. 2002). Resource variables and covariates

Table 3.1 Ecological land-cover classification scheme. Ecosite phase and plant community types are taken from Beckingham & Archibald (1996). Ecosite class combines these very fine community types into classes that are ecologically similar and land cover classes are broad groupings of ecological communities based on functional or physiognomic similarity. Alpha-numeric codes under the ecosite phase column can be cross referenced to Beckingham & Archibald (1996).

Land Cover Class		Ecosite Class	Ecosite Phase and Plant Community Type		
1	Jack Pine Dominated	Jack Pine Dominated	a1	Pj lichen	
			c1	Pj-Sb	
			b1	Pj-Aw blueberry	
		Regenerating Jack Pine			
2	Other Conifer	Black Spruce Dominated	g1	Sb-Pj hygric	
			d3	Cranberry Sw	
			e3	Dogwood Sw	
			f3	Horsetail Sw	
		Conifer	b4	Sw-Pj	
3	Deciduous	Deciduous	b2	Aw(Bw) submesic	
			d1	Aw cranberry	
			e1	Pb-Aw dogwood	
			f1	Pb-Aw horsetail	
		Deciduous Dominated	b3	Aw-Sw blueberry	
			d2	Aw-Sw cranberry	
			e2	Pb-Sw dogwood	
			f2	Pb-Sw horsetail	
4	Bog	Tamarack	k1	Treed rich fen	
		Open Black Spruce	j1	Treed Poor Fen	
		Shrubby Bog	i2	Shrubby Bog	
		Treed Bog	i1	Treed Bog	
		Shrubby Poor Fen	j2	Shrubby Poor Fen	
5	Shrub Fen	Shrubby Rich Fen	k2	k2.1	Dwarf Birch, Sedge, Willow
			k2	k2.2	Willow, Sedge
			k2	k2.3	Willow, Calamagrostis
6	Grass Fen	Graminoid Fen	k3	k3.1	Sedge Fen
			k3	k3.2	Marsh Reed Grass Fen
		Grasslands	Rare True Grasslands		
7	Wetlands	Wetland	l1	l1.1	Cattail Wetland
			l1	l1.2	Reed Grass Wetland
			l1	l1.3	Bullrush Wetland
8	Not Vegetated	Mud			
		Sand			
		Rock			
9	Water	Water			
10	Anthropogenic	Urban Residential			
		Urban Commercial			
		Access Major			
		Access Minor			
		Agricultural Cropland			
		Agricultural Pastureland			
		Cut Block			
11	No Data	NA			
12	Burn	Burn			

considered in the analysis are summarized in Table 3.2. K-fold cross validation was used to validate the habitat use models and further validation was obtained by generating probability of use maps outside the study area (Boyce et al. 2002, Huberty 1994).

3.1 Positional Data

Telemetry data were provided by Joly (2001), which were collected as part of a disease study measuring the apparent prevalence of tuberculosis and brucellosis in bison in WBNP and the growth-limiting effects of these diseases on the population. These data were supplemented by data from WBNP, from a movement and distribution study (unpublished data, 1998) and the Mackenzie Bison Sanctuary (Larter 1988). Aerial survey data were obtained for the Mackenzie Bison Sanctuary, Slave River Lowlands and WBNP from the Department of Resources, Wildlife & Economic Development (RWED),Government of the Northwest Territories and Wood Buffalo National Park, respectively. Approximately 7,700 telemetry relocations and 9,500 aerial survey locations were incorporated into the study as used locations and we generated 30,000 random points in order to define availability.

To account for spatial inaccuracies introduced from telemetry relocations, air and telemetry relocations, mapping errors and map errors, we calculated resource variables as the percentage of each resource class within a 300m buffer around each relocation (Erickson et al. 1998). A better estimation of total variability is obtained using this method (Samuel & Kenow 1992). We assigned covariate values directly to the point locations in the used data set since these covariates were found to have less spatially-related variance. 30,000 points were randomly seeded along a uniform distribution restricted to within 100 metres of the polygon boundary and greater than 100m of other points. Available points were not allowed to fall within 300m of used points; this reduced the overall variance in the dataset.

Following King & Zeng's (2000) recommendation we assessed variance by measuring the change in standard error with an increasing ratio of used to available points. Variance stabilized to less than one standard error as the number of available points exceeded two hundred (Figure 3.2). Statistical modelling of resource selection in SAS employed all used points for Wood Buffalo National Park (telemetry and aerial survey data) and over 30,000 available (randomly generated) points. We executed a Pearson paired correlation on all the covariates. When significant correlation (r^2>0.75) was found we dropped one of the pair of correlated variables from the modelling process (n=4).

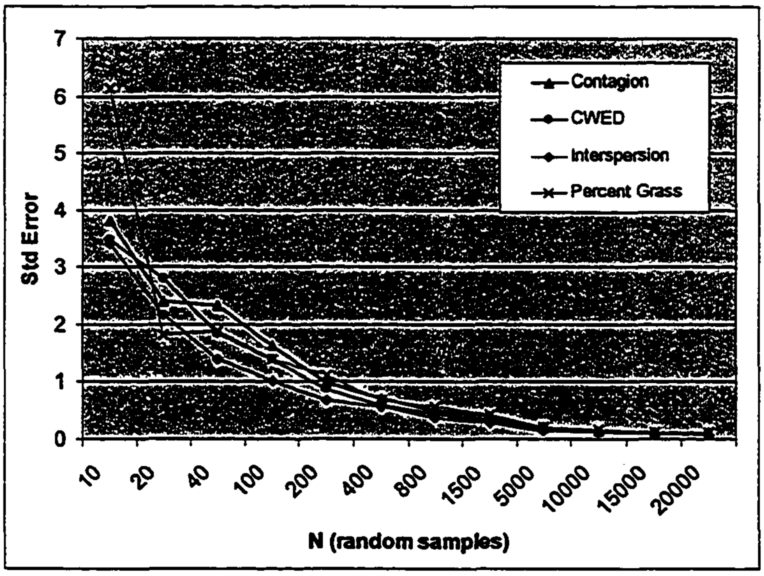

Figure 3.2 Change in variance as measured by standard error for selected variables. The metrics Contagion, Contrast-Weighted Edge Density (CWED), Interspersion, and Percent Grass are represented in the figure.

3.2 Delineation of populations

Populations are defined here to be spatially, genetically or demographically disjunct groups of animals; and meta-populations are understood to be spatially disjunct with some demographic or genetic connection (Wells & Richmond 1995). We used agglomerative hierarchal clustering (Podani 2001) to delineate populations of bison in the study area using median seasonal locations of each collared bison in the meta-population (Joly 2001; Taylor et al. 2001). We divided the data by season and generated dendrograms from agglomerative hierarchal clustering. We identified groups of bison from the dendrograms through qualitative analysis of the branches. Seasons were demarcated as Winter, November 7th to May 4th; Spring, May 5th to June 30th; Summer, July 1st to August 31st; and, Fall, September 1st to November 6th (Carbyn et al. 1993). As with Joly's (2001) analysis, we identified five distinct populations within the WBNP meta-population; Delta, Sweetgrass, Garden River, Little Buffalo and Nyarling (Figures 3.1 and 3.3). We recognized the subjective nature of the dendrogram analysis (Taylor et al. 2001). For each bison where n>20 in each season we calculated seasonal home ranges using 95% fixed-kernel home range method (Otis & White 1999). The sampling period and interval is felt to adequately capture the complete normal movements across each individual bison's home range and complications relating to auto-correlation should therefore not apply in these home range calculations (Otis & White 1999). We calculated annual home ranges from the overlay of these seasonal ranges and subsequently calculated population boundaries from the overlay of all seasonal home ranges for bison assigned to each population.

3.3 Defining resources and predictors of use

In this study resources are conceived as communities of plants called ecosites, which are ecological communities defined as *"a plant community of definite floristic composition, uniform habitat condition and uniform physiognomy"* (Ponomarenko & Alvo, 2002). Using Landsat 7 TM imagery we created a digital map of resources from a hierarchal, unsupervised classification. Training data was used to guide the classification process with radiometrically-corrected Landsat imagery that was segmented by ecological region. Classification was performed within each ecoregion and the resulting classifications were merged into a seamless grid for the entire study area (Jensen & Sánchez-Azofeifa, submitted). Prior to classification we created an element-based phytotopological classification scheme based on Beckingham & Archibald's (1996) "Field guide to the ecosites of Northern Alberta", which is relevant to the study area. From the agglomeration of functional groups of ecosites we created a resource map of twelve landcover classes; these were: jack pine, conifer, deciduous, bog, shrub fen, grass fen, wetlands, non-vegetated, water, anthropogenic, no data, and recent burns (Table 3.1).

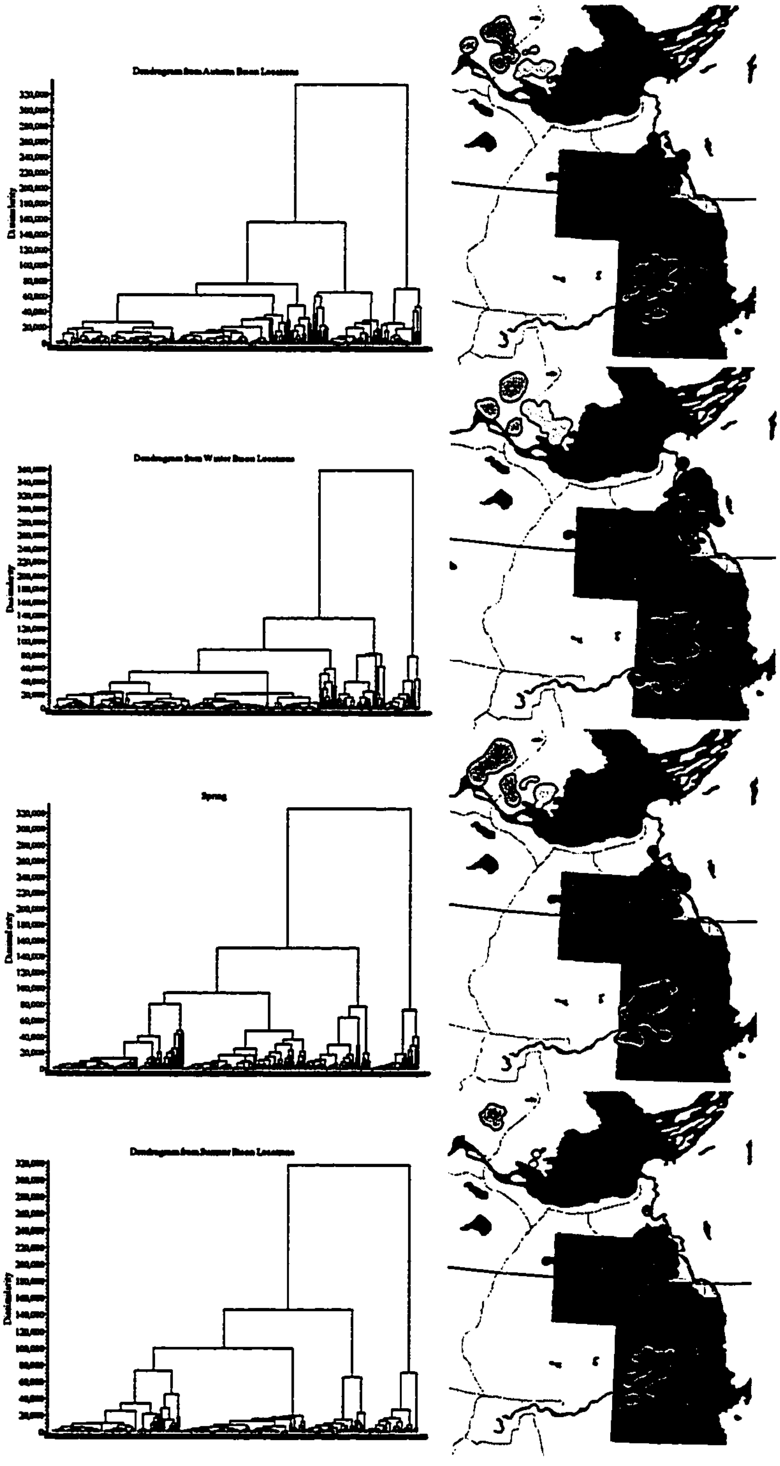

Figure 3.3 Dendrogram output from agglomerative hierarchal clustering and population boundaries by season for Wood Buffalo National Park, the MBS and the Slave River Lowlands. From top to bottom: fall, winter, spring and summer. Winter population boundaries for the Slave River lowlands were obtained from aerial survey data only.

Table 3.2 Resource variables and covariates considered for inclusion in Resource Selection Function (RSF) modelling.

Code	Covariate name	Description
Classification Variables		
ID	Observation ID	From bison observation database
Easting	X Location	Easting in UTM NAD83 Zone 12
Northing	Y Location	Northing in UTM NAD83 Zone 12
Used	Used	Used or Available location
Type	Type of Point	*Random, Telemetry or Aerial Survey Point*
Bison	Bison ID	Taken from field data tables
Group	Population	Population to which the individual is assumed to belong
GrpSize	Group Size	Observed group size at time of relocation
Season	Season	Season of observation
Patch Variables (Active Selection)		
Eco12	Land cover class	12 class Ecological Land Cover
Perimeter	Perimeter	Patch Perimeter
Area	Patch Area	Total size of the patch, regardless of landscape size
Fractal	Fractal Dimension	Patch fractal dimension
Rugged	Terrain Ruggedness Index	Local topographic variation derived from a 1:50 000 DEM
Local Landscape Variables (Active / Passive Selection)		
Elev	Elevation	Elevation derived from 1:50 000 DEM
Contag	Contagion	Measure of landscape homogeneity
Cwed	Contrast Weighted Edge Density	Quantity of edge for each landscape, weighted by type
Ed	Edge Density	Unweighted measure of edge density
DW	Distance to Water	Distance to nearest water source
Sidi	Simpson's Index of Diversity	Measure of landscape diversity
Per1-12	Percentage	Percentage of cells within 300m buffer around points
Ca1-12	Class Area	Class area for each class in the landscape
Clumpy1-7,9	Clumpiness	Measure of the proximity of similar patch types
Cwed1-7,9	Contrast Weighted Edge Density	Weighted edge density for each patch type
Enn1-7,9	Euclidean Nearest Neighbour	Straight-line distance to patch of same class
Frac1-7,12	Fractal Dimension	Measure of complexity of local landscape
Iji1,3-7,12	Interspersion Juxtaposition Index	Interspersion for class type
Pd1-7,9,12	Patch Density	Patch density for each class type
Teci1-6,12	Total Edge Contrast Index	Calculated for each class within the landscape
Iji	Interspersion Juxtaposition Index	Measure of landscape homogeneity
Landscape Variables (Passive Selection)		
SC	Soil Class	Slave River Lowlands soil class from 1974 survey

We agglomerated ecosites in order to improve the performance of RSF modeling by limiting the number of habitat types in the model to reduce overall variance (Alldredge & Ratti 1992). We re-sampled the digital ecosite map to create an integer grid whose pixel size is equal to one hectare and analysed the grid in FRAGSTATS v3.3 to create landscape physiognomy covariates for analysis (McGarigal et al. 2002). By passing a circular moving-window with a radius of 2000m over each cell in the resource grid and calculating landscape metrics within this window we calculated resource covariates; returning the subsequent landscape metric covariates to the cell at the centre of the window. We set the size of the window to approximate the average daily movement of a bison (Fortin et al. 2003). Additionally, we created a digital elevation model (DEM) from 1:50 000 digital topographic maps and a derived terrain ruggedness index map from the DEM. We obtained a 1:250 000 scale digital elevation model from Natural Resources Canada via GeoBase (http://www.geobase.ca) for the Mackenzie Bison Sanctuary (Table 3.1).

3.4 Modelling resource use with logistic regression

"*Habitat selection is usually a behavioural consequence of animals actively selecting where they live, or passively persisting in certain habitats*" (Boyce & McDonald 1999:268). A conceptual model of habitat selection by wood bison is presented in Figure 3.4. Abiotic factors, landform, elevation, distance to water, terrain ruggedness determine distribution at the highest levels while physiognomic and forage factors determine occupancy at the lowest levels. Active foraging decisions set within the context of optimal foraging theory determine occupancy within the patch, feeding site and camp (Bailey et al. 1996) while the distribution, quantity and quality of forage patches as well as landscape physiognomy determine persistence of an individual or group within the region. At the lowest levels resource selection is active, an individual bison or herd makes decisions about what plant it consumes and in what patch it will do so. Resource selection at this scale follows an energy maximization strategy (Bergman et al. 2001) and a simple gain function can be used to determine the value of a patch (Stephens & Krebs 1986). At larger scales bison behave as time-minimizers since their foraging behaviour is constrained by biting flies, predation risk and movement decisions made by the herd, to name a few. Notwithstanding these conflicting demands, long-term average rate-maximizing is the goal in order for the individual to maximize it's fitness (Stephens & Krebs 1986).

Persistence in a landscape depends on a landscape containing the necessary forage resources and landscape covariates to maximize its fitness over the long term. The marginal value theorem is one way to conceptualize and model the landscape metrics that might lead to an increased fitness and persistence. Marginal value theorem predicts that patches further away must be larger or more productive to be used in order to justify the energetic cost of movement through the intervening matrix of habitats. This conceptual model of fitness helped us to determine the biological relevance of the resulting models.

Resource Selection Functions (RSF) are a statistical tool for modelling the probability of use of a given resource given the properties of its covariates. We used logistic regression, a form of the Generalized Linear Model (GLM) to model habitat selection. Prior to analysis we created biologically plausible models based on a review of the literature relevant to wood bison in North America. Aikake Information Criteria (AIC) coefficients generated from full-model logistic regression in SAS were used to assess the models. We ran logistic regression models on the full dataset, and on subsets of the data grouped by season, by population and by observed group size. We created a conceptual model of habitat use, which incorporates foraging and hierarchy theory, and used this to create biologically-plausible models (Figure 4). We chose the most biologically-plausible model with the lowest AIC score as the best model and compared the stability of beta coefficients generated from logistic regression between subsets. Models that were rejected because they were not biologically-plausible were those that consistently showed selection for or avoidance of resources that have been documented in refereed journals. (Soper 1941, Fuller 1960, Fuller 1961, Reynolds et al.1978, Krasińska et al. 1987, Gates & Larter 1990, Larter & Gates 1991, Fortin et al. 2003). The model with the lowest AIC score across all subsets was subsequently chosen for k-fold and out-of-sample validation.

3.5 Model validation: *K* fold cross validation

We used k-fold cross validation to evaluate the predictive success of the resultant best model. Using this technique we divided the training and validation database (n=46,283) into four k-fold sets. We created an RSF for each set, each time withholding the n^{th} group. To assign probability values to each point in the n^{th} withheld group we used the probability surface generated from the RSF. To assess the quality of the RSF function we partitioned the testing set into bins containing roughly equal numbers of testing points and performed a Spearman-rank correlation between ranked bins and area-adjusted frequency of cross-validated use locations (Boyce et al. 2002). Using data from the Mackenzie Bison Sanctuary we performed predictive (out of sample) validation. As outlined above, we used classified Landsat TM data, a DEM and covariates derived from FRAGSTATS to created similar resource variables and covariates for the Mackenzie Bison Sanctuary. We assigned values from a probability of use map

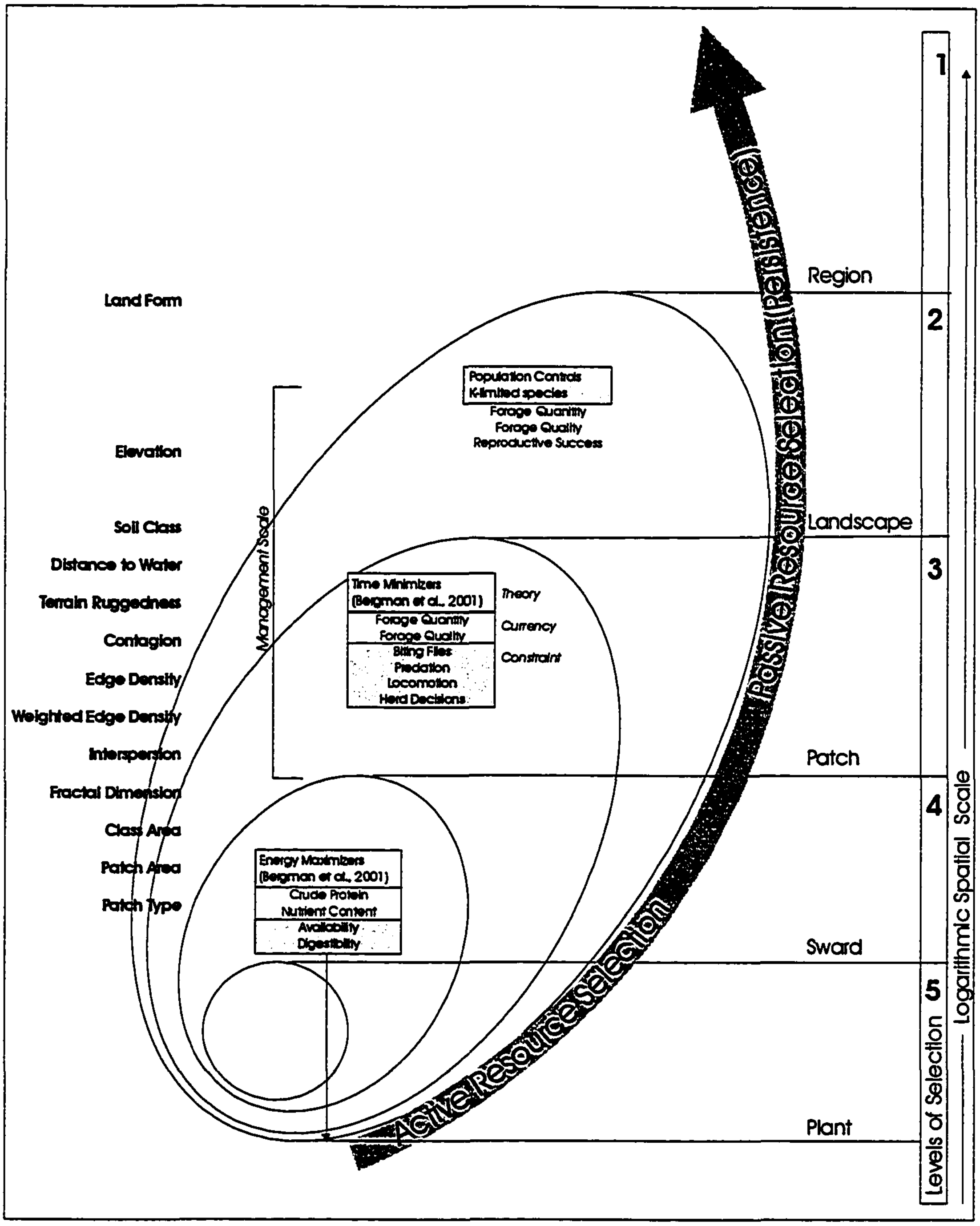

Figure 3.4 Conceptual model of habitat selection by wood bison. Johnson's (1980) levels of habitat selection are presented on the right side of the figure. Predictor variables are listed on the left side of the figure in relation to the scale at which they are applicable.

created using RSF models generated from the WBNP data to evaluate the predictive value of the model.

Using telemetry and aerial survey data obtained in the MBS we evaluated the predictive abilities of the final map through out-of-sample validation. We created a Habitat Suitability Index for the MBS using methods described above with data obtained using parallel methodology. Using the grid surface and point data in a GIS we obtained RSF values for each used location in the new area. We visually assessed the distribution of used locations over the categorical HSI map (Figure 3.8) and assessed the area adjusted frequency of used bison locations falling within ranked bins with the same dimensions as those used with the WBNP data.

4.0 Results

Agglomerative hierarchal clustering of median seasonal locations of bison indicates two discrete meta-populations, one within the Mackenzie Bison Sanctuary and a second in Wood Buffalo National Park (Figure 3.3). Analysis of dendrograms and home range maps suggest that no clearly demarcated populations of bison in the Mackenzie Bison Sanctuary but rather there are shifts in seasonal use of the range in this area. Mackenzie data are limited to telemetry data collected in 1992. The Mink Lake and Falaise herds are named for convenience only – analysis of the dendrograms in Figure 3.3 suggest plasticity in range boundaries. Falaise and Mink Lake herds, which form the Mackenzie Bison Sanctuary can be seen as the second main branch on the right side of the dendrogram. Analysis of dendrograms and home range maps for WBNP suggest five discrete populations of bison. Joly (2001) identified the same five spatially-discrete populations of bison. Although range overlap does exist for some populations, especially Delta, Sweetgrass and Garden River - these populations can be seen on the left side of the dendrograms and are clearly separated from the central branch of the dendrogram, which accounts for the Nyarling and Little Buffalo populations. In addition range overlap is a function of unusual movement vectors of <5% of individuals monitored in any population. Larter and Gates (1991) found that for bison in the MBS, mature females and young of the year males had larger home ranges than mature males, although these boundaries were found to be relatively stable. Older males are less likely to be associated with other groups of bison so they may restore body condition during the breeding season which results in longer movement trajectories (Komers et al. 1992). However, sporadic long distance movements have been observed in both males and females in WBNP. A 1995 Bison Movement and Distribution Study (WBNP unpublished data) found a female to have travelled some 80km between summer and winter ranges, and in one 15 day relocation period a bull was observed to have travelled 125km.

Proportional use of habitat was assessed for each population within the WBNP meta-population. Although general statements can be made about resource selection over the entire study area as measured using selectivity indices, resource selection appears to differ between populations and does change seasonally (Figure 3.6). In all populations, bison make use of grass and shrub fens, presumably for forage and use deciduous and jack pine forest for resting, ruminating and seasonally for forage. Proportional use of these resources changes

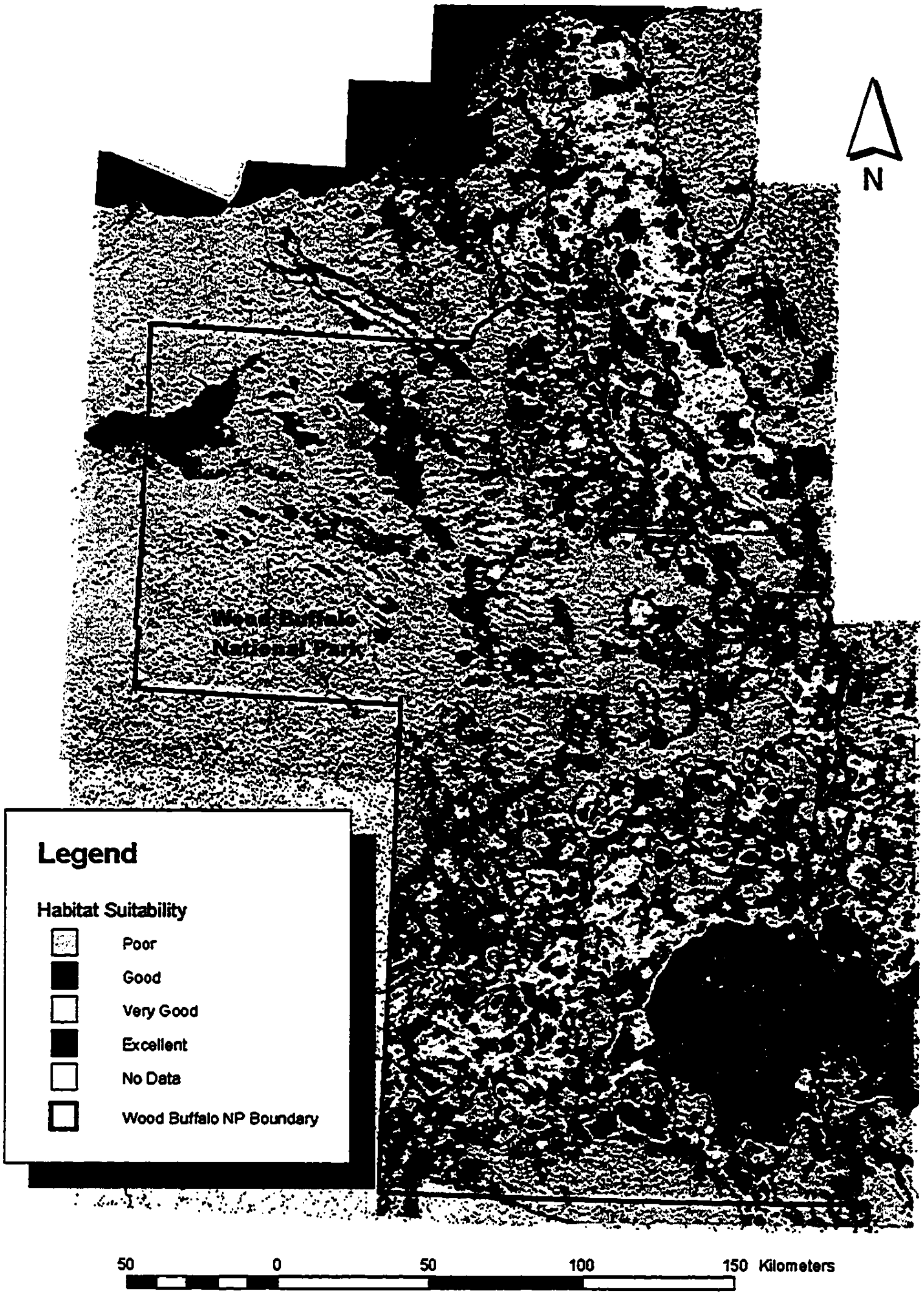

Figure 3.5 Categorical habitat suitability map developed from a resource selection model and resultant probability surface for Wood Buffalo National Park and the Slave River Lowlands.

seasonally: all populations use forage resources (grass and shrub fens) but especially so in the spring. Shrub fens are used increasingly in the fall. Deciduous forests are used more in the summer and for the Nyarling population jack pine forests are used in lieu of deciduous forest. Significant selection for deciduous forest, sedge and reed-grass fens was found for the Hay Camp population; selection for shrubby rich fens was not statistically significant at $\alpha=0.05$. The Little Buffalo population selects for deciduous forest more than would be expected by chance alone, grass fens and wetlands are not used more than would be expected by chance alone. However, the home range of this population contains a significant amount of reed grass and wetlands (40,058ha or 114ha per bison) so it can be assumed that selection for these habitat types are being made at the landscape scale. The Garden River population also selects for deciduous forests but appears to avoid ecosites classified as reed grass fens. Finally, the Delta population uses reed grass and sedge fen disproportionately to availability, surprisingly, since this area is dominated by large expanses of these ecosites. We assessed seventeen models using full-model logistic regression in SAS (Table 3.3). Biologically relevant and parsimonious models were created from a review of the literature (Burnham & Anderson 2001) and following the establishment of a conceptual model of habitat selection (Figure 3.4). Since simple null hypothesis testing is not as informative as testing multiple hypotheses we used AIC as the assessment criteria. Evaluation of model robustness is facilitated by the measure

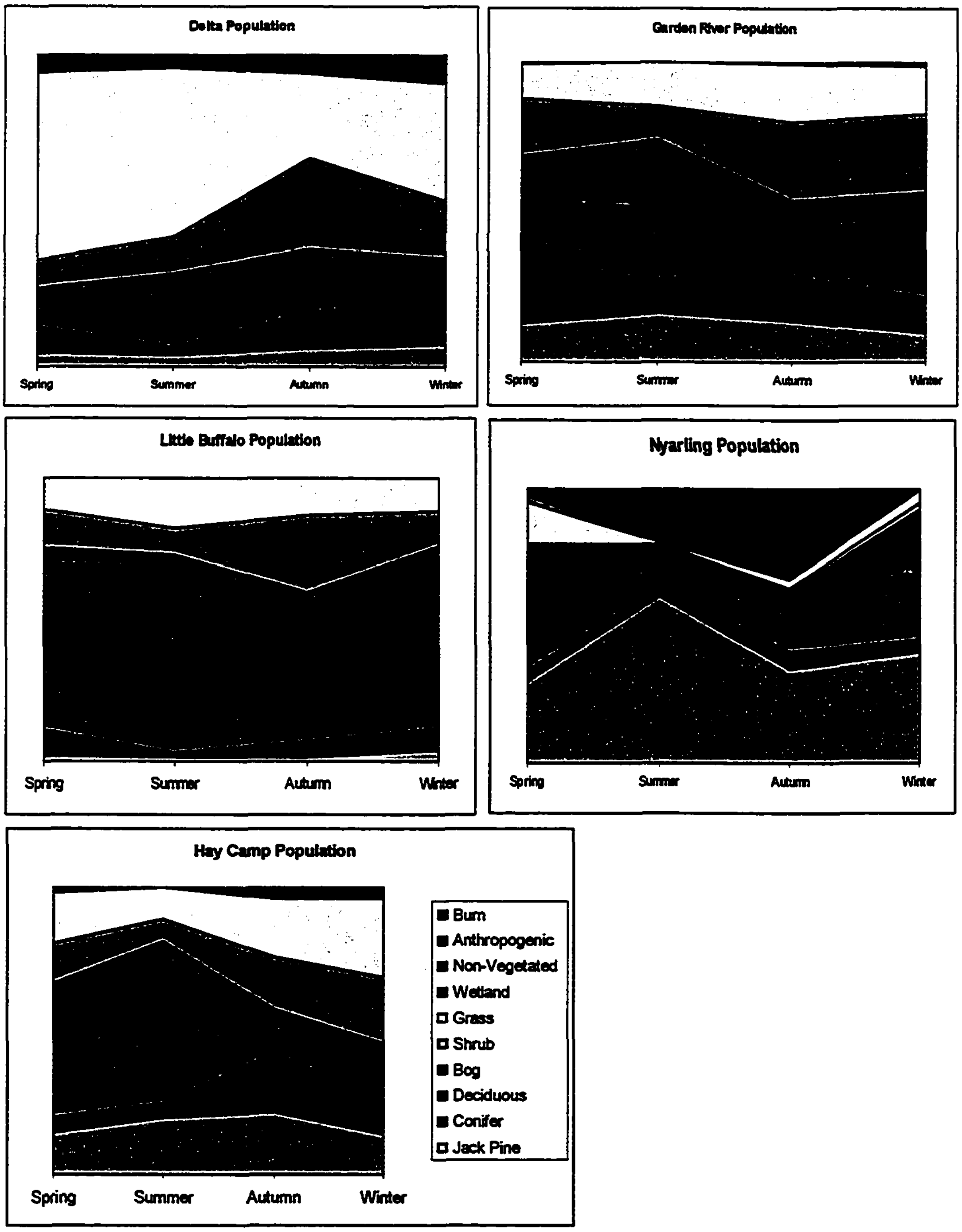

Figure 3.6 Seasonal changes in habitat selection for each population in Wood Buffalo National Park. Frequency of observations for each season by population.

of information loss inherent to AIC (Anderson et al. 2000). Model 17 (AIC = 1307.94) was selected for k-fold and out-of-sample validation. We rejected other models with lower AIC scores because, despite the fact that they apparently accounted for more of the variation in the data they contained biologically implausible results or SAS returned warnings due to insufficient data for all variables, or were later determined to have sacrificed plausibility for parsimony. Models containing the variables Patch Density (PD), Euclidean Nearest Neighbour (ENN), and Class Area (CA) for specific classes had to be excluded because the results depended on the landscape containing the variables of interest. Low AIC scores inevitably resulted from the analysis of these models because of the resultant restriction of the dataset. Models containing Simpson's Index of Diversity (SIDI) were later dropped. SIDI consistently appeared to be a good predictor of use but no biologically reason could be found to explain SIDI as a predictor variable. To examine the effect of ignoring telemetry relocation error in the modelling process we evaluated Model 2. The AIC score for this model was significantly higher as a result. Further, although the percentage of resources contained in a 300m buffer around used and available points is significantly correlated (Pearson r^2>0.75) with the class area within a 2000m radius, a model using only percentage resource use within the larger buffer explained much less variance and had a larger AIC score. Models 16 and 17 are two comparable models with low AIC scores and biologically sensical results. Each contains some measure of local resource selection (within 300m of a location), a measure of forage habitat within a single day's travel (2000m), and some measure of friction to movement.

Table 3.3 Models assessed using full-model logistic regression in SAS and the resulting Akaike Information Criteria (AIC) scores.

Model	***Resource Variables and Covariates***	AIC
1	per1 per2 per3 per4 per5 per6 per7 per12 DW TRI PA	973.20
2	eco12 DW TRI PA	32608.21
3	per1 per2 per3 per4 per5 per6 per7 per12 DW TRI PA PD2 PD4 PD5 PD6	756.49
4	per1 per2 per3 per4 per5 per6 per7 per12 CWED CONTAG IJI PA PD2 PD4 PD5 PD6	888.72
5	CA1 CA2 CA3 CA4 CA5 CA6 CA7 CA12 CWED CONTAG CLUMPY5 CLUMPY6 ENN5ENN6	16413.67
6	per1 per2 per3 per4 per5 per6 per7 per12 CWED CONTAG SIDI	706.59
7	per1 per2 per3 per4 per5 per6 per7 per12 ED CONTAG SIDI	661.16
8	per1 per2 per3 per4 per5 per6 per7 per12 CWED CONTAG ENN5 ENN6	559.66
9	per1 per2 per3 per4 per5 per6 per7 per12 ED CONTAG ENN5 ENN6 ENN7 DW	335.30
10	per3 per4 per6 per7 CWED CLUMPY5 CLUMPY6 CA5 CA6 CA7	679.35
11	per5 per6 per7ED CWED TRI CONTAG ENN6 CA3 CA4 ENN7	1375.61
12	CWED per5 per6 per7 CA1 CA3 CA5	6726.17
13	CWED per5 per6 per7 CA1 CA3 CA5 CA4	6706.82
14	CWED per5 per6 per7 CA3 CA5 PD2 PD4 PD6 CA1	6615.93
15	ED SIDI per2 per3 per5 per6 per7 Area	1036.00
16	CA5 CA6 CA7 CWED CA4 per3 per1 per5 per6 per7 CONTAG ELEV PD4 PD5 PD6 PD7	1311.78
17	CA5 CA6 CWED per3 per1 per5 per6 per7 CONTAG ELEV PD4 PD5 PD7	1307.94

We expect that some of the results of this analysis would change if the radius of the "landscape" were varied. However, we chose landscapes whose size was biologically relevant and our final models contained metrics that have been found to have a predictable response with changing landscape size, so a change in landscape size should not affect the analysis (Shen et al. 2004). Given the plausibility of the model, the logic of the beta coefficient scoring and the marginally lower AIC score, model 17 was selected for validation.

Prior to model validation we ran the final model again using full-model logistic regression but subset by population, group size, and season (Table 3.4). Because of decreased sample size for Garden River, Little Buffalo, and

Sweetgrass populations warnings were generated by SAS and these beta coefficients were excluded from the table. Beta coefficients are stable (within one standard error) for the most part, from model to model. Coefficients that vary more than one standard error from each other can be explained as seasonal differences in resource selection or differences resulting in the different proportions of resource availability in each range. Boyce et al. (2003) found that Beta coefficients varied as the scale of selection changed with respect to elk (*Cervus canadensis*) in Yellowstone National Park. In this case, when the scale of selection is static the coefficients are similar even as the sampling location changes.

We performed K-fold cross validation using data for Wood Buffalo National Park by splitting this dataset into four k-fold sets. From the RSF we generated a probability-of-occurrence surface for the study area, scaled from 0 to 1. We then ranked RSF scores for the available points and divided them into 23 bins containing an equal number of random points. The total landscape area contained in each bin was serendipitously equal which equates to a set of bins that have been histogram-equalized. We counted the number of used locations falling in each bin and performed a Spearman Rank Correlation on bin-rank and area-adjusted frequency of used locations in each bin (Figure 3.6). The mean Spearman Rank Order Correlation score is 0.988, indicating a good model with a strong relationship between predicted probability of occurrence and recorded bison locations (Table 3.5).

Table 3.4 Beta coefficients generated from full-model logistic regression for model 17, subset by season, population and group size

		Season							Group Size						
	Variable	Autumn	Spring	Summer	Winter	Delta	Nyarling	full	1	2-5	6-10	11-20	21-50	51-100	>100
Beta Coefficients	CA5	-0.01270	-0.01770	-0.00924	-0.01270	-0.00878	-0.11240	0.00000	0.00009	0.00008	0.00005	0.00039	-0.00007	-0.00082	-0.00320
	CA6	-0.00067	0.00565	0.00323	0.00118	0.00333	0.01720	0.00157	0.00105	0.00202	0.00182	0.00147	0.00132	0.00150	0.00385
	CWED	-0.22800	-0.06600	-0.08770	-0.07310	0.01340	-0.29050	-0.06210	-0.05410	-0.06430	-0.06900	-0.06800	-0.06310	-0.05700	-0.07170
	per3	1.65530	0.46500	0.39950	0.52430	0.14510	0.56710	0.82030	1.15640	0.73550	0.64460	0.75550	0.65110	1.02470	0.15980
	per1	1.89980	0.71840	0.73910	1.26660	2.79710	0.88310	0.64440	0.72630	0.44790	0.90120	0.60610	0.51350	0.51060	0.22140
	per5	4.28780	6.46580	1.27610	6.01820	0.97890	16.13280	0.23940	0.79730	0.08150	0.22760	0.35060	0.09760	0.32240	0.24520
	per6	1.73040	0.80260	0.43530	0.81910	0.11200	1.12200	0.97280	1.20980	0.41190	1.13160	1.20530	1.04850	1.71760	0.17940
	per7	0.69410	1.07890	1.01760	5.42570	1.68990	-157.80000	2.40590	2.39850	1.94670	2.70480	2.35480	2.12760	2.27510	2.60840
	CONTAG	-0.03490	-0.04440	-0.03160	-0.02240	-0.02040	-0.05450	-0.03100	-0.03150	-0.03310	-0.03460	-0.03490	-0.02080	-0.03220	-0.04300
	Elev	-0.00617	-0.00085	-0.00386	-0.00198	-0.09070	-0.04390	-0.00218	-0.00221	-0.00306	-0.00154	-0.00124	-0.00234	-0.00340	-0.00154
	PD4	0.33220	0.08740	-3.05110	-0.30780	-2.32100	1.42820	0.06220	0.03260	0.12510	0.04060	0.02510	0.04790	-0.04610	-0.81580
	PD5	-1.69150	-4.59030	-2.25100	-1.36550	-1.94670	1.97420	-0.17770	-0.21700	-0.11080	-0.16060	-0.25200	-0.19240	-0.33740	-0.67850
	PD7	2.22790	2.54870	2.20130	1.23580	0.43200	-83.20560	1.12630	1.03220	1.19190	1.12130	1.13420	1.15350	1.40870	1.39030
Standard Error	CA5	0.00790	0.00657	0.00289	0.00310	0.00281	0.05460	0.00014	0.00031	0.00023	0.00038	0.00046	0.00034	0.00063	0.00093
	CA6	0.00160	0.00099	0.00074	0.00076	0.00092	0.00235	0.00012	0.00030	0.00027	0.00035	0.00036	0.00034	0.00055	0.00044
	CWED	0.06270	0.03020	0.03160	0.02400	0.03920	0.05130	0.00225	0.00466	0.00440	0.00658	0.00745	0.00716	0.01080	0.01570
	per3	0.68080	0.21590	0.27070	0.13840	0.06720	0.18330	0.06410	0.14840	0.12700	0.17850	0.21660	0.18230	0.31680	0.07500
	per1	0.32150	0.30460	0.26800	0.39510	1.35800	0.19490	0.08400	0.25390	0.21730	0.29740	0.25720	0.13830	0.46690	0.17970
	per5	1.78670	3.15600	0.64250	1.28890	0.58960	5.31160	0.12490	0.33050	0.15640	0.28930	0.46050	0.16430	0.43410	0.33040
	per6	0.73280	0.27660	0.11920	0.20450	0.06840	0.32550	0.10610	0.28280	0.23710	0.30970	0.27480	0.27440	0.48520	0.16120
	per7	1.13130	0.80230	0.35510	1.07450	0.67710	524.70000	0.24160	0.62520	0.54060	0.69140	0.72300	0.69420	0.82110	1.27320
	CONTAG	0.01850	0.01740	0.01340	0.01310	0.01830	0.02130	0.00158	0.00342	0.00317	0.00446	0.00516	0.00482	0.00755	0.00940
	Elev	0.00568	0.00312	0.00413	0.00254	0.02690	0.01260	0.00026	0.00054	0.00053	0.00074	0.00076	0.00083	0.00158	0.00213
	PD4	0.61720	0.37490	0.87300	0.29210	1.37680	0.47390	0.01980	0.04140	0.03930	0.05750	0.06430	0.06310	0.10280	0.20230
	PD5	0.76980	0.88790	0.45700	0.33910	0.44990	1.41540	0.02020	0.04320	0.03950	0.05750	0.06580	0.06430	0.10020	0.15260
	PD7	0.60060	0.54500	0.37540	0.24210	0.31650	2138.60000	0.02930	0.07000	0.06640	0.07970	0.09140	0.08530	0.11520	0.14300

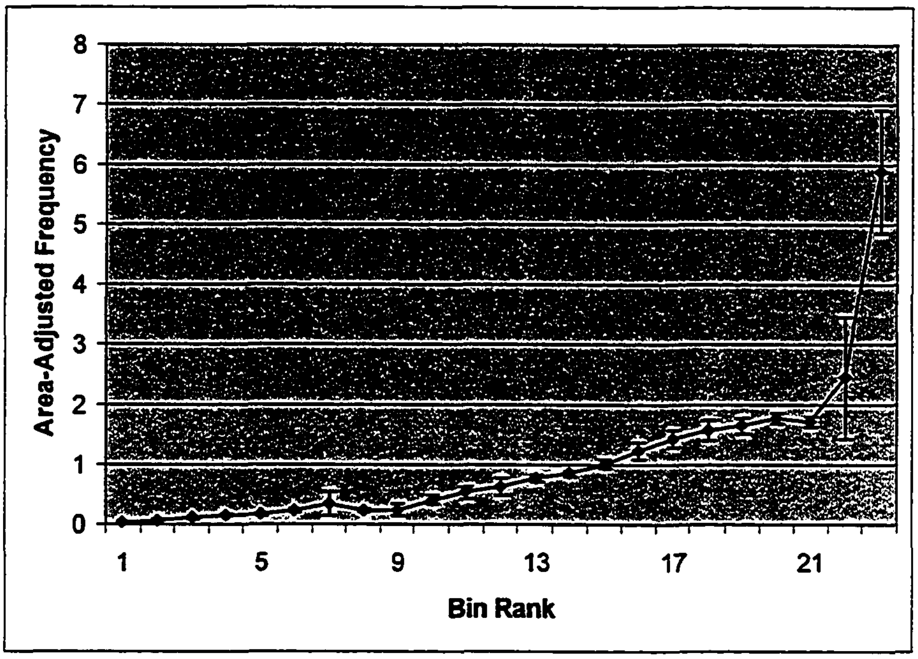

Figure 3.7 Area-adjusted frequency of used locations compared with bin rank. Bin dimension was determined by number of random points and used locations were counted in each bin. Frequency of occurrence was adjusted by the area (ha) represented by each bin.

The probability of occurrence surface generated from an RSF is essentially a habitat suitability index (HSI) but with statistical rigour (Boyce et al. 2002). We converted the resultant probability surface developed over WBNP to a categorical map (Figure 3.5) for display purposes. From an analysis of Figure 3.7 we developed categories by examining the relationship between increasing bin order and area-adjusted frequency of occurrence. We categorized poor habitat as having an area-adjusted frequency <1, good habitat >1 and <2 as very good habitat. Excellent habitat was categorized as falling within the dimensions of the last two bins.

Table 3.5 Spearman Rank Order Correlation results.

K-fold group	Spearman Rank-Order Correlation
kfold1	0.9830
kfold2	0.9870
kfold3	0.9880
kfold4	0.9940
Mean	0.9880

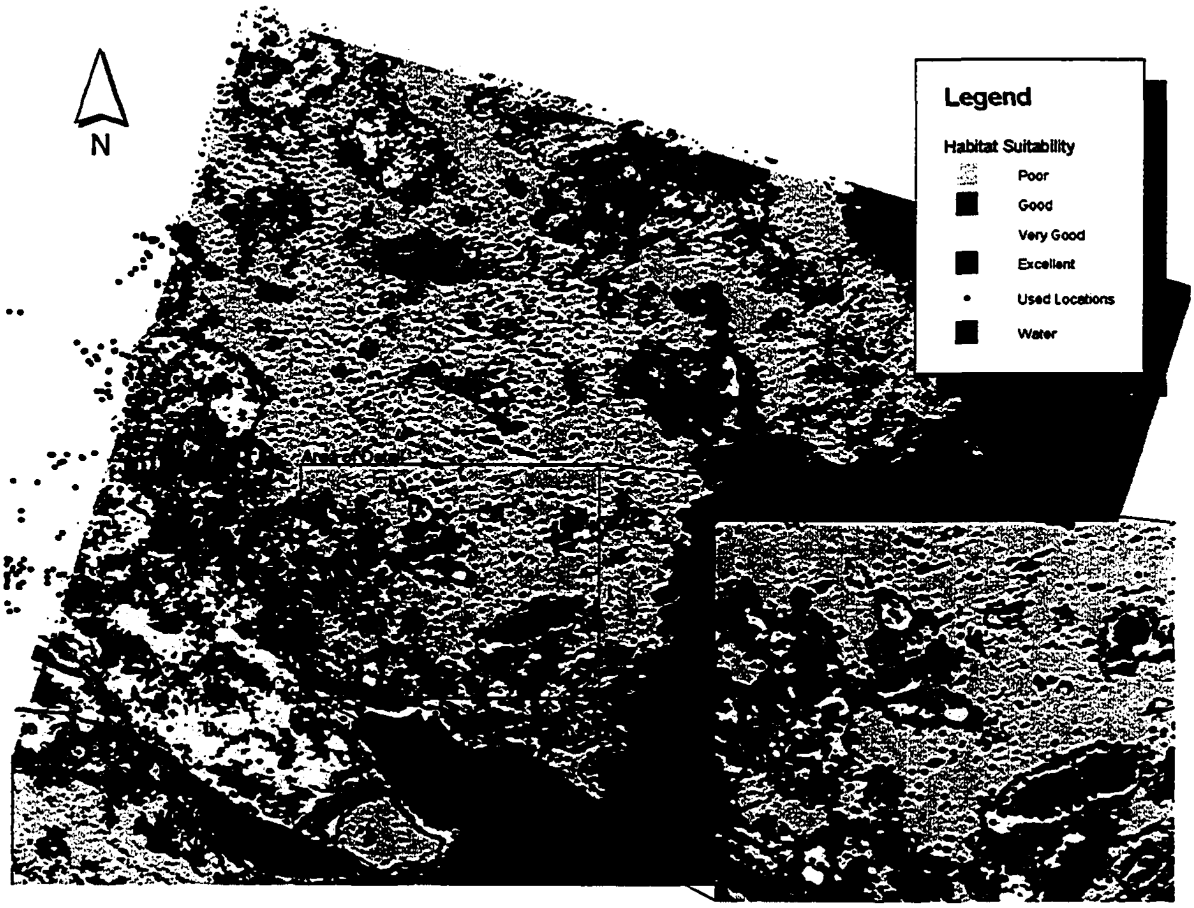

Figure 3.8 Habitat Suitability Index (HSI) developed for the Mackenzie Bison Sanctuary in order to assess the predictive qualities of a RSF model developed with data from Wood Buffalo National Park.

Out of sample validation using data from the Mackenzie Bison Sanctuary was performed and an assessment of the relationship between the categorical habitat map (produced using the RSF developed in WBNP) and bison observations was done using the RSF scores at each used point in the database. The area-adjusted frequency for points falling within bins with the same dimension of those for the WBNP model indicates a good model fit with an area-adjusted frequency in the "poor" category of 0.5244, 0.9636 in the "good" category, 1.9635 in the "very good" category and 18.4025 in the "excellent" category. Poor habitat is used less than would be expected through random selection while good habitat is used approximately equal to it's availability. Both the "very good" and "excellent" category are used in much higher proportion than would be expected by chance. The model appears to be a good predictor of use (Figure 3.8).

5.0 Discussion

Distribution patterns of herbivores over large areas are determined by forage availability and abiotic factors including distance to water and topography (Bailey et al. 1996). Animal behaviour and interactions with the environment determine distribution and resource use patterns within the boundaries created by these abiotic factors. Factors that determine resource selection differ within each level of a hierarchy of spatial scales (Hall et al. 1997). Occupancy is determined not only by forage quantity and quality but by landscape physiognomy, including composition, complementation and contagion. Landscape structure and the composition of habitats within a home range present considerably variability in terms of resistance to movement (Ricketts 2001). We modelled this structure explicitly in order to capture the link between landscape and habitat ecology (Lennon 1999). Landscape structure covariates are useful in that they provide a measure of the compatibility of a landscape for bison, indirectly measured by the trade-off between forage availability and energy loss and predation risk. This modelling approach assumes that the value matrix of intervening habitats surrounding forage habitat changes spatially. Modeling simultaneous multi-scale selection is important to generating good predictive models (Fortin et al. 2003).

Some constraints on active resource selection include predation (Carbyn et al. 1998), biting flies (Bergman et al. 2001, Fortin et al. 2003), distance to water (Fortin et al. 2003), and in winter, wind-hardened snow and snow depth (Fortin et al. 2003; Reynolds et al. 1978). The quality of the matrix of habitats surrounding forage habitat, the travel costs associated with movement through the matrix in which forage habitat is embedded will affect dispersal and survival of a population of animals (Bender et al., 2003, Ricketts 2001). Given this ecological context bison must act as time minimizers but at the smallest temporal scales maximize their long-term rate of energy intake by behaving as energy maximizers when conditions permit. Temporal and spatial scale is therefore important when behaviour is considered in the context of optimal foraging theory (Fortin et al. 2002).

At larger spatial scales bison are not so much selecting for qualities of the landscape but are being selected for within that landscape – selection is passive and individuals and herds are persisting in a suitable landscape. Covariates that are good predictors of use are those that express the energy loss incurred by a bison moving through a landscape. Contrast Weighted Edge Density (CWED) was found to be one of the best metrics to express energy loss and thus predicted use. CWED is a measure of the number of edges in a landscape that is the average daily travel distance for a bison (Fortin et al. 2003), weighted by the relative contrast between those edges. This contrast is measured from the assumed perspective of a bison and thus includes considerations of the energetic cost of miring, mud, dense brush, biting insects, and absence of forage. Saura and Martinez-Millan (2001) found edge density metrics to be robust compared to those that quantify the complexity of shapes. Since scale was held constant among landscapes scaling responses and the subsequent changes in metric response was not a concern (Shen et al. 2004). FRAGSTATS was used to construct a CWED grid, the edge weights for those calculations are presented in Table 3.6. Landscape physiognomy, measured here using landscape metrics can be linked to specific biological functions using the conceptual framework of foraging theory.

		Jack Pine	Conifer	Deciduous	Bog	Shrub Fen	Grass Fen	Wetland	NonVeg	Water	Anthro	No Data	Burn
		1	2	3	4	5	6	7	8	9	10	11	12
Jack Pine	1	0	0.4	0.1	0.8	0.7	0	0.5	0.3	0.9	0.4	0.0	0.2
Conifer	2	0.4	0	0	0.4	0.2	0	0.2	0.1	0.8	0.1	0.0	0
Deciduous	3	0.1	0	0	0.8	0.1	0	0.8	0.7	0.9	0.2	0.0	0.2
Bog	4	0.8	0.4	0.8	0	0.5	0.7	0.5	0.2	1.0	0.5	0.0	0.3
Shrub Fen	5	0.7	0.2	0.1	0.5	0	0.1	0.5	0.4	0.8	0.3	0.0	0.2
Grass Fen	6	0	0	0	0.7	0.1	0	0.4	0.1	0.7	0.2	0.0	0.1
Wetland	7	0.5	0.2	0.8	0.5	0.5	0.4	0	0.1	0.3	0.1	0.0	0.2
NonVeg	8	0.3	0.1	0.7	0.2	0.4	0.1	0.1	0	0.8	0.1	0.0	0.1
Water	9	0.9	0.8	0.9	1.0	0.8	0.7	0.3	0.8	0	0.1	0.0	0
Anthro	10	0.4	0.1	0.2	0.5	0.3	0.2	0.1	0.1	0.1	0	0.0	0.1
No Data	11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0
Burn	12	0.2	0	0.2	0.3	0.2	0.1	0.2	0.1	0.0	0.1	0.0	0

Table 3.6 Weights applied to the resource matrix in order to create a contrast-weighted edge density grid. A weight of zero implies no contrast between edges, whereas a weight of one implies maximum contrast.

A recognized potential weakness of the study design is the disparity between the collection period for distribution data and habitat data. Distribution data for the Mackenzie bison range was obtained from telemetry relocations collected from 1988 to 1991, in WBNP telemetry data from several studies were incorporated into the analysis spanning a period from 1988 to 2000. The Landsat imagery used to develop the habitat classification for the study area was collected from 1998 to 2002. The relatively long period of collection of distribution data shows that home range boundaries are relatively stable in WBNP adding strength to habitat selection inferences since the region in which selection occurs changes very little. We argue that the incongruity between the temporal sampling periods makes the inferences robust, perhaps more so than would be found for a sampling period of just two or three years since environmental variability is sampled over a longer time period and a large sample is obtained, variance is reduced. The validity of the model and the robustness of the model are supported by the predictive success of the final RSF model as presented in the final two figures.

Optimal foraging theory can be used to explain and predict foraging at the scale of the plant and the sward (Fortin et al. 2003). Within the patch, forage velocity is governed by "matching" forage time to forage quantity and quality and this, too, should be predictable even with the confounding effects of animal and herd behaviour. At these scales herbivores have demonstrated that they have accurate spatial memories that can last up to twenty days, though a narrower moving 'forage memory' window of four or five days is more likely (Fortin et al. 2002, Bailey et al. 1996). At these scales forage quantity and quality is the currency and availability and digestibility are the constraints (Figure 3.8). At the scale of the patch forage quantity and quality are retained as the foraging currency but the constraints are more complex and include predation, harassment by insects, and group behaviour. It is these more variable and stochastic events that result in bison switching from energy maximizers to time minimizers (Bergman et al. 2001).

At the patch and patch-assemblage scale, marginal value theorem can be used to understand distribution. Within this context animals move from a patch at a threshold where the marginal intake rate decreases below the average intake rate (Stephens & Krebs 1986). The value of the patch is determined in part by the forage quantity and quantity within it but also by its spatial context; the energy lost in travelling to and from the patch, which is a product of distance and land cover type as well as the predation risks associated with the patch. Large forage patches have a high theoretical value since they contain a large amount of forage but, as Carbyn et al. (1993) hypothesized, the predation risk may negate any benefit created from increased forage availability. Landscape metrics, which describe the physiognomy of the landscape are useful in indirectly quantifying the energy loss and, hence, value of a patch. Fractal dimension, interspersion, edge density and contagion express the potential energy lost in travel through the landscape habitat matrix. Conversely, patch type, patch area, and class area represent energy gain in terms of forage quantity. It should be possible to estimate carrying capacity from these increases in forage availability, however this would require a measure of forage quality and we did not directly estimate forage quality in this study. Biological interactions are constrained by abiotic factors and so, at the regional scale, terrain ruggedness, distance to water, elevation and landform can be used to determine what landscapes might be suitable habitat.

A useful model of habitat selection has predictive abilities (Boyce et al. 2002) and a model is more likely to be predictive when it is a more general model. Regardless, we assessed differences in habitat selection and resource for each population, by season and again by group size, as recommended by Schooley (1994). The selected model from the candidate set had general equality of beta coefficients (within one standard deviation) from one population, season, group and group size to another. We created predictive grids and performed k-fold model testing using the beta coefficients from the full model (all telemetry and aerial survey data) (Table 3.6). This model is considered to be the most generalized and therefore have the potential to be the most predictive.

The resources and conditions that produce occupancy by wood bison necessarily include forage: sedge-grass meadows. Wood bison require forage resources, preferably sedge-grass meadows; their foraging currency is crude protein and nitrogen. This does not necessarily preclude the use of other resources but this foraging currency appears to be maximized within sedge-grass meadows, especially those that develop on lacustrine deposits. Many authors including Gates et al. (1992) and Raup (1935) postulated that this habitat is constrained to the lacustrine plains within the Mackenzie Basin. Carbyn et al. (1993) went further to say that the bed of Glacial Lake McConnell in which we now find both Wood Buffalo National Park and the Mackenzie bison range was likely to be the only place where habitat for bison was likely to develop. However, bison are not limited to these areas only (Stephenson et al. 2001), reintroductions are being considered and have been undertaken in regions outside of these lacustrine plains (J. Nishi pers. comm.).

Other habitats that are important include deciduous and dry jack pine dominated forests, which are used for resting and ruminating and, at certain periods of the year, for forage. Bogs and other conifer-dominated forests are avoided. Maintenance of forage resources appears to be facilitated by fires, which discourage the encroachment of woody plants (Quinlan et al. 2003) and flooding, which encourages the growth of sedges and grasses.

The matrix of habitats in which forage habitat is embedded is important and this landscape structure has an influence on population and meta-population structure (Ricketts 2001, Wiegand et al. 1999). Thus, the quality of the matrix determines in part the minimum habitat or minimum area requirements of wood bison because population dynamics are sensitive to the landscape physiognomy and produce habitat-specific birth and death rates (Wiegand et al. 1999). As Fahrig (2001) points out, habitat quality is a function of landscape pattern and composition. When habitat comprises more than twenty percent of the landscape, habitat amount (forage habitat) is more important than configuration (Fahrig 1997, Flather and Bevers 2002). Ricketts (2001) found in a study of montane butterflies that the composition and thus quality of the matrix determined the resistance to interpatch movement. It is likely that for wood bison the matrix of habitats in which forage habitat is embedded also determines the resistance to interpatch movement. Larter and Gates (1994) hypothesized that home range size is a product not only of the availability of forage but also by its distribution characteristics. This relationship and the effect of matrix quality on daily caloric requirements and thus fitness is outlined in the conceptual model (Figure 3.4). This conceptual model is based on the rules of optimal foraging theory and as Dunning et al. (1992) suggested, optimal foraging theory can be a good starting point from which dispersal rules might be created, as is done here. A habitat matrix that facilitates locomotion and lowers inter-patch resistance to movement is preferred. Low Contrast-Weighted Edge Density and relatively high contagion are measures of the landscape physiognomy that are important.

Forage habitat must be embedded in a matrix of habitats where energy lost in dispersal and habitat selection is minimized. Forage embedded in a matrix comprised of deciduous or dry jack pine forests would likely meet these requirements while those embedded in a matrix of bog would not. Summer forage meadows must have soils that facilitate or do not severely limit locomotion; winter forage meadows need not be so. Landscapes differ in their composition and juxtaposition of forage and non-forage habitat and thus have different effects on survival and therefore would be expected to have different habitat-specific demographic rates (Wiegand et al. 1999). Finally, sedge-grass meadows need not be the only forage resource. For example, Fischer (2002) studied wood bison foraging in alpine meadows and European bison (*Bison bonasus*) forage in fresh and moist deciduous forests, without any apparent access to meadow systems comprised of sedges (Krasinska et al. 1987).

6.0 Conclusions

The information-theoretic method, exemplified here using AIC, does not allow the presumption that the best model in the set is a true parameterization of reality (Anderson & Burnham 2002). However, the results of predictive modelling indicate that the selected model is not only a good fit but predicts well in new areas. The predictive ability is an important consideration for evaluating RSF models (Boyce et al. 2002). However, just as hierarchy theory predicts constraints imposed by higher levels on lower levels in ecological systems, our modelling is restricted to bison observations within the bed of glacial lake McConnell and so the applicability of the model is likely constrained to other alluvial or fluvial derived systems. This hypothesis can be tested with land cover and distribution data from the Yukon. However, we expect that the conceptual approach using optimal foraging theory, hierarchy theory, marginal value theorem and measures of landscape physiognomy and abiotic factors to express energy loss and gain will be useful to other regions where bison are known to occur, for example, the Pink Mountain region of British Columbia, or where bison may be reintroduced, i.e., Yukon Flats, Alaska. Further, indirect measures of energy loss and hence fitness such as CWED are not location or site-specific. As long as the landscape in question is assessed from a bison's perspective, CWED should be an applicable metric in any region. Forage availability is obviously the most important consideration when assessing resource use and a simpler, even more widely applicable model might include forage habitat at the site and local landscape levels as well as contagion, which is also not site-specific, and CWED.

Regardless, this approach of using measures of landscape physiognomy allows us to link spatial attributes to biological factors, specifically energy budgets and fitness of individuals.

Conservation of wood bison requires two things; first, the species-habitat relationship be clearly defined and second, that critical habitat be identified from an understanding of this relationship. Management of wood bison, including reintroduction, requires that the resources and landscape features that result in persistence be clearly identified, biologically plausible and supported by research. These resources, both habitat and physiognomic have been identified in this paper. In the political context of SARA, critical habitat needs to be objectively determined and mapped. The background and results provided by this paper set the stage for this to happen.

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Chapter 4

Conclusions

1.0 Introduction

The research presented in this thesis is intended to serve the purpose of identifying critical habitat for a species at risk, the threatened wood bison. In making progress towards accomplishing this task I explored some improved techniques for generating land cover maps using remote sensing and gained insight into how this remote-sensing imagery might be used in a GIS to better understand species-habitat interactions. Within an ecosystems paradigm I developed an improved approach for mapping land cover over large areas of the boreal forest using image segmentation based on ecological regions. The subsequent land cover map was analyzed within a GIS to produce metrics of landscape physiognomy and these site (habitat) and landscape-scale (landscape metric) variables were assessed in a logistic regression resource-selection modelling approach to explore habitat use by wood bison at the landscape scale.

2.0 Summary of Research

Prior to a quantitative exploration of the species-habitat relationship for wood bison it was necessary to create an accurate and detailed map of land cover for the study area. An unsupervised classification of remote sensing imagery was undertaken to create a digital land cover map of the total study area, some 80 000km^2. This land cover map was further assessed in a GIS to create digital maps of resource covariates, specifically measures of landscape physiognomy. These metrics were assessed within a conceptual model of habitat use to be potentially important to understanding the species-habitat relationship for wood bison at the landscape scale.

Remote sensing image classification for boreal environments is challenging since field data collection is expensive, limiting the number of training sites available to the classifier. As well, the environment is heterogeneous at almost every spatial scale and, although floristic diversity is low compared to tropical environments the combination of different species within the multitude of ecosites creates a large number of objects that may be functionally very different but spectrally similar or the converse. In order to limit the number of necessary training sites and improve the classification by accounting for some of the spectral variance in an image I assessed a method of image segmentation using ecological regions as the segmentation criteria.

An unsupervised image classification technique employing image segmentation by ecological regions was evaluated using percent accuracies and *Tau* coefficients against an un-segmented two-stage classification. *K*-fold cross validation is used to partition the field data into training and testing sets. A *Z*-test of the *Tau* statistic and its variance was used to test for a significant increase in classification accuracy when using image segmentation. Results show a significant increase in classification accuracy ($\alpha = 0.05$, one-tailed) over two-stage approaches ($Z = 2.49$, $Z_{crit} = 1.65$ $p{=}0.0063$). This supports the hypothesis that spectral variance within information classes can be explained, in part, by ecological region. Multi-group discriminant analysis is performed using Jack Pine (*Pinus banksiana*) plant community spectral data, grouped by ecological region.

Significant spectral differences in a single information class within different ecological regions were found, which support the image segmentation approach to classification. The minimum mappable unit (MMU) is discussed in the context of Landsat Thematic Mapper (TM). The plant association, or ecosite, is presented as the MMU and the physical and ecological properties are discussed in relation to their spectral properties. The results suggest logical refinements for image classification and field data collection for remotely-sensed data in boreal environments.

The resultant land cover map was structured into a hierarchy of land cover classes with accuracy increasing towards the highest levels (highest level contain the smallest number of land cover classes). Although it is possible to display the land cover over the study area to the level of ecosite, I used the highest level of the hierarchy for further analysis. This approach was used to limit effects of compounding errors in analysis and was deemed appropriate when assessing resource selection at the landscape scale.

A conceptual model of habitat selection identified land cover as only one of many factors that can be important in quantifying resource selection by wood bison. At the landscape scale measures of landscape physiognomy were also identified as potentially important. A digital land cover map consisting of twelve land cover classes was assessed using landscape pattern analysis (FRAGSTATS) in order to derive a number of landscape metrics important to quantifying selection. Metrics were derived at the patch, or local, scale as well as within a landscape which consisted of a circular moving window analysis over the entire study area. The radius of the moving window analysis was set to a size equal to the average daily movement distance of bison.

The digital land cover map and its derivates – landscape metrics, were then assessed using logistic regression analysis to create a model of resource selection. I modelled resource selection by wood bison (*Bison bison athabascae*) using resource selection functions (RSF) at a scale relevant to the ecology, management and conservation of the animal. In this multi-scale project I considered ecological and foraging processes at finer spatial scales. However, the emphasis in this project is on an applied, predictive understanding of habitat use at the landscape scale. Model selection was constrained by considering the limitations imposed on lower scales of selection by those at higher spatial and temporal scales. I suggest that this landscape scale is more relevant to the problems of management and conservation. The predictive qualities of the model were assessed using k-fold validation within the study area and out-of-sample validation with data from the Mackenzie bison range in the Northwest Territories (NWT). Resource variables were obtained from a land cover map developed from the classification of remote-sensing data. Covariates in the analysis include metrics of landscape physiognomy. These include, class area (CA), edge density and contrast-weighted edge density (CWED), patch density (PD) and contagion measured within a circle with a radius of two kilometres, a local landscape equal to the average daily movement distance of a bison. On a smaller spatial scale, covariates included elevation and the resource variables which were calculated as the percentage of land cover type within a circle with a radius of three hundred metres. A used/available design was employed using telemetry and aerial survey data obtained over a ten year period. While the distribution of wood bison depends on the presence of forage habitat, factors such as edge density and contagion proved to be important predictors of use. We created *a priori* models of habitat use using a conceptual framework developed through the incorporation of optimal foraging and hierarchy theory. We postulated that while forage abundance can be used as a partial predictor of use, measures of landscape physiognomy might additionally be employed to model energy loss through different matrices of non-forage habitat. When validated by applying the model in a new area the model proved robust and a useful predictor of occurrence. The incorporation of landscape metrics into resource selection modelling proved to be an effective means of linking spatial landscape attributes to biological functions.

3.0 Defining Critical Habitat for Wood Bison

The conservation context for this work requires taking this information forward to develop a definition of critical habitat in order to meet the legislative requirements of SARA. This task can only be accomplished by placing the remote sensing, GIS and statistical work within the biological, ecological and political context of wood bison. The primary biological needs of the wood bison and vital rates including fecundity and survivorship are summarized in Table 4.1, and this table is supplemented by data for other bovids (Gaillard et al. 2000). Bison do not appear to have specific habitat requirements for rutting, mating or gestation as these activities appear to take place within the normal range of habitats of the species. However, calving adults appear to favour larger meadow systems; Calef and Van Camp (1987) observed pre-calving migratory movements to large meadows. Deciduous and jack pine forests appear to have value for resting and ruminating (Reynolds et al.1978) and the absence of these forests necessarily results in the reduction in perceived value of a forage patch not proximate to these habitats. Further, winter mortality resulting from cold temperatures and wind, snow-crusting and spring flooding can make forested areas adjacent to meadows more valuable in that they increase the chance of winter survival. Winter mortality also appears to increase when snow depth passes a critical depth threshold of 50-60cm (Carbyn et al. 1993); additionally, low temperatures do not appear to affect mortality rates until temperatures drop below -30°C, down to this point metabolic rates appear stable. Forage resources in regions with >60cm snow depth will likely preclude the persistence of populations of bison. Finally, regions where the temperature routinely drops below -30°C and winds are common will also be excluded because the increased metabolic rates during these periods can increase mortality.

Temporal variability in habitat value comes as a result of flooding and fire, or as outlined by Quinlan et al. (2003), by a lack of fire. Flooding has been reported as a stochastic source of mass mortalities in Wood Buffalo National Park by Carbyn et al. (1993) and in the Mackenzie Bison Sanctuary by Larter and Gates (1991) where bison are known to have drowned in large numbers. Though dramatic, these stochastic events are not likely to result in local extinction for healthy bison populations. Joly (2001) included drowning mortality as a factor in population modeling. Fire does not appear to be a significant mortality factor for wood bison. The gradual drying, caused in part by isostatic rebound of the Slave River Lowlands and a lack of fire has been postulated by Quinlan et al. (2003) and by Gates et al. (2001) to be a factor in reducing forage habitat over very long temporal scales. Both fire and flooding are thought to contribute to the long term maintenance of forage habitat in the sedge-meadow complexes growing on the lacustrine plains in the study area.

Table 4.1 Vital rates for disease-free herds of wood bison (with standard error given in parenthesis). Environmental variance in mortality rates used by Wilson & Zitlau (2004) for modelling Minimum Viable Populations with respect to genetic health was 0.02 – 0.19. (†estimated from a diseased population). Fitness for bovids in general is from Gaillard et al. 2000.

Fitness Component	(General) Bovids	(Specific) Bison	Citation
Pre-weaning survival	0.749 (0.084)		
Post-weaning survival	0.676 (0.048)		
Yearling survival	0.829 (0.021)	0.870	WBNP 1995
Prime aged ♀ survival	0.895 (0.013)	0.950 (0.100)	Joly 2001
Prime aged ♂ survival		0.930 (0.090)	Joly 2001
Senescent ♀ survival	0.825 (0.025)		
Fecundity young ♀	0.495 (0.077)		
Fecundity adult ♀	0.834 (0.048)	0.78 (0.05)†	Joly 2001
Fecundity old ♀	0.944 (0.013)		
Calf:cow ratio	0.411 (0.077)	0.380	Komers et al 1992
Juvenile survival	0.547 (0.041)		

Temporal differences in habitat use appear to be caused by moisture and soil type which increases foot loading during foraging and hampers locomotion. Wet sedge meadows are used during the winter while in summer these habitats are not available (Larter and Gates 1991). Calving season also leads matriarchal groups of bison to select larger meadows, the mechanism for this is unclear but is likely related to forage. While there does not appear to be any demographic differences in habitat use, home ranges for mature male bison is larger than for females. Again, this appears to be related to group size which necessitates the selection of larger meadows or larger home ranges in order to meet the forage requirements of an increased number of animals.

Rate-limiting steps in healthy bison populations include juvenile and calf survival, ingress and egress initiated by large-scale events such as fire and flooding, and, where present, disease which affects both fecundity and mortality rates. In healthy populations the most variable and important rate-limiting step is juvenile and calf survival (Gaillard et al. 2000). Critical snow depths and cold temperatures coupled with windy conditions can reduce survival of juveniles and the interplay between snow depth, wind-hardened snow and predation success have a large impact on yearling recruitment in northern bison herds (Carbyn et al. 1993, Hebblewhite et al. 2002). A matrix of habitats that does not provide adequate forage resources or cover will do the same. Finally, as outlined by Joly (2001) disease in combination with wolf predation has been demonstrated to limit population growth. Without disease, and in the context of habitat containing adequate forage and a suitable low-contrast matrix bison populations should increase until limited by carrying capacity (intra-specific competition for food).

Until recently meta-population theory reduced landscapes to binary components of habitat and non-habitat. Habitat is extremely variable and a more realistic reduction of real landscapes for modelling purposes would be to model habitat-specific demographic rates for a greater number of habitats, recognizing the gradation in habitat across the landscape rather than the presence of absolute boundaries. These habitat types should implicitly incorporate measures of landscape physiognomy since these attributes of habitat appear to affect habitat selection. Modelling could focus on females, since they are the reproductive unit (Gaillard et al. 2000) and adaptive time-step modelling could include the modification of mortality rates as a function of local habitat quality and competitor density.

Population goals of the recovery team outlined by Gates et al. (2001) require the establishment of four free-ranging and disease-free herds of at least four hundred animals. The amount and configuration of habitat features required to meet survival and recovery goals can be modelled using spatially-explicit meta-population models like Population Viability Assessment in a program like RAMAS (Akçakaya and Root 2002). The remote sensing techniques outlined in chapter two of this thesis combined with the conceptual model and resource variables used in the RSF in Chapter Two can be used to build the models. Finally, these spatially-explicit models can be used to assess new areas and ultimately to locate and describe the habitat required to meet survival or recovery goals.

Critical habitat is a term that has clear legal and management implications. For wood bison conservation and recovery, a definition of critical habitat is directly linked to the goals of the National Recovery Plan (Gates et al. 2001). In this context critical habitat must provide the forage resources and matrix of habitat conditions that will sustain a minimum population of 400 animals. The use of Habitat Suitability Index (HSI) maps that are based on biologically relevant RSF models provides the first step to developing an empirical definition of critical habitat and in the evaluation of potential reintroduction sites (see Schadt et al.

2002). I recommend that HSI maps be complemented with spatially-explicit population modelling in the form of Population Viability Analysis (PVA). An exploration of suitable habitat could comprise a modelling exercise that is not spatially explicit and the thresholds for model variables could be analysed in this context. However, since critical habitat is a legal definition that necessarily includes specific goals the modelling of critical habitat must be spatially explicit since the final product will include a map of some region that has been assessed to have some potential of supporting a given population of animals.

Four habitat types were created from an analysis of the area-adjusted frequency of used locations compared with bin rank (Figure 3.6) these are: poor, good, very good and excellent. Excellent and very good habitat could be grouped together and demographic rates established for these habitat types that are better than replacement ($\lambda > 1.0$), or modelled separately with excellent habitat as λ >1.0 and very good habitat $\lambda \geq 1.0$. Good habitat would allow for replacement but when considering temporal environmental stochasticity we would expect λ to vary in time above or below 1.0. Poor habitat could be considered matrix and is unsuitable. Good habitat in this scenario would be considered sink habitat over longer temporal scales. Landscape physiognomy is implicitly modelled in this approach.

Suitable habitat or "habitat" has been defined through a review of the relevant literature and an exploration of some important landscape metrics. Critical habitat could be defined, within the context of the recovery objectives for wood bison, in the following manner:

- A potential area for inclusion as critical habitat is identified by field biologists or other knowledgeable persons or communities.
- A digital map of habitat is created using the remote sensing and GIS techniques outlined in Chapter One of this thesis. Landscape physiognomy variables are created from an analysis of the habitat map using FRAGSTATS or similar landscape metric software.
- The RSF model selection for out-of-sample validation in Chapter Two is used to generate a habitat suitability index map for the area. The probability surface is then categorized into habitat classes – very good, good, and poor (matrix).
- Habitat-specific demographic rates and the vital rates summarized in Table 1 are used to populate a Population Viability Assessment model for analysis. The PVA is used to assess the probability of persistence of a population of bison over some time period and this information is used to guide the decision making process for determination of critical habitat.

Threats to habitat conceivably include loss of forage resources due to forest and woody vegetation encroachment although over long temporal and spatial scales this loss should be balanced by gains. In the southern part of their range habitat loss is due mainly to agricultural activities although it has been postulated that some industrial-agricultural activities including oil and gas exploration and forestry could be used to create or enhance habitat (Gates et al. 2001). This enhancement should be undertaken with caution since the climax stage of boreal forests used for commercial timber harvest is forest, not grassland and the maintenance of these ecological communities as grassland can only be done within an agro-industrial paradigm. Thus, we can hardly consider these forests cum rangelands as sustainable in an ecological context. In the central and northern part of their range human activities are limited and the dominant processes on the landscape are fire and flooding. However, the continuing expansion of the oil and gas industry into northern Canada, fuelled by improving technology and the increasing value of fossil fuel may well introduce these anthropogenic threats to habitat. Seismic activities, road-building, and the development of new mines will bring immediate and cumulative impacts to the ecology of the north. Threats to habitat can include climate change but the direction and magnitude of climate-change-induced habitat change can not be presently determined. Since wood bison population growth is limited by ecological carrying capacity, threats to habitat include those that reduce the ecological carrying capacity of the land. However, Joly (2001) has demonstrated that in the presence of disease, bison population growth is limited by wolf predation. A threat to population growth and recovery is therefore the presence of the exotic diseases tuberculosis and brucellosis which limit population growth and result in a large part of the historic range of this species being unavailable for reintroduction and recovery.

4.0 Research Needs

4.1 Remote Sensing

Given the widespread use of Landsat and satellite platforms of similar resolution for land cover classification further investigation and definition of the object under investigation would be useful to mapping. The spectral, spatial and radiometric properties of Landsat limit its utility for mapping fine features of the boreal forest, those <0.5ha; the object under investigation lies somewhere in this half-hectare range. Ecosite associations in the Braun-Blanquet definition are thought by Nilsen et al. (1999) to be un-mappable. The electro-optical properties of these ecosites, at the spatial scale of the sensor, would be useful to explore since it can help to shed some light on the objects being classified. The spectral properties of individual trees would be less useful to explore, in a large scale, boreal context than would be the properties of ecosites containing these trees.

Collection of training sites in remote boreal environments is time consuming and expensive. Classification techniques that maximize the usefulness of these training sites would be valuable. Further investigation of k-fold classification techniques especially in an automated context can prove useful in maximizing the use of training data. Since k-fold techniques in a manual classification context are time consuming and thus expensive they are probably most useful when used with automated procedures. Further, k-fold techniques can prove to be a more rigorous and statistically-valid means of reporting classification error.

Finally, classification of spectral data in an ecosystem context would benefit from algorithms that are spatially informed. Unsupervised classification groups spectral space according to the similarities of data in spectral bands. Spatially-informed classification algorithms that classify spectral space but incorporate spatial proximity into the classification rules may help in mapping ecosites. Textural classifiers and other algorithms that take advantage of other elements in the data will further improve the accuracy and utility of the resultant maps.

4.2 Resource Selection Functions and Critical Habitat

Further validation of the model should be carried out in order to assess the utility of the model for predicting use. Model validation could be performed in the Hay Zama lowlands region in northern Alberta and in the Interlake region of Manitoba. Should the model provide a good fit to existing occurrence data a good case would be made to using the model as a tool for delineating suitable habitat. As part of an exercise in modeling population persistence over time in a spatially-explicit population viability assessment model, habitat-specific carrying capacity would need to be estimated.

Critical habitat first requires that the biological and ecological needs of a species be identified. Further, the relationship between habitat and demographics must be established, recognising that demographic rates vary by habitat. Habitat, "*the resources and conditions present in an area to produce occupancy – including survival and reproduction, by a given organism*" (Hall et al. 1997) is by definition "suitable habitat". Critical habitat, however, is a legal definition that implies the persistence of a population in a specified place and over some specified time period. The Canadian Species at Risk Act (SARA - Government of Canada. 2002. Species at Risk Act (http://laws.justice.gc.ca/en/S-15.3/index.html) has defined critical habitat as "*the habitat that is necessary for the survival or recovery of a species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species*". Survival is defined as no net loss in abundance or distribution; and, recovery as the downlisting of the species to Special Concern or Not At Risk which means the species remains sensitive to human activities or natural events, or simply is not at risk. Critical habitat, since it pertains to the entire species, is a population level definition and thus implies persistence over some time period. Therefore, population goals need to be established and spatially explicit models of population persistence need to be created in order that a region can be objectively assessed as "critical" in the context of the Canadian Species at Risk Act.

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