CORE AREAS OF HABITAT USE: THE INFLUENCE OF SPATIAL SCALE OF ANALYSIS ON INTERPRETING SUMMER HABITAT SELECTION BY MOOSE (*ALCES ALCES*)

BY

ERIC VANDER WAL

A THESIS
PRESENTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGY
LAKEHEAD UNIVERSITY
THUNDER BAY, ONTARIO

DECEMBER 2004

Your file Votre référence
ISBN: 0-494-10675-1
Our file Notre référence
ISBN: 0-494-10675-1

Abstract

I investigated summer habitat selection patterns within the home ranges of 60 GPS-collared adult female moose (*Alces alces*) in northwestern Ontario. I developed a model that identified the 'summer' period for moose and I suggest and test a new approach for objectively delineating areas of intense use, or 'core' areas. Once summer and core areas were established, I tested two competing hypotheses to identify differences in habitat selected between the core areas and home range peripheries; (1) core areas represent superior spatial configurations of habitats when compared to home range peripheries; and (2) core areas are selected to contain a subset of 'preferred' forage species with higher individual densities or a higher total density of all forage species than home range peripheries. The study was conducted in 2 landscapes characterized by different disturbance patterns created by different timber harvesting systems: modified "guidelines" cut (MGC); and progressive, contiguous clear cut (PCC).

Moose move more and faster during the summer than the winter to exploit available forage. I defined moose 'summer' as the period during the calendar year when an animal maintains a rate of movement greater than the annual mean. Using a sub-sample (n=32) of animals collared in 2000, I determined 1 May 2000 as the median date for the 'winter-summer' transition (range: 2 April-24 May) and the median transition from 'summer-winter' was 25 August 2000 (range: 1 Aug-23 October).

Moose home ranges were designated using a 90% adaptive kernel. Within the home range, moose devote a disproportionate amount of time to a fraction of the total area. The area of

intense use, termed 'core' area, was delineated using a time-maximizing – area-minimizing function. On average, core areas were used 2.17 (mean) times more intensely than home range peripheries and comprised 67% (range: 57-79%) of animal relocations. Core areas represented a mean of 26% (863 ha) of over-all home range size (range: 14-55%; area range: 115-6514 ha).

I calculated spatial metrics regarding area, density and size, shape, edge, and interspersion within 10 habitat categories determined from a Forest Resource Inventory of the study area; 9 categories based on forest composition and age and 1 category for wetlands. Metrics were calculated separately for the core areas and the home range peripheries of GPS-collared adult female moose (n=60). Browse density data for core areas and home range peripheries, to determine whether core areas are established on the basis of food availability, were collected using two-stage cluster sampling (n=780 sites). Binary logistic models were developed for each data set and competing hypothesis. Candidate models were then selected using Akaike's Information Criterion (AICc) and evaluated using Receiver Operating Characteristic (ROC) curves.

Spatial habitat models explained between 52-60% and 44-51% of the variation between core areas and home range peripheries in the MGC and PCC landscapes, respectively. When evaluated, models were determined to be reasonable discriminators; the ROC area under the curve (AUC) ranged from 80-84% in the MGC and 84-86% in the PCC landscape. The variation explained using browse density models was 13-15% in the MGC and 10-12% in the PCC landscape, for models constructed using individual preferred

species; models for the MGC and PCC constructed using total browse density explained 22% (MGC) and 17% (PCC) of variation between core areas and home range peripheries. Models constructed using individual species were poor discriminators (AUC < 70% for all models). Total browse models were evaluated and had reasonable discrimination ability (AUC was 74% for the MGC and 73% for the PCC landscape).

Core areas and home range peripheries comprise similar habitat – primarily young seral patches. Cores, however, have a refined size, shape, and interspersion of the habitat, such that ecological factors affecting core use change monotonically with scale. Thus, core areas are not a distinct ecologically significant spatial scale for moose. Rather, they are an ambiguous scale which incorporates patch and home range level habitat selection characteristics.

Acknowledgements

"...ignorance more frequently begets confidence than does knowledge: it is those who know little, and not those who know much, who so positively assert that this or that problem will never be solved by science." – C. Darwin The Descent of Man xvi

Support for this thesis was provided by Lakehead Univeristy, an Ontario Graduate Scholarship, the Ontario Ministry of Natural Resources, and the National Science and Engineering Research Council.

I could not have completed the thesis without the help from the people at the Centre for Northern Forest Ecosystem Research. There is no program in the building that did not help me at some point or another. In particular, Brad Allison, whose logistical assistance throughout the thesis process was invaluable.

I would like thank several people who critically reviewed drafts of the proposal or thesis: the committee, Dr. Murray Lankester, Dr. Peter Lee, and Dr. Rob Rempel; Dr. Brian McLaren, Nancy Dewar, and Dr. William Muir Graham.

I'd like to recognize Gabe Lamarche for his assistance with the calculus. This marks close to 2 decades of math help Gabe has provided me.

The browse density data were tirelessly collected by a physically and mentally strong crew of individuals, each of whom I am indebted to: Mark Jantunen, Lindsey Barnes, and Chris Carli. Collectively, I think we would all like to thank saunas for existing.

I would like to thank Dr. Art Rodgers, not only for his support and the opportunity to study on this project, but for his flexibility, for encouraging me to push my own limits of understanding, and for challenging me to go beyond the practical or the obvious.

Of course I would like to recognize, my folks, Jake and Susan. In particular I would like to thank them for a decision they made 33 years ago to uproot themselves, and all they were familiar with, to move from the Golden Horseshoe to the remote, rugged wilderness of the Lakehead. Without that decision I would likely have become an economist, or accountant, probably out of touch with nature's vast and valuable beauty.

And I would like to thank Carissa for being with me while I am around or there for me while I am away.

Table of Contents

List of Figures

List of Tables

Preface

In 1989, the Ontario Ministry of Natural Resources initiated the Moose Guidelines Evaluation Program (MGEP) to study the efficacy of the *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR 1988) and provide increased understanding of timber management effects on moose populations. The program radio-collared 124 moose between 1995 and 2000, resulting in a data set exceeding 1,000,000 relocations. By putting an emphasis on individuals, the MGEP design has been able to address questions regarding moose genetics and morphometrics, condition and productivity, calving sites, use of aquatic feeding sites, and moose habitat use (Rempel et al. 1997; Welch 2000; Welch et al. 2000; Crouse 2003; Wilson et al. 2003). In addition, the program has gathered detailed habitat data pertaining to the study area in a Geographic Information System (GIS). This thesis capitalizes on a subset of MGEP information to address questions about animal movements, patterns of space use, and habitat selection; though none necessarily in terms of timber management systems.

The central question of this thesis is not addressed until Chapter 3: Detecting how spatial scale relates to habitat selection within core areas of moose home ranges during summer? Prior to answering that question I needed to first know, what is summer (Chapter 1), and second, which areas comprise the 'core' of the home range (Chapter 2)? Both Chapter 1, with the objective to designate summer based on an animal's rate of movement, and Chapter 2, which presents a synthesized method for designating core areas and tests whether the method delineates areas of intense use, required creating unambiguous definitions and techniques, currently absent or insufficient in the literature. For that reason, rather than writing Chapter 1 and 2 into the Methods section of Chapter 3, I wrote these

chapters to stand on their own merit. Thus, each includes additional information which goes beyond the scope of the central thesis of this project.

To reduce internal replication in this document the study area and collaring description sections appear only once.

Study Area

The study area is located in Northwestern Ontario, between 49.61°N and 46.68° N, latitude; and 91.98° W and 93.48° W, longitude (Figure 1).

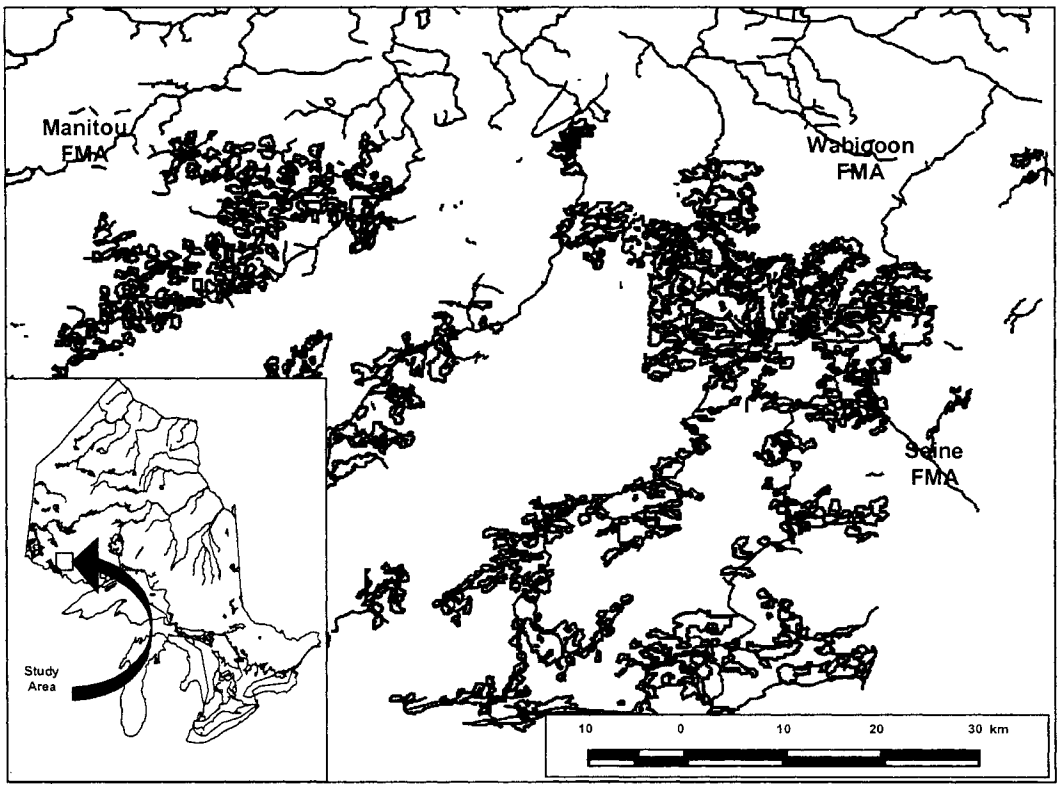

Figure 1. This study comprised 3 forest management areas (FMAs), Manitou, Wabigoon and the Seine, in Northwestern Ontario, Canada. The area consists of Boreal forests and Quetico-Great-Lakes St. Lawrence temperate forest (Rowe 1972). The boundaries of the area are 49.61°N and 46.68° N, latitude; and 91.98° W and 93.48° W, longitude (from Welch et al. 2000).

The study area straddles the ecotone between the Boreal forest to the north and the Quetico-Great Lakes-St. Lawrence forest to the south (Rowe 1972). The forest is dominated by pure to mixed stands of conifers: jack pine *Pinus banksiana*, black spruce *Picea mariana*,

white spruce *P. glauca*, and hardwoods (trembling aspen *Populus tremuloides*, balsam poplar *P. balsamifera* and white birch *Betula papyrifera*). Other species that are present include: balsam fir *Abies balsamea*, eastern white cedar *Thuja occidentalis*, eastern larch *Larix laricina*, eastern red pine *Pinus resinosa*, and eastern white pine *Pinus strobus*. Active forest management occurs in the study area; the result is recent clear-cuts in a mosaic of mature forests of up to 120 years in age (Rodgers et al. 1995).

Water bodies comprise an estimated 45 % of the area. In addition to lakes, many streams and rivers occur, ranging from primary tributaries to rivers 10 m in width (Rodgers et al. 1995). The landscape is oscillating Canadian Shield and ranges in elevation between 300 and 500 m above sea level (Rodgers et al. 1995).

The landscape experienced two separate timber harvesting systems. The forest management area (FMA) originally named the Manitou (1989-1992 moose density 0.224 km^{-2} ; Rempel et al. 1997) and FMA formerly known as the Seine were harvested in accordance with the *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR 1988) beginning in 1981 and are referred to as modified guidelines cuts (MGC). These areas were harvested using a 2-pass, dispersed block-cut harvesting system (Welch 2000). This created a landscape mosaic of different cut sizes (80-130 ha), shapes, and blocks left unharvested, comprising areas of approximately 15-km by 40-km and 15-km by 30-km in the Manitou and Seine FMAs, respectively (Welch 2000).

Portions of the FMA previously known as the Wabigoon (1989-1992 moose density 0.496 km^{-2} ; Rempel et al. 1997) were harvested as a contiguous clear-cut, often described as a

progressive clear-cut (PCC), since 1978 (Rodgers et al. 1995). The disturbance encompasses an area 15-km by 30-km in size (Welch 2000). The PCC technically complies with the *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR 1988); i.e., buffers remain around aquatic sites, but the clear-cut size is large, averaging 1,184 ha (Rempel et al. 1997).

Road access, and consequently access by hunters, differed between the forest management areas owing to the timber harvesting pattern (Rempel et al. 1997). The guidelines-cut FMAs require more roads in order to harvest the timber than the PCC. Additionally, hunter access was restricted in the PCC between 1978 and 1986 and again from 1990 to 1992 (Rempel et al. 1997).

Collaring

Relocation data from 60 free-ranging adult female moose, selected at random from a total of 124 animals that were fitted with NAVSTAR-based Global Positioning System (GPS) collars (GPS 1000, LOTEK Engineering Inc., Newmarket, Ontario) between 1995 and 2000 (Crouse 2003), were included in the determinations of 'core' areas (Chapter 2) and subsequent habitat analyses (Chapter 3). GPS collars attempted relocations of animals a minimum of every 4 hours until battery failure or collar removal in February each year. Locations were subsequently differentially corrected. Only 3-dimensional, differentially corrected data points were used in the analysis, resulting in a location accuracy of 3-7m (Rempel and Rodgers 1997). The mean number of relocations per animal during the summer was 466 (range: 48-1225) for these 60 adult female moose.

Development and evaluation of the rate of movement model as a method for designating seasonal boundaries (Chapter 1) required relocation data that were collected throughout the year. GPS technology improved substantially over the course of the MGEP study (Rodgers 2001) such that animals collared in the final year of the field program (2000) had the most complete data sets. Of those animals, I selected individuals for which data were available in all seasons between the time the GPS collar was deployed and retrieved, resulting in a subset of 32 free-ranging female moose that were all collared in 2000. For this subset of 32 individuals, used in Chapter 1, the mean number of relocations per animal throughout the year was 1130 (range: 664-2075), which averages to 1 location every 7.75 hours.

Chapter 1. Designating Seasonality: the Rate of Movement Model

Introduction

Movement provides the interconnection that links spatial and temporal relations among animals, their populations, and environments (Turchin 1998; Brillinger et al. 2004; Preisler et al. 2004). At different times moving is motivated, for example, by the social need to interact with con-specifics, as an anti-predator response, and by the need to acquire resources. Resulting patterns of animal movement provide information on behaviour and decision processes. However, identifying patterns of movement, and understanding the reasons for moving, are confounded when animals experience distinct seasonality. These animals are required to adapt and subsequently acclimate to differing supplies of resources and changing environmental conditions. Such species must use seasonally available foods that will, in part, sustain them through periods of resource drought. Studying animals on a seasonal time scale captures much of the variation inherent in animal response to a dynamic environment but requires delineation of periods between or among which behaviours are expected to differ. Identification of these time periods provides temporal definition to subsequent home range analyses.

Proxies of when animals are affected by seasonal change are widely used to designate seasonal boundaries. Typically these consist of single variables, such as climate, precipitation or phenology (Bowyer 1991; Jackson et al. 1991; Stewart et al. 2002; Oehler et al. 2003). Using single explanatory variables, however correlated to an animal's environment, cannot fully represent the suite of factors influencing behaviour. Use of such factors can perpetuate regional and local inaccuracies, which fail to capture the natural variation of individuals and the ecosystem. To properly understand specifics for an

animal's 'summer', for example, one must understand what is biologically important and which factors influence the animal during that time period, then designate the beginning and end of the season.

Exempting mammals that migrate or hibernate to avoid the inclemency of northern environments, the remainder have evolved to persist throughout the year. Northern cervids exhibit transhumance (Senft et al. 1987); i.e., their life requisites change with the seasons based on a repeated and patterned response to predictable seasonal shortages in forage availability. The North American moose (*Alces alces*) is differentially adapted to exist during the seasons of the year. Researchers have often divided the moose's season into three time periods: 'summer', 'early winter' and 'late winter' (Bowyer 1991; Jackson et al. 1991; Stewart et al. 2002; Oehler et al. 2003). 'Summer' is purported to begin early in May, at the onset of calving, and runs through first oestrus until late September. 'Early winter' is when moose have not been forced into coniferous habitats to avoid the largest snow accumulations, which constitutes 'late winter'.

Seasonal divisions can be based on available forage and feeding patterns. The moose is a seasonally adaptive concentrate selector (Schwartz 1992) and an energy maximizer (Belovsky1978) that capitalizes on the abundance of green forage during the 'summer' months to supplement its fibrous browse diet during the 'winter'. As an obligate herbivore in a dynamic environment, moose switch their feeding strategies with the seasons. Moose have a diet of green forage in the 'summer' and twigs and buds in the 'winter'. Selecting for different foods results in changes in handling time (*sensu* Holling 1959). For a

ruminant, such as the moose, handling time consists of two components: acquisition (i.e., leaf stripping or twig clipping) and rumination (i.e., regurgitation and repeated mastication) (Belovsky 1978); where 'winter' browse requires longer handling time than 'summer' forage (Hjeljord et al.1982; Renecker and Hudson 1985). Additionally, abiotic conditions influence moose behaviour between seasons. Though adapted to deep snow environments, the energy costs of movement are still higher in the 'winter' than the 'summer' (Coady 1974).

Stewart et al. (1977) describe differences in phenologies of moose forage in Saskatchewan. They compared total digestible nutrients and crude protein in forage species between leaf inception (mean = 17 May) and abscission (mean = 4 October), and of winter browse species. These dates have been used in studies across North America to designate seasons (Jackson et al. 1991). The phenological method for designating when an animal perceives seasonal change is coarse and is predicated on availability of foliar forage as the sole driver of behavioural change.

I suggest that a more precise method is to examine an animal's rate of movement, which is a comprehensive proxy of animal behaviour and is not solely contingent on environmental variables. It incorporates factors known and unknown that influence an animal's behaviour. Global Positioning System (GPS) biotelemetry collar technology yields high resolution near-continuous tracking data (Kernohan et al. 2001; Rodgers 2001) that can be used to quantify rate of movement. The resultant data describe a trail from which the researcher can infer movement response to seasonal resource availability.

I created a global set of theoretical models illustrating potential movement patterns of moose through the seasons of the year. Six movement models, constrained by the assumptions of cumulative data (i.e., the slope of the curve must be ≥ 0), were hypothesized (Figure 1.1), where the slope of the curve indicates the rate of movement. Rate of movement is affected by a combination of time spent searching and handling time for food (Holling 1959) in different seasons. A steeper slope indicates a higher rate of movement and implies shorter processing time.

Each model (Figure 1.1) is separated into seasons: 'summer' and 'winter', which is further divided into 'early winter' (EW) and 'late winter' (LW). The null model (Model 1) represents an animal which does not move, or moves very little. Model 2 is of an individual that moves at a constant rate throughout the year, unaffected by differences in 'summer' or 'winter' conditions. Model 3 indicates increased movement during the 'summer' when the animal has the greatest access to highly nutritious forage. This model predicts lower rates of movement in the winter when locomotion is encumbered by snow accumulation and food digestibility is at its lowest. Model 4 suggests that in 'summer', movement is at a minimum due to a seasonal overabundance of resources, resulting in reduced search and acquisition time, whereas the 'winter' months resource dearth results in greater search times. Model 5 suggests that only 'late winter' proves a hindrance to moose movement, due to accumulated snow depth, and individuals will search for foods, at a constant rate, throughout the remainder of the year. Model 6 presents a higher rate of

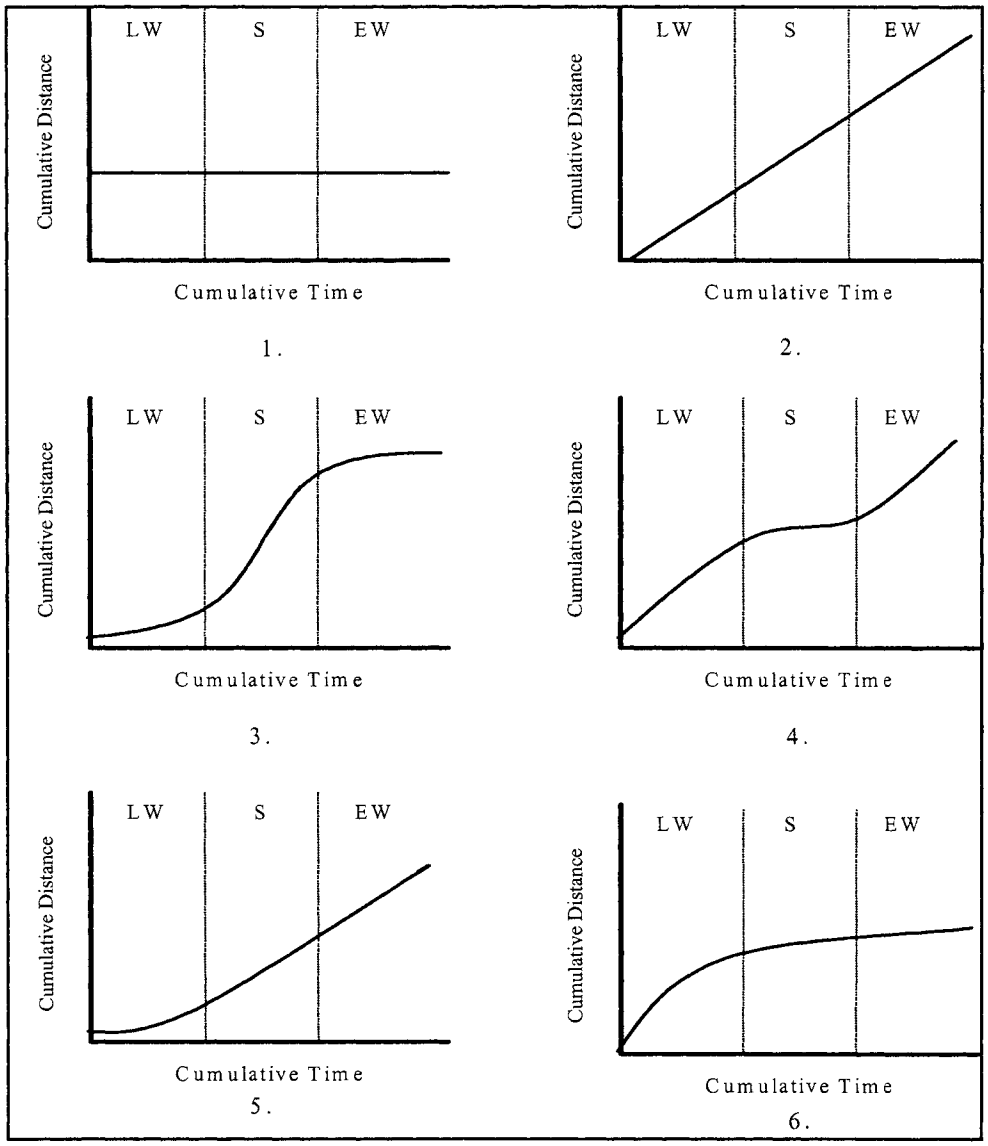

Figure 1.1. Six theoretical models of distance against time through the seasons of the year (LW = late winter, S = summer, EW = winter), given the constraints of cumulative data, where the slope indicates the rate of movement.

movement occurring only during 'late winter' when access to resources is most difficult. Of the 6 potential models, Models 3-6 represent movement patterns that have thresholds.

It is my objective to: (1) determine the pattern of female moose movements through the seasons of the year for comparison with theoretical models (Figure 1.1); (2) define and develop a method for demarcating seasonal boundaries based on changes in seasonal movement rates of female moose that can provide temporal definition to subsequent home range analyses (Chapter 3); and (3) compare seasonal boundaries based on changes in movement rates with previously used proxies based on single variables, such as phenology.

Methods

Designating Seasons

Cumulative distances (in meters) and associated times (in seconds) between successive animal relocations were calculated using the Home Range Extension (Rodgers and Carr 2002) in ArcView 3.2a (ESRI, Redlands, California, USA). Both distance and time were standardized and ranged from 0-1, viz., each sample is divided by the maximum cumulative distance or time: standardized cumulative distance (*SCD*) and standardized cumulative time (*SCT*), respectively. Values were standardized to make all graphs interpretable with a similar method at a similar scale.

Standardized cumulative distance for all animals was plotted against *SCT* for comparison with possible models (Figure 1.1). As the general relationship in the data approximated a sigmoid curve (Figure 1.3) most similar to Model 3 in Figure 1.1, a logistic curve fitting technique (SPSS v.11.5, SPSS Inc., Chicago, Illinois, USA) was selected and used to obtain equations for the curves of individual female moose.

In each case, standardized cumulative distance was regressed against *SCT*. The relationship was fit with a logistic curve:

$$SCD = \frac{1}{(\frac{1}{u} + b_0(b_1{}^{SCT}))} \qquad [1]$$

Where, u is the upper boundary value for the logistic model, b_0 is a constant and b_1 is the regression coefficient. The animal's instantaneous rate of movement was calculated as the first order derivative:

$$\partial SCT/\partial SCD = -\frac{b_0 b_1^{SCT} \ln(b_1)}{(\frac{1}{u} + b_0 b_1^{SCT})^2} \quad [2]$$

Consequently, due to the standardization procedure, the mean annual rate of movement is:

$$\partial SCD/\partial SCT = 1 \quad [3]$$

Whenever the slope of the logistic curve exceeds the mean annual rate of movement the animal is designated *in* the 'summer' season. Thus, seasonal boundaries are demarcated along the abscissa (*SCT*), where the first order derivative exceeds the mean annual rate of movement (the instantaneous transition from 'late-winter' to 'summer') and then recedes below the mean annual rate of movement (the instantaneous transition from 'summer' to 'early-winter') (Figure 1.2). The animals' rate of movement exceeds and recedes below the annual mean at:

$$\partial SCD/\partial SCT > 1 \text{ and } \partial SCD/\partial SCT < 1, \text{ respectively } [4]$$

Where SCT=1 is:

$$SCT = \frac{\ln(-u \ln(b_1) - 2 \pm \sqrt{u^2 \ln(b_1)^2 + 4u \ln(b_1)}) - \ln 2ub_0)}{\ln(b_1)} \quad [5]$$

The resulting values were multiplied by their respective maximum cumulative times yielding an interpretable date; i.e., calendar dates.

Additionally, the instantaneous point that designated the maximum rate of movement (i.e., when an animal's rate of movement began to decelerate) was determined using the second-order derivative of the *SCD* regression upon *SCT*, where it equals 0:

$$\partial SCD^2 \Big/ \partial^2 SCT = 0 \qquad [6]$$

Deceleration begins at the inflection point on the sigmoid curve:

$$SCT = \ln\left(\frac{1}{b_0 u}\right) \Big/ \ln(b_1) \quad [7]$$

Regressions were run on 32 individual female moose and on pooled data for all individuals with locations in the year 2000. Dates for 'pre-summer' and 'post-summer', and peak rates of movement were calculated.

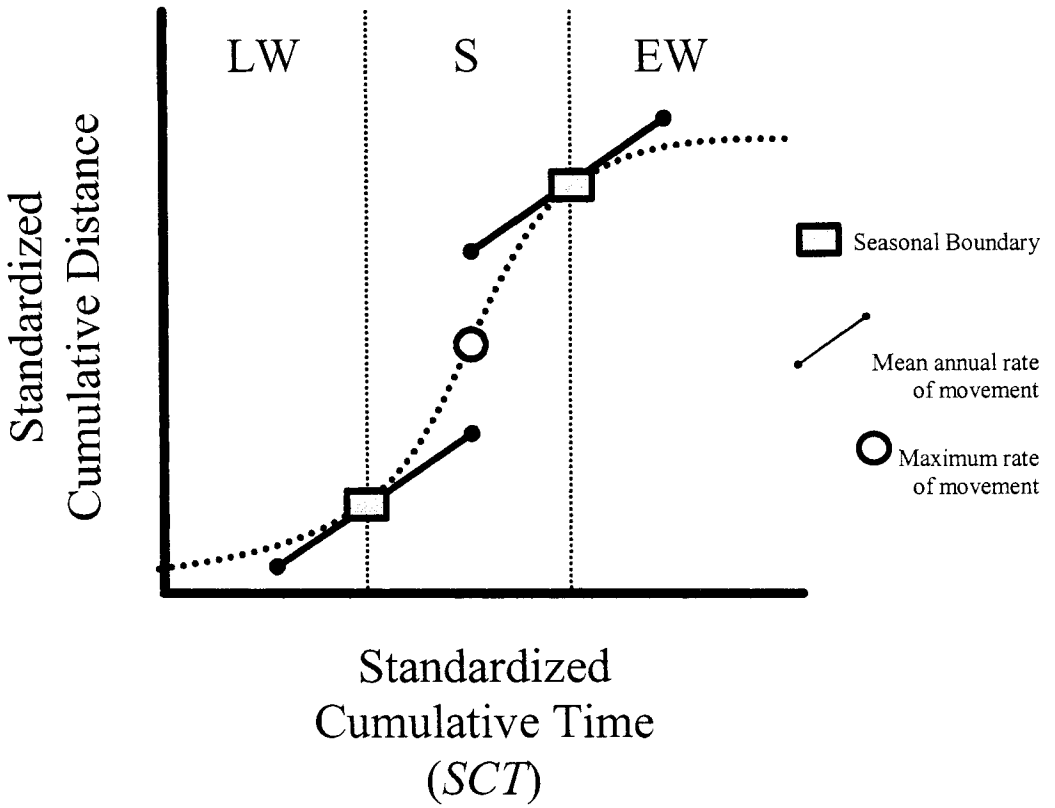

Figure 1.2. A hypothetical model of Standardized Cumulative Distance (*SCD*) regressed against Standardized Cumulative Time (*SCT*) and its key dissections. The shape is congruous with the sigmoid pattern of the data. The abscissa follows the calendar year, beginning in January. The model is divided into three sections: 'early winter', 'summer', and 'late winter'. Where ▭ denotes $\partial SCD/\partial SCT = 1$, and thus the area between ▭ is when rate of movement is greater than the annual mean. This area is designated as the 'summer'. Furthermore, ○ is when $\partial SCD^2/\partial^2 SCT = 0$, where the maximum rate of movement occurs.

Results

The rate of movement had a sigmoidal relationship over the calendar year (Figure 1.3), with the rate of movement for moose being less during the 'winter' months than the 'summer'. The median and mean dates at which moose exceeded the annual mean rate of movement were 01 May and 30 April, respectively (Table 1.1; range: 02 April – 24 May). The dates when the rate of movement fell below the annual average were: median = 25 August; mean = 31 August (Table 1.1; range: 1 August – 23 October). The global model resulting from analysis of pooled data yielded mean dates of 04 May and 13 September when the rates of movement exceeded and receded below the annual mean, respectively. Mean and median dates of individual and pooled-data models for maximum rate of movement and subsequent deceleration were 04 July (range: 17 June – 25 July). The number of days where the rate of movement exceeded the annual mean ranged between 96 and 173 (mean: 122, median = 119).

Table 1.1. Coefficient of Determination and Seasonal Transition Dates for GPS-collared adult female moose in Northwestern Ontario in 2000

	Adjusted R^2	'Late Winter'-'Summer' Transition Date[1]	Maximum Rate of Movement Date[2]	'Summer'-'Early Winter' Transition Date[3]
Median	0.92443	05/01/00	07/04/00	08/25/00
Mean	0.92341	04/30/00	07/04/00	08/31/00
Range	0.85-0.97	04/02-05/24	07/17-07/25	08/01-10/23
Pooled	0.91633	05/04/00	07/04/00	09/13/00

[1] 'Late-Winter'-'Summer' Transition Date is the day where the animals sustained rate of movement exceeded the annual mean rate of movement.
[2] The maximum rate of movement date corresponds to the second order derivative and demarcates the time when the animal is at its annual peak rate of movement, as well as the time when it begins decelerating.
[3] 'Summer'-'Early-Winter' Transition Date is the day where the animals sustained rate of movement receded below the annual mean rate of movement.

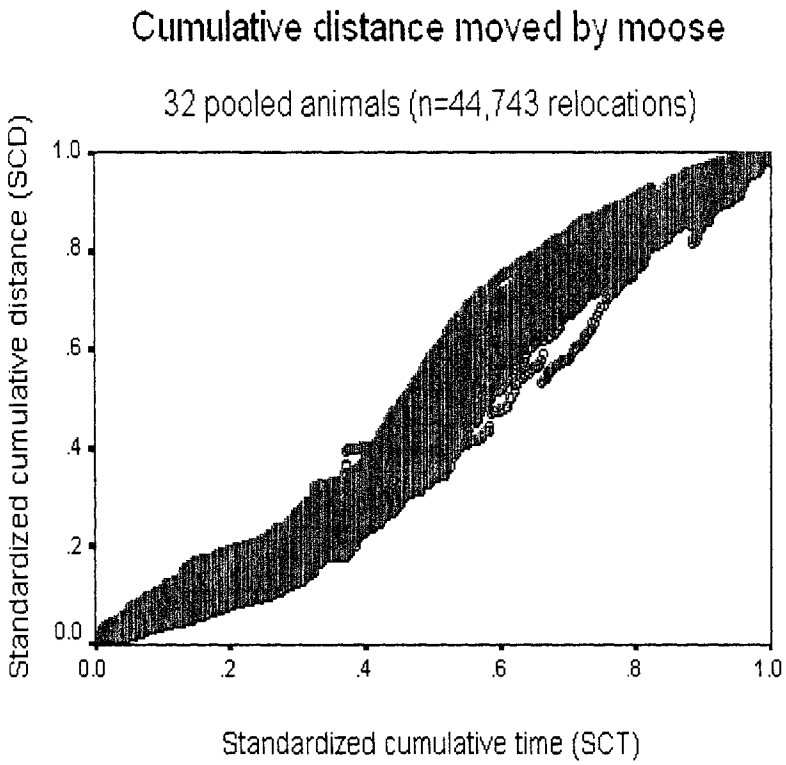

Figure 1.3. A scatter-plot of pooled cumulative-distances (n = 44,743) by cumulative-time for 32 GPS-collared adult female moose in Northwestern Ontario throughout 2000. Time on the abscissa approximates the calendar year (bound by the sampling regime), where values near 0 occur in late January and early February and the maximum value 1 occurs in late November and December. The graph outlines the distinct sigmoidal relationship between movement and season. This relationship indicates increased rate of movement throughout the 'summer' months when compared to the rate of movement throughout the remainder of the year.

Although the scatterplot of the global model indicated a sigmoidal relationship between *SCD* and *SCT* (Figure 1.3), differences existed among individual moose in the amount of variation and the appropriateness of the model. The mean amount of variation in *SCD* explained by *SCT* was 92.4% (range: 85.4% – 97.0%), which was comparable to the R^2 of the pooled model: 91.6%. Differences among individuals, however, are illustrated by extreme contrasts; e.g., Figure 1.4 and Figure 1.5. Figure 1.4 is a quintessential example of the sigmoid outcome and appears similar to the global model. Figure 1.5, an aberrant case, might be casually described as a linear relationship.

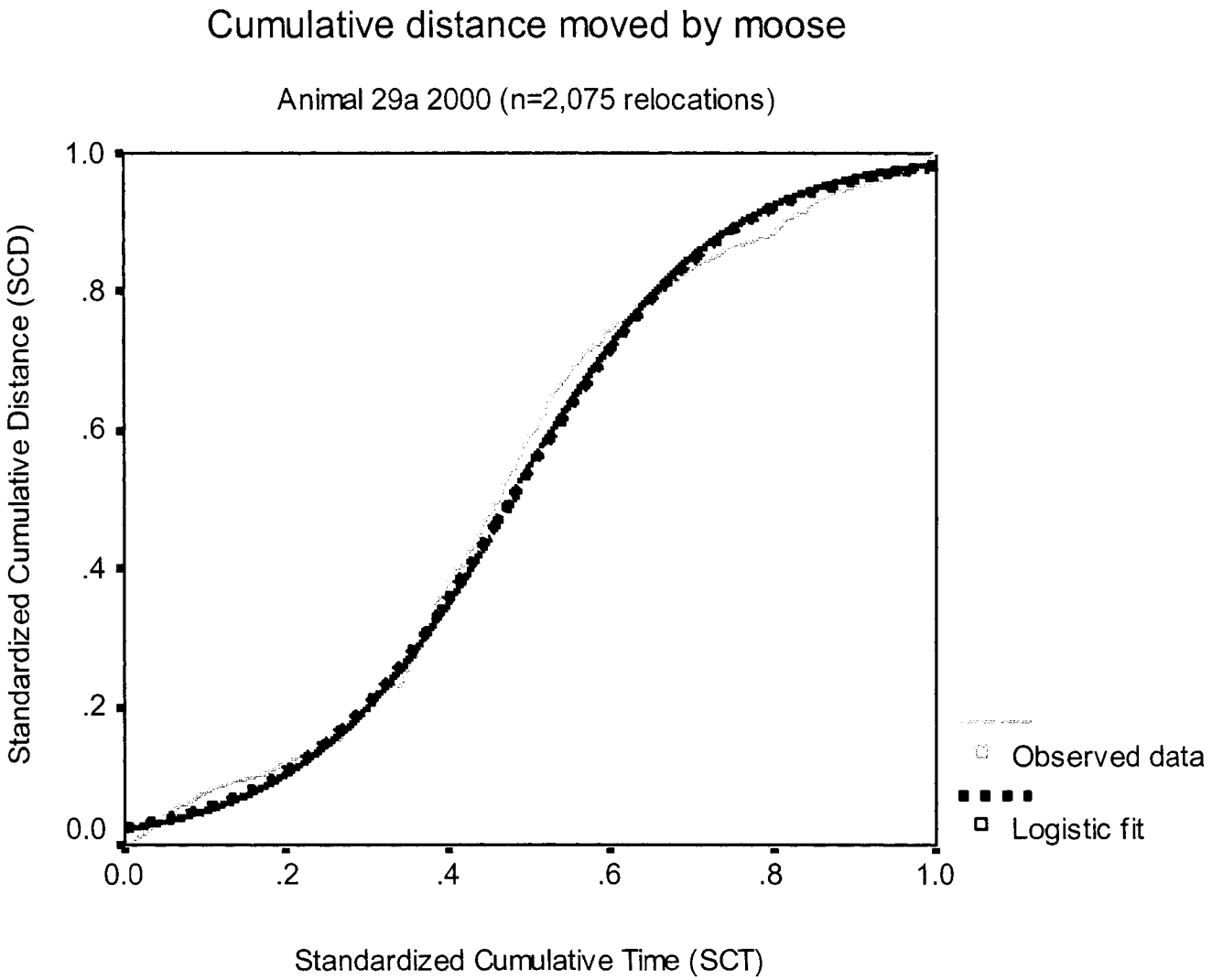

Figure 1.4. A quintessential example of model result: logistic curve-fit of Standardized Cumulative Distance (*SCD*) moved by a GPS-collared adult female moose in Northwestern Ontario against Standardized Cumulative Time (*SCT*) during the year 2000, which shows a sigmoid relationship (throughout the calendar year) and illustrates the rate of movement exceeding the annual mean during the 'summer'. The solid grey curve is the observed data distribution and the dashed black curve demonstrates how effectively the equation fit the curve. The coefficient of determination in this case was 97.0%.

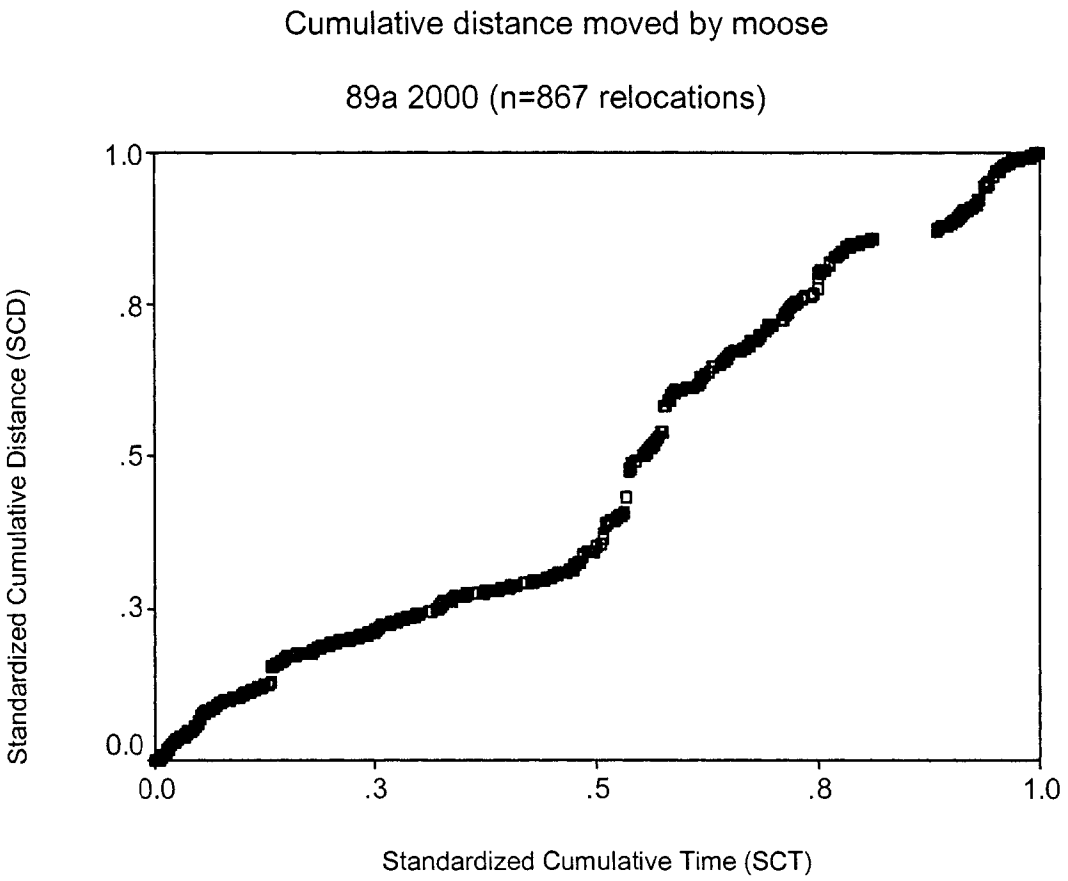

Figure 1.5. In contrast to Figure 1.4, this is a scatter plot of an atypical movement sequence of Standardized Cumulative Distance (*SCD*) moved by a GPS-collared adult female moose in Northwestern Ontario against Standardized Cumulative Time (*SCT*) during the year 2000. The relationship is poorly described by a logistic function. The coefficient of determination is 85%, however, there is a pattern in the residuals. The rate of movement does appear to increase temporarily during the 'summer', but the increase occurs only briefly and differs little from the remainder of the year.

Discussion

Moose had a greater rate of movement during the 'summer' relative to the 'winter', where the 'early summer' was a period of acceleration and 'late summer' a period of deceleration (Figure 1.3), similar to my hypothesized Model 3 (Figure 1.1). A proposed reason moose move more in the 'summer' than the 'winter' is that they are hyperphagic (Schwartz 1992) during the 'summer', exploiting a variety of forage species to increase digestibility and provide more nutrients in the diet; e.g., terrestrial and aquatic vegetation (Belovsky 1978). Moose increase their rate of intake (Renecker and Hudson 1986) to exploit available resources, accommodate lactation, and store fats for the 'winter' months (Timmermann and McNicol 1988). Additionally, moose consume 2.6-3.5% of their body weight in dry matter per day in summer compared to 0.5-1.3% in winter (Schwartz et al. 1984). The maximum rate of this consumption reaches different asymptotic maxima during different times of the year, reflecting the available diet, such that ingested usable biomass is markedly less in January than in July (Renecker and Hudson 1986). Consequently, the consumption of less digestible 'winter' browse increases ruminating time (Hjeljord et al. 1982; Renecker and Hudson 1985) and limits nutrient acquisition (Saether and Andersen 1989). Combined, the result is decreased foraging time and fewer large movements in the winter, as illustrated in the movement model (Figure 1.3). Moreover, with changes in food digestibility and availability, metabolism fluctuates throughout the year, peaking during the 'summer' and ebbing during the 'winter' (Schwartz 1992). Additionally, the increased energy costs of travel through snow in 'winter', which increases basal metabolic rate in a time of limited resources, can discourage animals from making large movements (Coady 1974).

Discrepancies between the phenological model (Stewart et al. 1977) and the rate of movement model exist in the transition from 'late winter' to 'summer' and 'summer' to 'early winter' (Figure 1.6) – at least in part because the phenological model was developed in eastern Saskatchewan and the rate of movement model in northwestern Ontario. Stewart et al. (1977) report mean dates of leaf inception and abscission in Saskatchewan were 17 May and 25 October, respectively. In comparison to northwestern Ontario, moose began to accelerate their movements 2 weeks prior to leaf inception. As all sample animals were females in this study, this may represent spatial shifts prior to calving, which occurs in mid-May (Testa et al. 2000; Welch et al. 2000). Additionally, increasing movement is likely related to snow loss simply decreasing the energy expense of locomotion, providing extra opportunities to search for foods at low cost (Coady 1974). Similarly, the transitions from 'summer' to 'early winter' do not coincide between the phenological model (Stewart et al. 1977) and the rate of movement model. Maximum rate of movement (04 July) of female moose coincided with the decline in total digestible nutrients, as measured by Stewart et al. (1977) using *in vitro* digestion techniques with sheep rumen innoculum, which peak and decrease during the first half of the summer. Subsequently, the rate of movement model indicated a decline in moose movements 2 months prior to leaf abscission. This may, in part, be a product of dry matter increasing and digestibility decreasing in forage plants as they prepare to abscise their leaves, thus increasing rumination time relative to earlier in the summer (Gasaway and Coady 1974). As well, the rate of movement of females falls below the annual mean near the time of first oestrus in August. Thus, a relationship might exist between rutting behaviour and lower movement rate in female moose. Overall, the

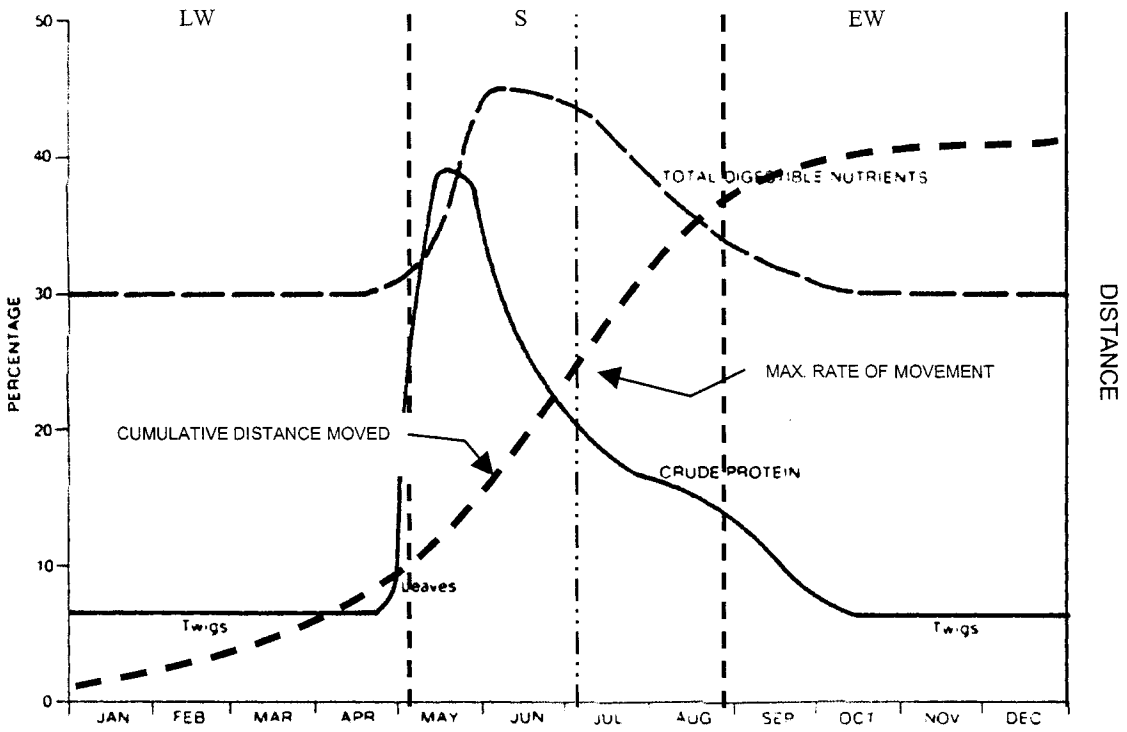

Figure 1.6. This figure, modified from Stewart et al. (1977), illustrates the nutrients in forage throughout the year overlain by a hypothetical cumulative moose movement curve with its associated seasonal boundaries and maximum rate of movement point. At a coarse level, the curve illustrates the increased rate of movement near the time of leaf inception. Rate of movement appears to increase in tandem with increased total digestible nutrients available in forage. The rate of movement peaks in early July and continues to decrease throughout the remainder of the 'summer' into the 'winter'. The inflection point coincides with a reduction in total digestible nutrients. Rate of movement recedes below the annual mean prior to leaf abscission near the end of August.

phenological model suggests a summer period of 140 green days (range: 121–168; Stewart et al. 1977) contrasted to animal movement response of 122 days (range: 96 – 173).

Variation existed among individual moose when fitting the rate of movement model. Scenarios such as Figure 1.5 were anomalies. However, counter-examples such as these can provide important information about an animal's ecology or circumstance. The typical sigmoid example (Figure 1.4) is a moose that exhibits an increased rate of movement during the 'summer' months, and limited movements during the 'winter' months. This relationship agrees with movement patterns suggested by previous authors. Risenhoover (1986) and Renecker and Hudson (1986) suggested that seasonal differences in handling time and search time are based on forage density and quality. Furthermore, Risenhoover (1986) suggested that movements related to foraging are inversely related to browse density. From a broader perspective, optimal foraging theory dictates that animals which are unsated will travel farther distances based on increasing time since their last meal (Charnov 1976). Thus, anomalous rate of movement patterns (e.g., Figure 1.5) might represent moose inhabiting landscapes with low density browse and having to travel further to fill the rumen with digestible browse and invest greater energy in searching. Renecker and Hudson (1986) found that the largest movements during feeding bouts occurred in 'winter' and were associated with widely spaced forage. This relationship could be used as an index of relative habitat quality and animals that do not conform to the sigmoid rate of movement (e.g., Figure 1.5) may be exploiting habitat with a low density of forage where they must maintain a higher rate of movement throughout the 'winter' to remain sated.

Superficially, this contradicts the hypothesis of Vivas and Saether (1987), which is predicated upon the handling time required for a ruminant to process its food. They hypothesize that moose, in 'winter', will devote more time searching for highly digestible browse to reduce rumination time (Vivas and Saether 1987; Saether and Andersen 1989; Andersen and Saether 1992), resulting in an increased rate of movement. Here the limits of the rate of movement model become apparent. The issue is scale dependant: where movements related to intra-patch search effort (i.e., selection at Johnson's (1980) fourth order) are too fine to be detected at 4 or 8 hour intervals (the inter-fix time of the GPS biotelemetry data). Rather, increased rates of movement during 'winter' are indicative of inter-patch relocations. These movements may be exacerbated by having to travel among patches of low browse density (selection at the third order; Johnson 1980). Renecker and Hudson (1986) found that large movements in 'winter' were associated with feeding on sparse forage. Suffice it to say that the model is contingent on relocation data that are too coarse to infer intra-patch level selection. The model can, however, provide insight into forage quality at the level of patch dispersion, and inter-patch exploitation by moose, where moose using small patches cannot sustain themselves for long periods of time and must frequently move among patches to provide sufficient 'winter' browse.

Similar to intra-patch movements the rate of movement model is too coarse to factor in fine scale movements resulting from encounters with predators. These encounters may result in a temporarily increased rate of movement, which may exceed the mean annual rate of movement. This increase is ephemeral, and thus will have a minimal effect on the sigmoid curve fit to illustrate seasonal boundaries. Presumably predator avoidance strategies

change at different predator densities: where an animal may either increase its movements to avoid predators; or conversely move less frequently to be inconspicuous. Furthermore, predation may force an animal into marginal habitats (Edwards 1983; Molvar and Bowyer 1994) where less digestible forage exists, thereby affecting rumination time. These strategies and their consequences might be seasonally specific as vulnerability to predation may change throughout the year.

Calving and having young at heel may also affect rates of movement. Female moose reduce their rates of movement following calving (Bowyer et al. 1998), however, similar to fine scale predation, this event is ephemeral and occurs at a small time scale and is thus unlikely to have an exclusive defining effect on the rate of movement model's seasonal boundaries. Perhaps using a higher order polynomial to fit the curve could reveal more information about fine scale events. Alternately, females with young at heel will choose to trade-off exploiting patches of high forage availability for patches in proximity to protective cover (Stringham 1974; Langley and Pletscher 1994; White and Berger 2001) and this might affect the selection of digestible forage and in turn movement rates. Ultimately, however, the rate of movement model is a proxy for multiple variables and would factor the effects of calving, presence of young at heel, and predation on an animal's perception of seasonal change.

Moose seasonality is traditionally divided into 3 periods (Jackson et al. 1991): 'summer', and 'early' versus 'late' 'winter'. The rate of movement model fails to distinguish between the 2 divisions of 'winter'. Though the potential exists for moose rate of movement to

decrease inversely with snow depth (Coady 1974), this change throughout the winter is gradual and indistinguishable to the rate of movement model if, as suggested above, the rate of movement model is related primarily to changes in the availability of high and low quality browse between 'summer' and 'winter' seasons, respectively. Since moose feed on low quality browse throughout the winter, the rate of movement model is unable to detect a change in behaviour between 'early' and 'late' 'winter'. The primary means of differentiating between 'early winter' and 'late winter' thus remains analyzing what habitats are being used in each period (Jackson et al. 1991).

The rate of movement model does not apply exclusively to moose, or large mammals for that matter. Rather, it can be applied to any animal that experiences changed requirements and environments between or among seasons. Nor is its use limited to studies that use GPS collar technology; all that is required are location data collected around the periods of expected seasonal changes. Although issues related to spatial scale are relevant, recognizing whether the model is influenced by intra- or inter-patch selection is affected primarily by inter-fix time. Thus, given small enough sample intervals (e.g., 2-3 days), traditional VHF radio-telemetry data would be suitable to build an inter-patch rate of movement model. When inter-fix time becomes increasingly small, the rate of movement model for moose – which is largely limited by time spent ruminating– can be interpreted, conversely, as the time spent *not* moving: *ergo*, the curve is a coarse scale temporally-explicit functional response of moose to food digestibility, where inferences on foraging strategies at the intra-patch level, such as energy maximizing versus time minimizing (Belovsky 1978), might be further explored.

The model has limits, but it also has strengths. Primarily it designates seasonality based on individual behaviour rather than a single driving variable (e.g., phenology). It is apparent that moose are responding to factors beyond foliar flush and leaf abscission: these can be speculated upon, but the model is a composite of known and unknown variables that affect moose movement and behaviour. Thus, for a utilitarian dissection of an animal's yearly cycle of behaviour, movement rates act as a comprehensive proxy for animal decisions. A designation of 'summer' that encompasses all activities expressing several behaviours is more precise than 'summer' contingent on a single independent variable. It is important to construct biologically significant seasons. Be it for conservation of important summer habitats used for birthing or feeding, for maintaining structure in disturbed landscapes that will sustain healthy populations, or studying seasonal changes in predation rates and other ecological processes, meaningful seasonal compartmentalization offers increasingly clear results when quantitatively designated using rate of movement. Moreover, these results can be used for temporal definition in subsequent analyses such as seasonal survival or home range estimation (Chapter 3).

Chapter 2. Synthesizing core area designation for moose (*Alces alces*): a quantitative approach

Introduction

Burt (1943) first described a "home range" as the area traversed by an individual in its normal activities, including refugia for protection, feeding, mating and other life history requisites. Since its conception, home range has been a main focus and useful tool in animal ecology. Hierarchically, home range is considered to be the second order spatial scale of selection (Johnson 1980). Between second order selection and patch selection (third order selection) is a dynamic category termed the 'core' area (Kaufmann 1962). The 'core' area does not conform to any prescribed spatial scale, *per se,* and can constitute a small percentage or the majority of a home range, depending on the study species or descriptive technique used. Currently 'core' area is defined as an area of intensive use (Samuel et al. 1985; Hodder et al. 1998; Wray et al. 1992). The uncertainty surrounding 'core' area definition is in part due to the vagueness of the term 'intensive'.

If they can be identified, intensive areas of use within-home-range patterns can offer biological information on animal movements, forage and other aspects of resource selection. Within-home-range patterns of use were originally termed "centres of activity" (Hayne 1949). The concept of centre of activity has expanded to incorporate multiple centres of activity (Samuel et al. 1985). These multiple centres of activity have been considered by many to comprise 'core' areas, and have been the focus of numerous studies (Michener 1979; Springer 1982; Samuel et al. 1985; Christian et al. 1986; Jaremovic and Croft 1987; Doncaster and Macdonald 1991; Heikkila et al. 1996; Hubbs and Boonstra

1998; Hodder et al. 1998; Chamberlain et al. 2000; Kitchen et al. 2000; Passinelli et al. 2001; Samson and Huot 2001; Kalmer et al. 2003; Glenn et al. 2004).

The delineation of 'core areas' has been approached in several ways. Many authors select "arbitrary" values, or values that qualitatively fit their data, to delineate 'core' areas (Chamberlain et al. 2000; Kitchen et al. 2000; Kilpatrick et al. 2001). Often they use subjective isopleth values ranging from 30% to 50% of the volume under individual utilization distributions to describe core areas (Heikkila et al. 1996; Chamberlain et al. 2000; Kitchen et al. 2000; Kilpatrick et al. 2001). Although arbitrary assignment of 'core' area is perhaps a suitable method for some studies, there exist inherent problems with replicability and comparability. In addition, arbitrary selection of isopleths, merely as a way to distinguish areas, may result in a loss of biological significance.

Several authors have appreciated the drawbacks related to arbitrary methods of designating core areas (Samuel et al. 1985; Hodder et al. 1998; Glenn et al 2004). Most of these studies fall into one of two associated families of techniques: the first using variations on percent inclusion of animal locations (Hodder et al. 1998; Kalmer et al. 2003) and the second using probability density functions (Samuel et al. 1985; Christian et al. 1986; Wray et al. 1992; Glenn et al. 2004). Hodder et al. (1998), for example, suggest using incremental cluster polygons; i.e., the plot of percent area against percent inclusion of fixes that has a distinct elbow designating the switch-point where home range size (or 'core') is stabilized – this point is akin to identifying the difference between simple foraging activities and excursive movements. Hodder et al. (1998) use the inclusion of points because utilization

distributions create a smooth curve, which they purport to be uninterpretable. On the other hand, these authors concede that their technique is subjective. In contrast, probability density functions, or utilization distributions, are used by Samuel et al. (1985). They suggest utilization distributions provide a measure of probabilistic space use based on time spent in a single area versus the total area used (Ford and Krumme 1979) and describe the 'core' area within the home range as the area where the probability of occurrence is greater than would be expected with uniform use.

However difficult 'core' areas are to quantify, their enigmatic existence persists. Moreover, 'core' areas are conspicuous features within home ranges of animals across taxa: in Mammalia (Michner 1979; Heikkila et al. 1996; Chamberlain et al. 2000; Kitchen et al. 2000), Aves (Hodder et al. 1998; Passinelli et al. 2001), and herpetofauna (Christian et al. 1986), for example. Besides being biologically ambiguous, there is no agreed upon method for calculating what components of the home range constitute the 'core' area. As a result, comparability among studies is difficult. This chapter places additional limits on the definition of 'core' area and subsequently marries the strengths of two accepted techniques, resulting in a quantitative, replicable method. I suggest that, conceptually, an area of *intensive* use or 'core' area is the minimum area within which an animal spends a maximum amount of time.

The moose (*Alces alces*) exists across Johnson's (1980) spatial scales and different components of moose ecology are associated with distinct spatial scales (Voigt et al. 2000). For example, inter- and intra-specific competition and predator-prey relationships occur at a

scale smaller than the selection of habitat elements, such as calving sites or protective cover, which is yet a smaller scale than landscape level habitat selection; i.e., selection of patch size or proximity to browse (Voigt et al. 2000; Kie et al. 2002). Thus, limiting a study to a single spatial scale can restrict ecological understanding —especially with respect to habitat selection (Bissonette et al. 1997). Recent technology, particularly Global Positioning System (GPS) biotelemetry collars (Kernohan et al. 2001; Rodgers 2001), has allowed collection of accurate and precise data in appropriate quantities for multiple-scale habitat studies of animals. Multi-scale approaches are imperative in capturing the hierarchical manner in which animals perceive their habitat: from 'core', or usual area, to the overall perception of a familiar area, or home range (Bissonette et al. 1997; Hodder et al. 1998). For instance, habitat selection for browse may occur at a different spatial scale than mate selection; thus describing selection on a single scale will fail to capture key components of an animal's biology (Bissonette et al. 1997). Selection results in non-uniform use of moose home ranges and consequently the apparent occurrence of 'core' areas (Heikkila et al. 1996). Prior to understanding what role, if any, areas of intensive use play in moose ecology, the 'core' areas themselves must be identified. This chapter hypothesizes a methodology for delineating core areas using a maximized-time – minimized-area approach that can be used to distinguish intensively used habitats from peripheral habitats within home ranges of individual moose for later comparison (Chapter 3).

Methods

Core Area Designation

The 90% isopleth from a kernel analysis (Silverman 1986; Worton 1989) of animal locations was used to designate home ranges. Strictly speaking, kernel analysis describes a utilization distribution and not a true home range. As kernel analysis only provides a probability that an animal may be found in a specified area, it cannot definitively describe 100% of the area an animal uses. For consistency with previous work by others, however, this study will adhere to the misconception that home range and utilization distributions are often considered synonymous. The 90% isopleth value was arbitrarily selected for the boundary of the home ranges, as it is a value near the statistically improbable 100%. In some cases, using the 90% isopleth may result in apparently fragmented home ranges, which may not be intuitively realistic, but this chapter will demonstrate that the isopleth value used to denote a home range has little bearing on the designation of 'core' area.

As the study of core areas is one of internal range configuration, an adaptive kernel was used rather than a fixed kernel. The adaptive kernel, although purported to over-smooth range boundaries compared to the fixed kernel (Silverman 1986; Kernohan et al. 2001), best describes the 'inner anatomy' of a home range (Worton 1989; Kernohan et al. 2001). Silverman (1986) and Worton (1989) suggest that the choice or shape of the kernel (e.g., Gaussian or Epanechnikov) is not as significant as selecting the bandwidth or bin size of the kernel histogram. The method of selecting bandwidth is, however, in debate (Worton

1989; Kernohan et al. 2001; Gitzen and Millspaugh 2003; Gitzen et al. in press). This study used the reference, or optimum bandwidth (h_ref), which determines the width of individual kernels placed over animal locations assuming an underlying bivariate normal distribution in the data, and ultimately controls the amount of smoothing in the utilization distribution; narrow kernels expose fine details whereas wide kernels reveal the general shape of utilization distributions (Silverman 1986; Worton 1989; Kernohan et al. 2001). An alternative method for calculating the bandwidth is least-squares-cross-validation (LSCV) (Silverman 1986; Worton 1989; Kernohan et al. 2001). The LSCV method tests potential values to determine the bandwidth that minimizes the mean integrated square error (i.e., the difference between the true density function and the kernel density estimate). However, LSCV has high sampling variability and is reported to choose overly small values, thereby under-smoothing the data (Kernohan et al. 2001; Gitzen and Millspaugh 2003; Gitzen et al. in press). All animals had minimum sample sizes for kernel analysis as suggested by Seaman (1991) and Nicholson (1997); i.e., at least 50 independent locations or greater. Independence between relocations was calculated using Swihart and Slade's (1985) index in the Home Range Extension (HRE) software package (Rodgers and Carr 2002). Kernel analysis was performed on the location data of 60 GPS collared adult female moose using the HRE software package (Rodgers and Carr 2002) in conjunction with ArcView 3.2a (ESRI, Redlands, California, USA).

A plot of utilization distribution (home range) area versus utilization distribution volume from adaptive kernel analysis of individual relocation data results in an exponential relationship (Figure 2.1) from which a core area can be derived for individual animals. The

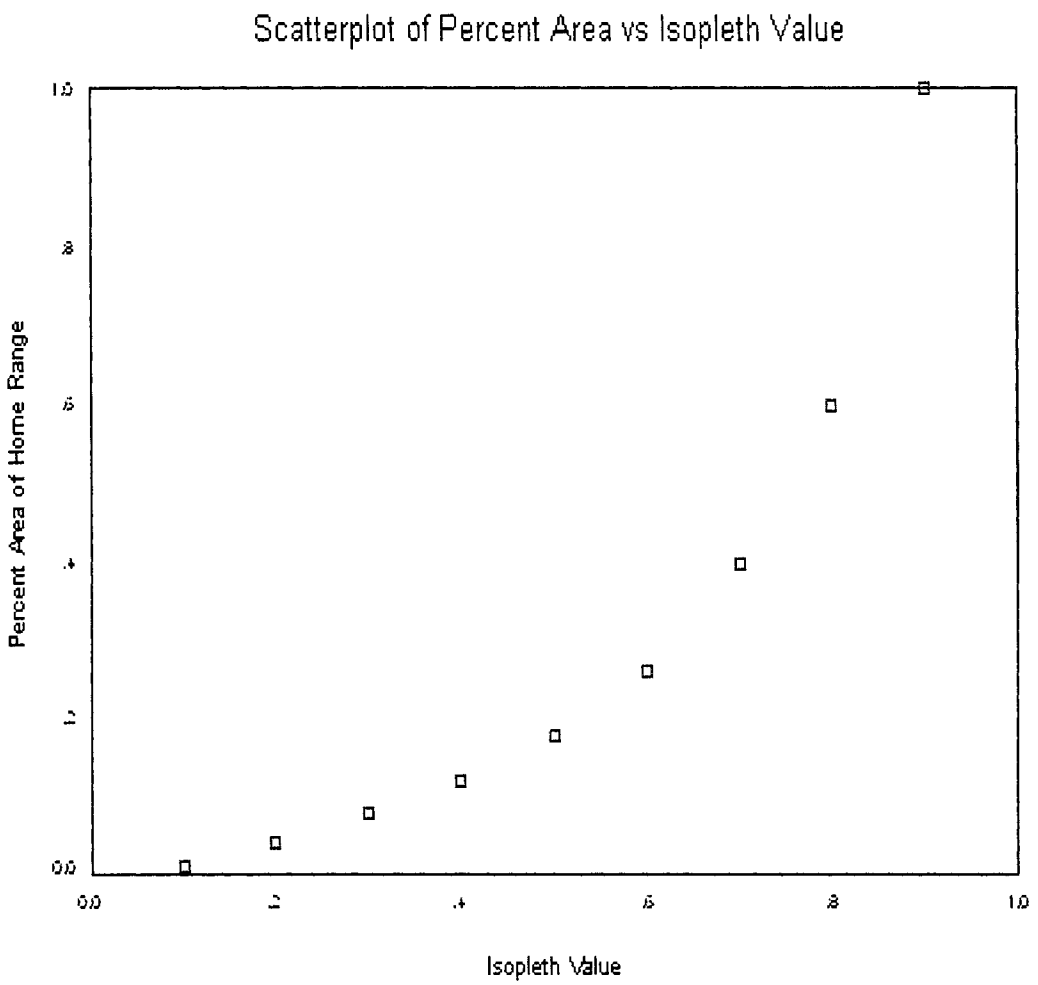

Figure 2.1. A scatterplot of percent area of the home range versus isopleth value (i.e., utilization distribution volume) determined by adaptive kernel analysis. There is a distinct exponential trend in the plot.

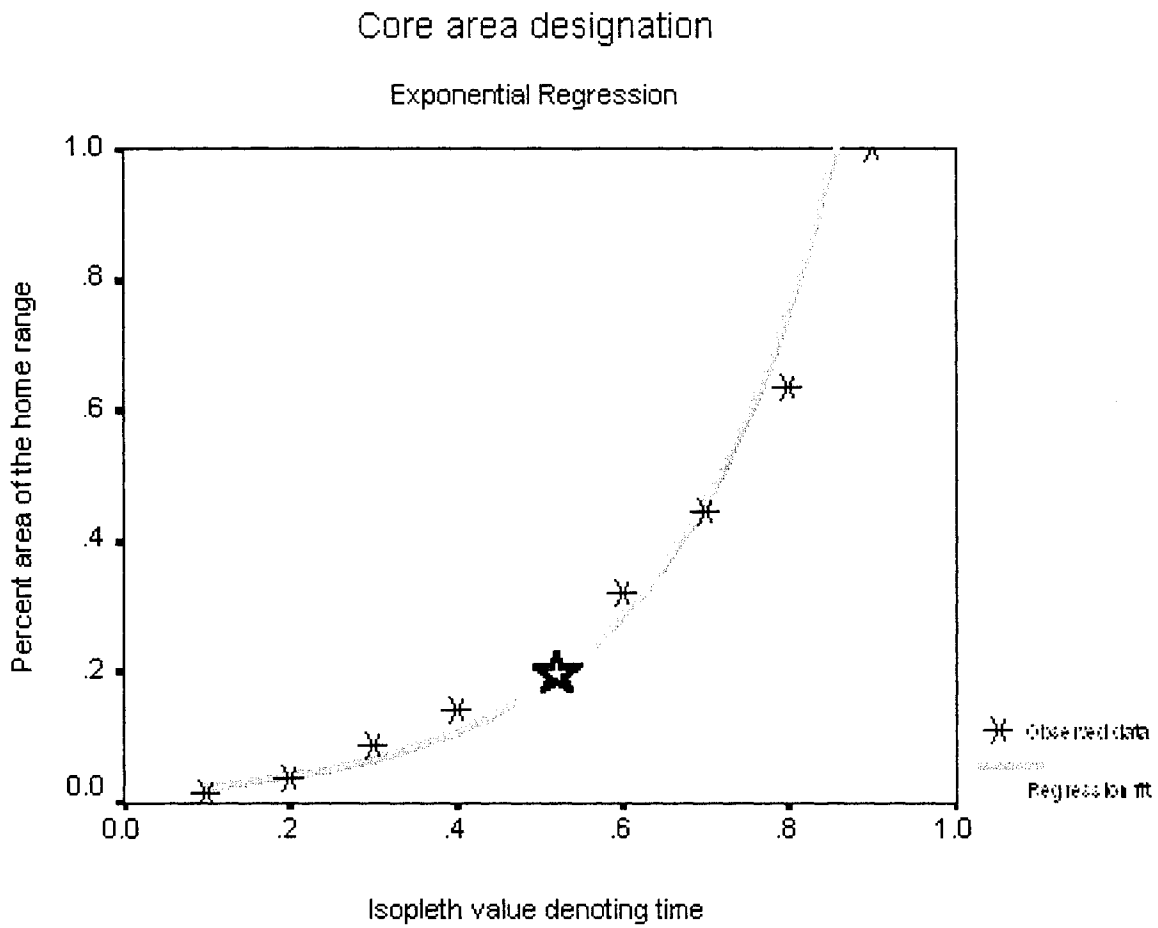

Figure 2.2. The observed curve of scaled utilization distribution area versus isopleth volume was derived from an adaptive kernel analysis (asterisks) of 329 locations of a GPS-collared adult female moose in Northwestern Ontario during the year 2000. It was fitted with an exponential regression, yielding an adjusted R^2 of 96% (grey curve). The star indicates where the slope of the fitted curve equals 1; i.e., the area to the left of the star represents the minimum area within which the animal maximized time spent. In this case, the 'core' area is subsequently defined by the isopleth that contains 53% of the utilization distribution volume.

area is the 2-dimensional coverage of the animals' utilization distribution (or home range) and the volume under the utilization distribution (i.e., the third dimension) – delineated by isopleths– is indicative of the likelihood of the animal spending time within different portions of its home range. To interpret the curve, the axes must be congruent; thus, home range area is standardized proportional to the total area covered by the utilization distribution and displayed as a percentage ($0 \leq$ total area ≤ 1: similar to $0 <$ distribution volume < 1) (Figure 2.2). This relationship of distribution volume versus area can be approximated with an exponential regression (Figure 2.2):

$$\ln(PA) = \ln(b_0) + b_1^{IV} \quad [1]$$

Where, PA is the Percent Area (y axis), IV is the Isopleth Value (on the abscissa); b_1 is the y-intercept; and b_0 is the exponential regression equation constant, as determined below.

The curve is asymptotic; thus, when differentiated, the point at which the slope is equal to 1 reflects the vertex where an animal's time spent is maximized within a minimum area. Therefore, generating an equation with statistical software (SPSS version 11.5, SPSS Inc., Chicago, Illinois, USA) and subsequently setting the first derivative [2] equal to 1 [3], the cut off point for the core area on the curve can be identified [4].

Where the first derivative is:

$$\frac{\partial PA}{\partial IV} = b_0 b_1 e^{b_1 * IV} \quad [2],$$

and where the area is minimized and time is maximized when the first derivative [2] equals 1:

$$\frac{\partial PA}{\partial IV} = 1 \text{ [3]},$$

such that substituting equation [3] into equation[2] and solving for *IV*, delineates the isopleth value that demarcates the outer boundary of the 'core' area:

$$IV = \frac{\ln(\frac{1}{b_0 b_1})}{b_1} \text{ [4]}.$$

For comparison among individual female moose, I calculated the isopleth value designating the 'core' area for each animal, the number of relocations within the 'core', the area defined by the 'core', and the proportion of the total home range enclosed by the 'core' area. To test whether 'core' areas in fact represent areas of intense use, I also calculated relative intensity of use using a method modified from Samuel et al. (1985):

$$I = \frac{\%Use}{\%HomeRange}$$

where, *I* is intensity of 'core' area use, *%Use* is the isopleth value (or probability of occurrence) associated with minimized area and maximized time, and *%HomeRange* is the proportion of the total home range occupied by the 'core' area. Values >1 indicate that the 'core' area is being used more intensely than the remainder of the home range, whereas values ≤ 1 indicate the contrary. This approach provides a way to verify the existence of a 'core' area within the home range of individual animals: if an area is not being used with greater intensity than the remaining home range it deviates from the definition of 'core' area.

Results

The 'core' area model produced isopleth values that ranged from 49% to 63% with a mean of 54% for 60 female moose. The mean coefficient of determination from fitting observed data with exponential regressions was 0.96 (range: 0.93 – 0.99). Core areas included a mean of 67% of animal relocations (range: 57 - 79%) and ranged in size from 115 ha to 6514 ha where the mean size was 863 ha (±129 ha). Proportionally, this represents a mean of 26% of the over-all home range (or area within the 90% isopleth; range: 14 - 55%). The mean relative intensity of use (I) was 2.17 (range: 0.91 – 4.00), where a single individual out of the 60 female moose included in these analyses did not use the area designated within the core proportionally more than the remainder of the home range; i.e., this individual had the lowest calculated value of I = 0.91.

Three examples illustrate the way in which multiple patches of intense use may be distributed within the home range of individual animals (Figure 2.3). Animal 31a (Figure 2.3 a) was the single female moose out of 60 which had a relative intensity of use value < 1. This indicates that the animal did not necessarily disproportionately use the core area relative to the home range peripheries. Dispersion of animal locations is less concentrated when compared to r75 (Figure 2.3 b) and r43 (Figure 2.3 c), both of which represent typical examples of animals that exhibit concentrated patch use, where the 'core' areas were used 2.17 and 4.0 times more intensely than home range peripheries, respectively.

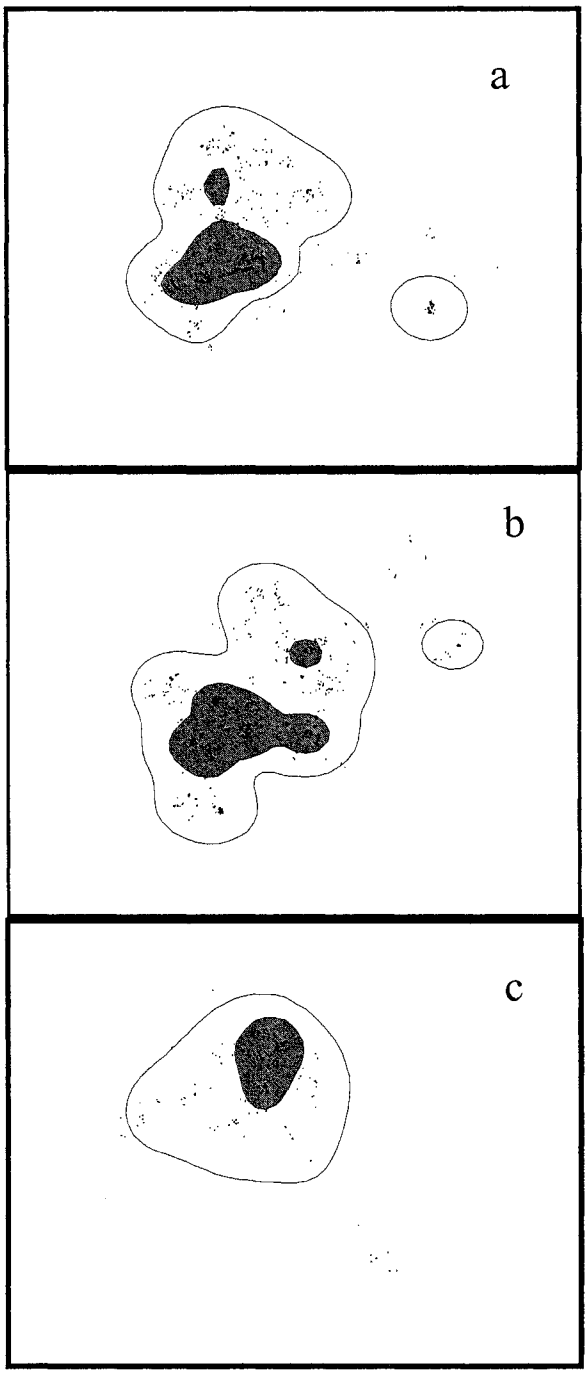

Figure 2.3. Examples of 'core' areas (hatched) nested within home ranges (90% utilization distribution) of GPS-collared adult female moose in Northwestern Ontario overlain with locations for (a) moose 31a (year 2000), (b) r75 (2000) and (c) r43 (1999), which have relative intensity of use values (I) of 0.91, 2.17 and 4.0, respectively.

Discussion

"Core areas are those areas used more frequently than any other areas and probably contain the home-sites, refuges and [the] most dependable resources" (Samuel et al. 1985). They are areas of *intense* use that can be described as the minimum area within which an animal spends a maximum amount of time. The method proposed in this Chapter identified areas that were used more intensely (mean relative intensity of 'core' area use, I = 2.17) by adult female moose than home range peripheries and contained, on average, 67% of relocations. Looking at 'core' areas as a maximizing function adds three key strengths: quantitative repeatability, probability of occurrence that implies time, and captures the variation in area used by individual animals.

Though the method of bandwidth selection used in kernel analyses remains subjective (e.g., h_ref versus LSCV), the method I have presented is objective beyond that point. Once the maximizing function [1] is accepted, the researcher no longer has control of the outcome. This is a strength (i.e., ensures repeatability), but, as in the case with moose, creates 'core' areas that have large spatial variation (1 order of magnitude). Less variation exists when 'core' areas are expressed as a percent of overall home range; i.e., the usual area as a proportion of the familiar area (*sensu* Hodder et al. 1998) remains relatively constant. In this study, the mean isopleth value that delineated the 'core' area for moose was 0.54; i.e., there was a 54% probability of finding the animal within a 'core' area that comprised an average 26% of the overall home range or 90% isopleth. Isopleth values for individual

adult female moose can thus be used to distinguish 'core' areas within overall home ranges for subsequent determination and comparison of habitat characteristics within (Chapter 3).

Samuel et al. (1985) espoused the qualities of using utilization distributions for describing internal range configurations: utilization distributions incorporate probability of use, detail internal range configurations, and consequently are more realistic in representing animal space use patterns. The technique described herein incorporates these strengths. Conversely, Samuel et al. (1985) expressed concern in using a technique, based on unbounded utilization distributions (e.g., kernel analysis), where selecting different maximum isopleth values to designate the home range will alter the results of 'core' delineation. Kernel analysis is a continuous asymptotic technique which uses probabilities rather than certainties (utilization distributions are not true home ranges; *sensu* Burt 1943). The maximum isopleth chosen for the technique is inconsequential, as the approximation of the curve simulates the asymptotic (i.e., infinite) nature of kernel analysis; viz., in theory, the 100% isopleth from a kernel analysis equals infinity, much the same as the upper limit of an exponential function, such that the equation for the exponential regression curve (which ultimately equals infinity) simulates the probabilities of the outer isopleths of a kernel analysis. Thus, whether the home range is bounded, for example, by the 90% isopleth or the 95% isopleth, it will not influence the outcome of the core area designation.

The main limitation of my approach is the ability to successfully fit an equation to the isopleth probabilities versus standardized area regression (Figure 2.2). The technique I have proposed is also constrained by kernel analysis assumptions and minimum sample

size requirements (Seaman et al. 1991). Of particular concern is the debate surrounding bandwidth selection methods (Worton 1989; Kernohan et al. 2001; Gitzen and Millspaugh 2003; Gitzen et al. in press): analyses using the least squares (LSCV) method may not be comparable to studies that use the reference bandwidth (h_ref). Similarly, fixed and adaptive kernels should not be compared, although it is recommended that adaptive kernels are more suitable for within home range patterns of use than fixed kernels (Worton 1989; Kernohan et al. 2001). Additionally, it is important to understand the scale at which questions are posed, and determine whether it would be more appropriate to look at finer scale patch level (third order) processes, or fourth order (Johnson 1980) selection, which could have less spatial variation than a 'core' area. I suggest that this method be tested on other taxa to see if it can be used to isolate areas of intense use as it can for moose. Moreover, it would be beneficial to use animals that have different foraging strategies than ungulates: e.g., central place foragers, predators, highly mobile or migratory animals.

Chapter 3. Detecting the effects of spatial scale of analysis on habitat selection within the home range of moose: tests of two hypotheses of disproportionate space use by moose (*Alces alces*)

Introduction

Consideration of scale is essential for understanding ecological processes (Wiens 1989). Different processes operate at different temporal and spatial scales, relevant to a particular organism (Holling 1992) resulting in distinct ecological neighbourhoods (Addicot et al. 1987). The hierarchical structure of scale is fundamental to interactions in nature, termed domains (Wiens 1989). The implications of hierarchy theory affect foraging strategies (Senft et al. 1987), and in turn influence a species' goal of maximizing fitness (Schoener 1971) through optimal foraging (Pyke et al. 1977), the outward manifestation of which is habitat selection. Consequently, habitat selected is impacted differentially at multiple spatial scales or domains. Rettie and Messier (2000) go further to suggest that each domain pertains to a specific limiting factor, or set there-of, and that selection at coarse scales has a larger impact on over-all fitness than fine scale decisions. Thus, to understand why an animal selects specific habitats, one must understand how processes in different domains impact on an individual.

Second and third order selection (Johnson 1980) pertain to habitat selection for home ranges (*sensu* Burt 1943) and the patch matrix within the home range, respectively. Disproportionate use of resources relative to their availability within the home range often results in a centre of activity (Hayne 1949) or multiple centres of activity (Samuel et al. 1985) comprising 'core' areas (Chapter 2). It is imperative that these core areas are evaluated as to whether they are spatial artefacts related to resource use and availability (i.e., selection) or behavioural responses to intra- or inter-specific interactions (Kaufmann 1962); i.e., any distribution can be fit with a core area – whether the core area is

biologically significant relative to the remainder of the home range, however, requires further examination. For example, coyote (*Canis latrans*) core areas are arranged to reduce interactions between competing individuals and while home ranges may overlap, areas of high intensity use often do not (Chamberlain et al. 2000). Also, with buzzards (*Buteo buteo*), where foraging is concentrated into core areas, these areas exclude excursive exploratory movements (Hodder et al. 1998). As home ranges are complex assemblages of economical (e.g., forage) and structural (e.g., cover) resources, many factors may explain the existence and intensive use of core areas.

Animals with home ranges that exist at a large spatial scale are suitable subjects for studying the effects of forest landscape heterogeneity on habitat selection. This is because natural variation is incorporated by large home ranges that encompass habitats which consist of heterogeneous patches on the landscape. Thus, both home range and core areas can be affected by landscape level spatial heterogeneity. Li and Reynolds (1994) describe spatial heterogeneity as the "complexity and variability of a system's property in space." Landscape heterogeneity can be considered in at least two ways: landscape composition, including patch composition and proportion, and landscape physiognomies (Dunning et al. 1992) which comprise configuration, sizes, shapes, arrangements, and inter-patch contrasts, among other characteristics (Li and Reynolds 1994). These landscape characteristics affect the way animals persist within their habitats and can explain some aspects of selection: for example habitat complementation (i.e., using a combination of proximal patches where one contains a specific resource that is suitable to some life requirement and unsuitable for another requirement and vice versa, such that in combination one complements the other) or supplementation (i.e., where animals can exploit patches with substitutable resources

extraneous to their focal patch, thereby supplementing available resources) (Dunning et al 1992).

Landscape characteristics of forests are dynamic; they are subject to change by different processes; e.g., competition, disturbance, etc. Disturbance, natural or anthropogenic, can change spatial configurations as well as compositional and seral characteristics of patches within the landscape. As a result, disturbance can have a detrimental effect on some species, or conversely create habitat for species adapted to systems with those qualities. In some cases animals that have adapted to feeding on early successional plants may exploit landscapes affected by disturbance; e.g., moose.

Moose populations are primarily affected by three processes: competition for available forage, predation by wolves (Messier 1991), black bears (Ballard and Van Ballenberghe 1998) or humans (Rempel et al. 1997), and snow accumulation (Mech et al. 1987). These different processes manifest themselves in selection patterns at different spatial scales or domains. First order selection (Johnson 1980) for moose is the Boreal forest – a biome that has evolved with disturbance. Consequently, this affects the processes which dominate moose behaviour. Historically, forest fire was the major form of disturbance in the Boreal forest, driving landscape structure both spatially and temporally and resulting in a mosaic of stand size, age, patch shape, and tree species composition (Thompson 2000). Moose, which are selective-generalists (Peek 1998) or coarse-grained foragers (*sensu* Rosenzwieg 1981), feed on early succession vegetation and have evolved with disturbance, acclimating to, and exploiting changing conditions (Voigt et al. 2000). Existing within this mosaic of disturbed patches and contiguous forest, moose have adapted to persist across large spatial

scales; with a home range size of 20-40 km^2 (Crête 1988). In addition, landscape level disturbance affects how moose select habitat that maximizes foraging opportunities and minimizes the risk of predation.

Several investigators have purported that moose have "core" areas (Cederlund and Okarma 1988; Heikkila et al. 1996). None, however, has determined what drives the clustering of moose locations. Cederlund and Okarma (1988) found that core areas had a large degree of overlap among individuals, which consequently rules out the influence of negative competition-mediated interactions between conspecifics (Fretwell and Lucas 1970); i.e., "spacing away" or intra-specific avoidance to reduce competition for resources. More likely, core areas for moose represent the culmination of selection for food and habitat characteristics relative to their availability within the overall home range; i.e., the distribution and abundance of positive attributes will be greater and negative attributes will be less in core areas than the remainder of the home range. Consequently, comparison of resource attributes between intensively used core areas and the remainder of the home range can be used to assess the relative importance of variables to the selection process at each scale.

I looked at within-home range habitat selection of moose at different spatial scales to determine which variables are important at each level of organization. I examined multiple spatial scales of habitat selection with respect to spatial organization and composition of habitats and availability of forage. This study embodies a multi-scale approach, with defined spatial and temporal extents (Wiens 1989), imperative in capturing the hierarchical

manner in which animals and their habitat interact. The temporal extent of this study is limited to the summer (Chapter 1). Summer habitat selection of female ungulates, moose included, is critical to accumulating sufficient fat stores to successfully reproduce (Cameron et al. 1993; Schwartz and Huntermark 1993) and survive through the winter (Moen et al. 1997). Spatially, the comparison is between the "core" or "usual" area and the "familiar" area or "home range periphery" (Bissonette et al. 1997; Hodder et al. 1998; Chapter 2).

I tested 2 competing hypotheses that may determine habitat selection at 2 spatial scales (core areas and home range peripheries): (1) core areas represent different spatial configurations of habitats when compared to home range peripheries; and (2) core areas are used more intensively (i.e., selected) to contain a subset of 'preferred' forage species with higher individual densities or a higher total density of all forage species than home range peripheries.

Methods

Season Reference

The focus of this study is on habitat use during the summer season. Summer is designated as the time period when an animal exceeds its annual mean rate of movement. For a detailed description of the technique used to define the beginning and end of the summer season see Chapter 1.

Core Designation

Core area designation followed the maximized-time—minimized-area method outlined in Chapter 2.

Spatial Approach

Data Collection (GIS)

To test whether core areas represent different spatial configurations of habitats relative to peripheral areas, spatial data were collected from a Forest Resource Inventory (FRI; OMNR 1999) of the 3 forest management areas occupied by GPS collared moose in this study and interpreted using ArcView 3.2a (ESRI Inc., Redlands, California, USA). Habitats were grouped by composition and age into a matrix of deciduous, mixed-wood and coniferous types following Courtois et al. (2002) of: (1) less than 20 years of age (maximum browse production; Crête 1988); (2) between 21 and 60 years; and (3) greater than 60 years since disturbance. FRI working groups were first clustered into standard forest units with the Strategic Forest Management Model Tool (SFMM Tool version 2.2;

Watkins and Davis 1999), then grouped further into the 3 aforementioned categories based on age (see Appendix 1 for SQL used). Each of the resulting 9 groups, plus a separate classification of wetlands, had spatial metrics calculated for their area, density and size, shape, edge, and interspersion.

To retrieve spatial information, Patch Analyst (Elkie et al. 1999) was used as a front end for Fragstats (McGarigal and Marks 1995). Comparisons were made between two areas of unequal size (i.e., cores versus home range peripheries; Chapter 2), so metrics that were neither indexed nor proportional were avoided; e.g., total edge, number of patches, etc. However, to ensure that the results were not biased, the sizes of core and home range periphery areas of all moose (n=60) were plotted against individual spatial metrics within each habitat category; no statistically significant relationships were found between area and the values of the spatial metrics in any of the 10 habitat categories, suggesting the metrics used were unaffected by differences in the size of core areas versus home range peripheries. All spatial metrics are based on similar variables, such as area and perimeter, creating multi-collinearity among metrics. Subsequently, collinearity was eliminated by variable selection, prior to model construction. Multi-collinearity was evaluated using Variance Inflation Factors (VIFs) coupled with non-parametric cluster analysis (Harrell 2001); all variables had a VIF<10 and a condition index <15.

Area Metrics:

- Class Area (CA; a measure of landscape composition) and Total Landscape Area (TLA; which define the extent of the landscape) were used as a ratio to calculate the proportion of each forest type within the core and home range periphery.

- "Core Area Density (CAD)" (*sensu* McGarigal and Marks 1995) was also calculated. "Core", is henceforth referred to as Stand Interior to avoid confusion with core areas of intense animal use (Chapter 2). Stand Interiors were calculated as the interior area of a stand that was greater than 100 m from an edge (Courtois et al. 2002). Stand Interior Density is a measure of the number of disjunct interior stand patches per 1 ha (Elkie et al. 1999).
- Total "Core Area" Index (TCAI) or Total Stand Interior Index was calculated to describe the percentage of stand interior within the landscape.

Patch Density and Size Metrics:

- Median Patch Size (MDPS) was calculated and selected preferentially over Mean Patch Size because the data were non-normal.
- Patch Size Coefficient of Variation (PSCV) was calculated. This metric was preferentially selected over Patch Size Standard Deviation, as it generally provides a better comparison between landscapes (McGarigal and Marks 1995).

Edge Metrics:

- Edge Density (ED), which standardizes edge per unit area, was calculated.

Shape Metrics:

- Mean Shape Index (MSI) and Area Weighted Mean Shape Index (AWMSI) are measures of patch complexity, whereas Mean Patch Fractal Dimension (MPFD) and Area Weighted Mean Patch Fractal Dimension (AWMPFD) are measures of patch morphology. Fractal dimensions are measures of tortuosity, where values near 1 are linear (or have simple perimeters) and values near 2 describe patches that are more

sinuous (or have complex perimeters). All four, however, are highly collinear so MPFD was used preferentially as an easily interpretable metric.

Interspersion

- An Interspersion and Juxtaposition Index (IJI) was calculated to characterize the diversity of patches dispersed throughout the core area and home range periphery.

Data reduction

Analyses were divided by timber harvesting system (modified guidelines cut, MGC; and progressive contiguous clear-cut, PCC), as each landscape had a distinct set of first order statistics. Pooling all the data for both landscapes would have confounded analyses and interpretation. Furthermore, data were randomly subdivided for k-fold cross validation (Fielding and Bell 1997). Two-thirds of the data were dedicated to developing the model ("Dvlp" in Tables 3.1-3.4) and the remaining 1/3 were used to evaluate the validity of the model ("Test" in Tables 3.1-3.4, see below).

Logistic regressions (using SPSS v.11.5, SPSS Inc., Chicago, Illinois, USA) were calculated for individual explanatory variables to evaluate the role that each plays in determining the dependent variable; i.e., whether an area is core (1) or periphery (0). Those independent variables that explained greater than 10% of the variation between core area and home range periphery were retained and tested in a global set of models.

Core and Home Range comparison using Logistic Regression

Retained variables were subsequently used in a model selection procedure suggested by Shatland et al. (2003), which maximizes the variable selection strengths of stepwise regression in predictive and exploratory studies (Menard 1995), and the ability to avoid arbitrary alpha values by using an information-theoretic approach (Burnham and Anderson 1998). First, I calculated a series of forward stepwise logistic regressions following Shatland et al. (2003). Then, Akaike's Information Criterion for small sample sizes (AICc; Burnham and Anderson 1998) was used to select the most parsimonious of the candidate models. Suites of final models with the lowest evidence ratios were selected for interpretation: evidence ratios are calculated by dividing a model's Akaike weight by the largest Akaike weight in the set of possible models (Burnham and Anderson 1998). Burnham and Anderson (1998) suggest that evidence ratios from 2-4 are weak evidence that the models are not the best approximation of the Kullback-Liebler distance; whereas ratios between 4-7 and 7-10 suggest definitive and strong evidence, respectively, that the model is not the best fit. Thus, for the purposes of full analysis and discussion, all models with evidence ratios less than 10 are presented.

The candidate models were tested using Receiver Operating Characteristic (ROC) curves (SPSS v.11.5, SPSS Inc., Chicago, Illinois, USA). Receiver Operating Characteristic curves allow evaluation of the predictive power of the logistic regression models and reflect how accurately and robustly the models classify the data (Boyce et al. 2002). Receiver Operating Characteristic curves were created for both the model development ("Dvlp"; 2/3) and evaluation ("Test"; 1/3) data.

Forage Availability

Data Collection

Browse density data, to determine whether core areas are a product of food availability, were collected using two-stage cluster sampling to minimize variance with a minimum sampling effort (Cochran 1977). Within the core area and home range periphery of individual moose, 3-5 cluster centriods were selected. Each cluster centroid was a known location for that individual that was randomly selected using the Animal Movement 2.0 (Hooge and Eichenlaub 2000) software program. Cluster centroids were buffered with circles using XTools ArcView Extension (DeLaune 2000). Each circle had a radius equal to the mean distance between summer relocations of the individual animal. Within the circle, 3- 6 sample sites (UTM co-ordinates; n=780) were randomly selected using Random Points in Polygon (Cederholm 2000) with the caveat that sample sites were required to correspond to their prescribed area; i.e., core or home range periphery.

Variable length belt transects were used to quantify browse density and composition at each sample site. The Universal Transverse Mercator (UTM) co-ordinate pair of the sample site was located at one end of the belt transect. Belt transects were run North from the sample site. Sampling was accomplished by walking the transect while holding a meter-stick horizontally 1 m from the ground surface. The belt transects were thus 1m wide and 1m off the ground. Each browse stem that fell within the transect was counted and the species recorded. The variable length belt transects were terminated once 30 stems of browse had been encountered.

Browse densities were calculated for 8 preferred summer forage genera (Peek et al. 1976): *Populus* spp., *Acer* spp., *Amelanchier* spp., *Betula* spp., *Salix* spp, *Prunus* spp., *Corylus* spp. and *Sorbus* spp.. Total browse density was also calculated.

Core and Home Range comparison using Logistic Regression

Two sets of logistic regression models were calculated: one each for the MGC and PCC landscapes, either including over-all browse density or individual species' densities. The model selection used a forward stepwise technique (Shatland et al. 2003). Akaike's Information Criterion (AICc) was calculated for candidate models, where those with the lowest evidence ratios < 10 were selected (Burnham and Anderson 1998) for further interpretation. Each of the resulting models was compared with the others using ROC curves on both the development and evaluation data.

Results

Spatial Approach

MGC Landscape

Five logistic regression models resulted from the MGC landscape classification using the information-theoretic approach (Table 3.1), 3 of which had evidence ratios of less than 4. All models explained 52-60% of the variation among the spatial metrics within the core area and the home range periphery. Every model consisted of 3 key explanatory variables: the patch size coefficient of variation (PSCV) of mixed-wood stands that were less than 20 years of age; interspersion (IJI) of deciduous patches less than 20 years of age; and the shape, or morphology, (MPFD) of mixed-wood stands greater than 20 and less than 60 years of age. This comprises model 1 (MGC-1).

The second model (MGC-2) –which had the lowest evidence ratio – also included the morphology (MPFD) of young coniferous patches. Compared to MGC-1, the evidence ratios varied only by 0.04, and MGC-2 explained only 2.9% more variation. Also, the area under the ROC test curve was 1% greater for MGC-2, and the standard error was 0.04 less than MGC-1.

The third model, MGC-3, was affected by the stand interior (CAD) of young deciduous stands. This model, with an evidence ratio twice both MGC-1 and –2, explained 56% of the variation between core and home range periphery. The area under the test ROC curve was only 1% greater than the previous model.

The remaining 2 models, MGC-4 and –5, incorporated the morphology of middle-aged mixed-wood stands (MPFD) and interspersion and juxtaposition (IJI) of middle-aged deciduous stands, respectively. Neither explained more than 60% of the variation, and both had ROC test curves with areas of 84%.

The value of the coefficients and the odds-ratio were used to further interpret the logistic regression models (Menard 1995; Table 3.1). Although the area statistic PSCV of young mixed-wood stands contributed strongly to explaining the variation in the models, it had a small coefficient and an odds-ratio near 1 (< 0.98). Thus, stands within the core area had less variation in their size (Figure 3.1; Table 3.2). Similarly, the interspersion indices for young and middle-aged deciduous stands had odds-ratios that were marginally less than 1 (except for MGC-5=1.05). The morphology indices all had a negative influence on the models, as indicated by their coefficients (Table 3.1), though more strongly than the other metrics discussed so far. The morphology of middle-aged mixed-wood and deciduous stands, as well as the young coniferous stands, all had smaller odds-ratios (range: 0.120-0.198). Therefore, core areas were likely to have had a less complex patch shape than home range peripheries in the MGC landscape.

Table 3.1. Modified Guidelines Cut (MGC) Landscape Candidate Models for Core Areas versus Home Range Peripheries of GPS-collared adult female moose in Northwestern Ontario between 1995-2000 (n Dvlp=40; n Test=20).

Candidate Model	Variables[1]	Coefficients	Exp B[2]	R^2[3]	AICc[4]	Evidence Ratio[5]	ROCc[6] Dvlp (A[7], s[8], Sig)	ROCc Test (A, s, Sig,)
MGC-1	PSCV_M-2	-.019	.981	0.520	83.095	1.04	.876 .057 .000	.800 .101 .023
	IJI_D-2	-.037	.964					
	MPFD_M-26	-1.621	.198					
		3.601	36.622					
MGC-2	PSCV_M-2	-.017	.983	0.549	83.009	1.00	.890 .054 .000	.810 .097 .019
	IJI_D-2	-.035	.966					
	MPFD_M-26	-1.737	.176					
	MPFD_C-2	-1.945	.143					
		6.019	411.366					
MGC-3	PSCV_M-2	-.017	.983	0.563	84.505	2.11	.893 .053 .000	.820 .094 .016
	IJI_D-2	-.040	.961					
	MPFD_M-26	-1.661	.190					
	MPFD_C-2	-1.907	.149					
	CAD_D-2	1.425	4.157					
		5.920	372.311					
MGC-4	PSCV_M-2	-.019	.981	0.573	86.662	6.214	.898 .054 .000	.840 .089 .010
	IJI_D-2	-.040	.961					
	MPFD_M-26	-1.454	.234					
	MPFD_D-26	-.568	.567					
	MPFD_C-2	-2.124	.120					
	CAD_D-2	1.405	4.076					
		6.352	573.647					
MGC-5	PSCV_M-2	-.021	.979	0.598	87.336	8.704	.900 .051 .000	.840 .089 .010
	IJI_D-2	-.051	.950					
	MPFD_M-26	-1.880	.153					
	MPFD_D-26	-2.129	.119					
	MPFD_C-2	-1.874	.154					
	IJI_D-26	.055	1.057					
	CAD_D-2	1.506	4.507					
		6.746	850.724					

[1] Each variable is identified in a sequence: Spatial Metric_Stand Type-Age. Where 'C', 'D', and 'M' denote coniferous, deciduous and mixed wood stands respectively. Age decodes into: '2', for less than 20 years; '26' for between 20 and 60 years of age; and '6' for greater than 60 years old. The spatial metrics are: Patch Size Coefficient of Variation (PSCV) Interspersion and Juxtaposition Index (IJI); Mean Patch Fractal Dimension (MPFD); and Core Area Density or Stand Interior Density (CAD).

[2] Exp B is the odds-ratio from the logistic regression.

[3] Coefficient of determination from the logistic regression.

[4] AICc is Akaike's Information Criterion for small sample sizes.

[5] Evidence ratio from the AICc.

[6] Reciever Operating Characteristic curve for both the development (Dvlp) data and the evaluation (Test) data sets.

[7] Area under the ROC curve.

[8] Standard Error.

Table 3.2. Summary Statistics (mean, range, and standard deviation) of important spatial variables from logistic regression of core areas versus home range peripheries of 60 GPS-collared adult female moose in Northwestern Ontario between 1995-2000.

Variable[1]	Core Area Mean	Core Area Range Min.-Max.	Core Area Std Dev.	Home Range Periphery Mean	Home Range Periphery Range Min.-Max.		Home Range Periphery Std Dev.
MGC[2]							
PSCV_M-2	51.3296	.00	140.53	45.8391	92.3980	.00	219.95	42.5535
IJI_D-2	14.4024	.00	62.31	22.2027	33.9240	.00	94.78	34.4226
MPFD_M-26	.5429	.00	1.39	.6824	1.1361	.00	2.50	.7572
MPFD_D-26	.2661	.00	1.38	.5462	.5382	.00	1.41	.6766
MPFD_C-2	1.2309	.00	1.49	.4233	1.4241	1.33	2.71	.3025
IJI_D-26	7.6479	.00	69.77	19.4866	20.7378	.00	73.35	28.2491
CAD_D-2	.1167	.00	1.91	.4251	8.408E-02	.00	.74	.1828
PCC[3]							
PSCV_M-2	50.1083	.00	170.90	52.6373	84.3268	.00	178.70	61.7217
TCAI_C-6	2.9640	.00	15.48	4.3039	7.4201	.00	16.66	4.4695
TCAI_M-6	4.9766	.00	13.76	4.4407	7.5538	.06	16.14	3.6728
PSCV_WL	75.6261	.00	114.91	31.3018	105.8351	.00	159.13	37.2837
PSCV_C-6	100.2689	52.92	146.65	23.0514	113.4681	.00	166.61	29.6613
MPFD_D-2	.5987	.00	1.42	.6797	.8775	62.14	1.51	.6622
IJI_D-2	22.1599	.00	81.53	29.2657	38.7291	.00	88.91	34.9165

[1] PSCV_M-2 = Patch size coefficient of variation for mixedwood stands less than 20 years of age.
IJI_D-2 = Interspersion and juxtaposition of deciduous stands less than 20 years of age.
MPFD_M-26 = Mean patch fractal dimension of mixedwood stands between 20 and 60 years of age.
MPFD_D-26 = Mean patch fractal dimension of deciduous stands between 20 and 60 years of age.
MPFD_C-2 = Mean patch fractal dimension of coniferous stands less than 20 years of age.
IJI_D-26 = Interspersion and juxtaposition of deciduous stands between 20 and 60 years of age.
CAD_D-2 = Core area (i.e., stand interior) density of deciduous stands less than 20 years of age.
TCAI_C-6 = Total core area (i.e., stand interior) index for coniferous stands greater than 60 years of age.
TCAI_M-6 = Total core area (i.e., stand interior) index for mixedwood stands greater than 60 years of age.
PSCV_WL = Patch size coefficient of variation for wetland areas.
PSCV_C-6 = Patch size coefficient of variation for conifer stands greater than 60 years of age.
MPFD_D-2 = Mean patch fractal dimension for deciduous stands less than 20 years of age.
[2] Modified Guidelines Cut (MGC); Core Area n=40; Home Range Periphery n=40.
[3] Progressive Clear Cut (PCC); Core Area n=40; Home Range Periphery n=40.

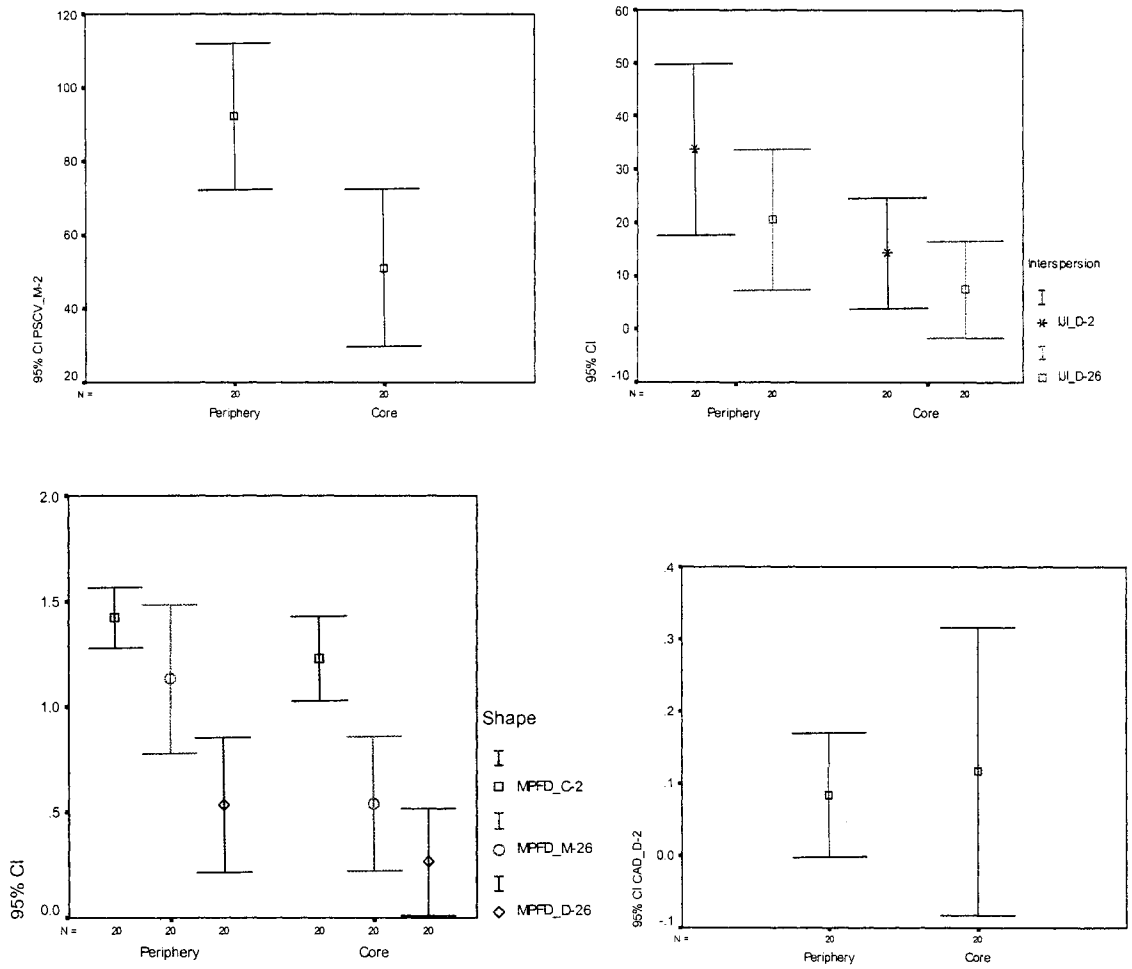

Figure 3.1. Error bar plots of MGC landscape selection model spatial variables from analyses of core area and home range periphery use of GPS-collared adult female moose in Northwestern Ontario between 1995-2000. Clockwise from the top left hand corner are the variation in patch size of young mixed-wood stands (PSCV_M-2); the interspersion and juxtaposition of young and middle aged deciduous stands (IJI-D-2, asterisk; and IJI_D-26, square); stand interior density of young deciduous stands (CAD_D-2); and the morphology of young coniferous (MPFD_C-2, square), middle-aged mixed-wood (MPFD_M-26, circle), and middle aged deciduous (MPFD_D-26, diamond) stands.

PCC Landscape

Three models qualified for analysis in the PCC landscape (Table 3.3). Overall, these models explained less variation in their landscape than their respective counterparts in the MGC (range: 44-51%). Of the maximum 7 variables selected in the PCC models (Table 3.2), only the patch size coefficient of variation of young mixed-wood stands (PSCV_M-2) and the interspersion of young deciduous stands (IJI_D-2) were common to the models selected from the MGC landscape.

The model with the lowest evidence ratio, PCC-2, consisted of 6 variables: percentage of stand interior of old (>60 years) conifer (TCAI_C-6) and mixed-wood stands (TCAI_M-6), the variation in wetland and young mixed-wood patch size (PSCV_WL and PSCV_M-2, respectively), the interspersion of young deciduous stands (IJI-D-2), as well as the morphology of young deciduous stands (MPFD_D-2). The interesting comparison was between PCC-2 and PCC-1, where PCC-1 differs only by lacking the morphology variable for young deciduous stands (MPFD_D-2). PCC-1 explained 6% less variation between the core area and the home range periphery than PCC-2; however, the test ROC curve had 2% more area under the curve than PCC-2, thus classifying better, with fewer variables. The evidence ratio for PCC-1 was, however, 2 times greater than PCC-2.

Model PCC-3 had one additional variable: the variation in old conifer patch size (PSCV_C-6). This changed little from PCC-2; the coefficient of determination for PCC -3 was 1%

higher and the test ROC curve was virtually identical to PCC-2. The evidence ratio for PCC-3 was 3 times that of PCC-2.

All variables, save for the morphology of young deciduous stands, had a negative influence on the models. Increased complexity of young deciduous stands had a strong influence on whether an area was classified as a core. The odds-ratio for morphology of young deciduous stands (MPFD_D-2) in PCC-2 was 14; thus, with increases in MPFD for young deciduous stands, there was a 14 times greater probability that the area was classified as a core. The odds-ratios for the remaining variables were less influential, ranging from 0.78-0.99 for all models. See Figure 3.2 for summary plots and Table 3.2 for associated values of these spatial variables.

Table 3.3. Progressive Contiguous Clear Cut (PCC) Landscape Candidate Models for Core Areas versus Home Range Peripheries of GPS-collared adult female moose in Northwestern Ontario between 1995-2000 (n Dvlp=40; n Test=20).

Candidate Model	Variables[1]	Coefficients	Exp B[2]	R^2[3]	AICc[4]	Evidence Ratio[5]	ROCc[6] Dvlp (A[7], s[8], Sig)	ROCc Test (A, s, Sig)
PCC-1	TCAI_C-6	-.138	.871	0.445	95.877	2.802	.878 .059 .000	.860 .089 .007
	PSCV_WL	-.017	.983					
	TCAI_M-6	-.136	.873					
	PSCV_M-2	-.009	.991					
	IJI_D-2	-.013	.987					
		4.260	70.833					
PCC-2	TCAI_C-6	-.243	.784	0.501	93.816	1.000	.873 .059 .000	.840 .095 .010
	PSCV_WL	-.016	.985					
	TCAI_M-6	-.146	.865					
	PSCV_M-2	-.011	.989					
	IJI_D-2	-.060	.942					
	MPFD_D-2	2.628	13.847					
		4.362	78.399					
PCC-3	TCAI_C-6	-.217	.805	0.513	96.067	3.083	.885 .055 .000	.840 .095 .010
	PSCV_WL	-.017	.983					
	TCAI_M-6	-.154	.857					
	PSCV_M-2	-.011	.989					
	PSCV_C-6	-.014	.986					
	IJI_D-2	-.065	.937					
	MPFD_D-2	2.921	18.553					
		5.808	333.084					

[1] Each variable is identified in a sequence: Spatial Metric_Stand Type-Age. Where 'C', 'D', and 'M' denote coniferous, deciduous and mixed wood stands respectively. Alternatively WL is the wetland designation. Age decodes into: '2', for less than 20 years; '26' for between 20 and 60 years of age; and '6' for greater than 60 years old. The spatial metrics are: Total Core Area Index or Total Interior Area Index (TCAI); Patch Size Coefficient of Variation (PSCV) Interspersion and Juxtaposition Index (IJI); and Mean Patch Fractal Dimension (MPFD).

[2] Exp B is the odds-ratio from the logistic regression.

[3] Coefficient of determination from the logistic regression.

[4] AICc is Akaike's Information Criterion for small sample sizes.

[5] Evidence ratio from the AICc.

[6] Reciever Operating Characteristic curve for both the development (Dvlp) data and the evaluation (Test) data sets.

[7] Area under the ROC curve.

[8] Standard Error.

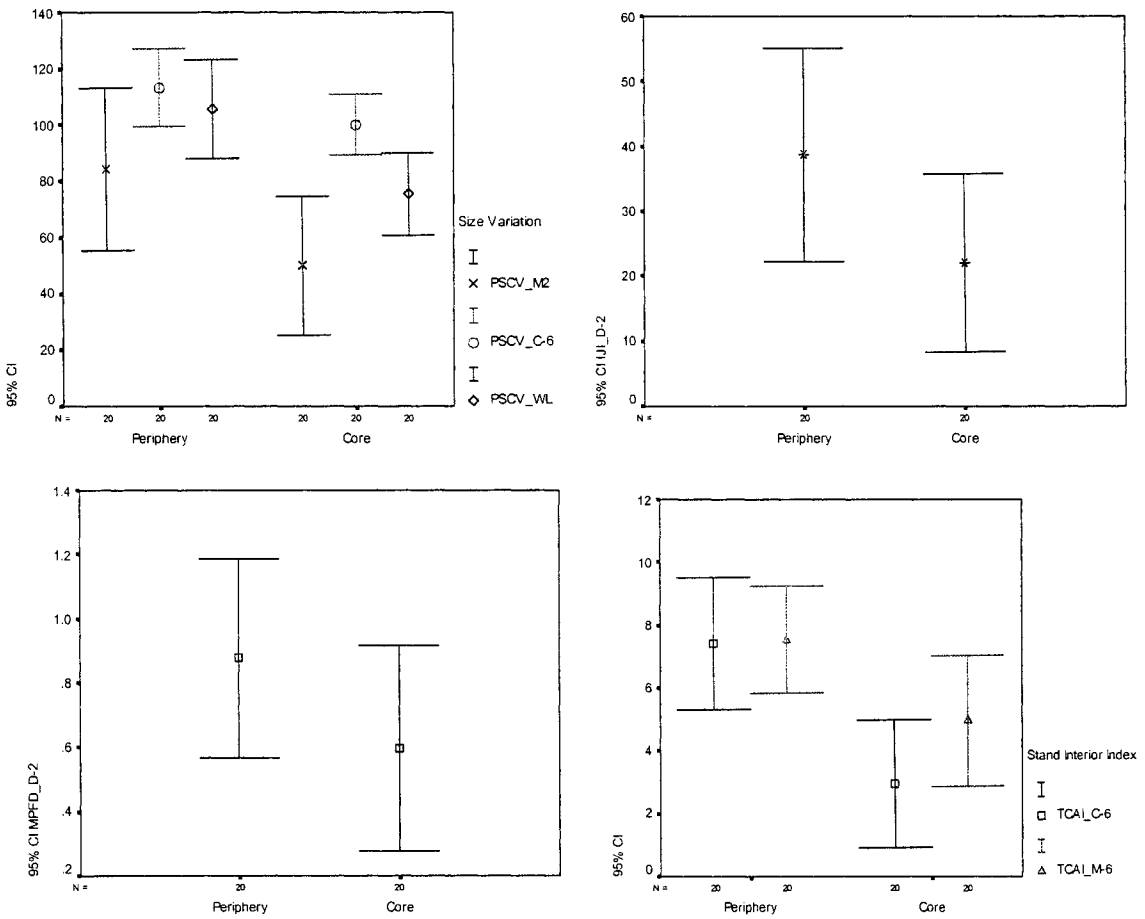

Figure 3.2. Error bar plots of PCC landscape selection model spatial variables from analyses of core area and home range periphery use of GPS-collared adult female moose in Northwestern Ontario between 1995-2000. Clockwise from the top left hand corner: variation in patch size for young mixed-wood (PSCV_M2, cross) and old coniferous stands (PSCV_C6, circle), and wetlands (PSCV_WL, diamond); interspersion and juxtaposition of young deciduous stands (IJI_D2); the total density of stand interiors for old conifer (TCAI_C6, square) and old mixed-wood stands (TCAI_M-6, triangle); and the morphology of young deciduous stands (MPFD_D-2).

Forage Availability Approach

MGC Landscape

Of the potential models for individual browse species, 6 qualified in the MGC landscape based on Akaike's Information Criterion (AICc) (Table 3.4). No combination explained greater than 15% (model MGC-6) of the variation in forage availability (range: 13-15%). Also, when the ROC curve was run on the test data set (n=140) the largest area under the curve was 61% (MGC-4; range: 56 - 61%).

The only variable that did not have a positive effect on the models was *Sorbus* spp (MGC-3 – MGC-6). Of the remaining species, *Populus* spp. had the largest effect, with an odds-ratio >36 for all candidate models. The next most influential group was *Acer* spp., followed by *Amelanchier* spp., *Salix* spp., *Prunus* spp., and *Betula* spp..

The model created using total browse density irrespective of species, explained 22.3% of the variation between core area and home range periphery. The test ROC curve area was also better than the individual species models at 74%. As this model was constructed using the same data as those with the individual species group variables, the log-likelihood values and AICc values are directly comparable. The evidence ratio from the total browse density model was smaller than all models using the individual species (minimum 25 orders of magnitude). Therefore the total browse density model, which does not distinguish the characteristics of individual species, was a better fit and a better discriminator than the models which incorporated information on individual species. See Figure 3.3 and Table 3.5 for comparisons among individual browse species densities and pooled density.

Table 3.4. Modified Guidelines Cut (MGC) Landscape Candidate Models for Browse Density in Core Areas versus Home Range Peripheries of GPS-collared adult female moose in Northwestern Ontario between 1995-2000 (n Dvlp=279; n Test=140).

Candidate Model	Variables[1]	Coefficients	Exp B[2]	R^{2}[3]	AICc[4]	Evidence Ratio[5]	ROCc[6] Dvlp (A[7], s[8], Sig)	ROCc Test (A, s, Sig)
MGC-1	*Populus* spp.	3.605	36.771	0.133	722.969	3.45	.614 .034 .001	.562 .049 .207
	Acer spp.	1.388	4.005					
		-.324	.723					
MGC-2	*Populus* spp.	3.663	38.978	0.142	720.884	1.22	.647 .033 .000	.579 .048 .108
	Amelanchier spp.	.631	1.879					
	Acer spp.	1.391	4.019					
		-.394	.674					
MGC-3	*Populus* spp.	3.707	40.747	0.147	720.492	1.00	.636 .033 .000	.571 .048 .148
	Amelanchier spp.	.621	1.861					
	Sorbus spp.	-3.147	.043					
	Acer spp.	1.477	4.382					
		-.359	.698					
MGC-4	*Populus* spp.	3.754	42.685	0.150	721.472	1.633	.643 .033 .000	.607 .048 .030
	Betula spp.	.386	1.470					
	Amelanchier spp.	.632	1.881					
	Sorbus spp.	-3.299	.037					
	Acer spp.	1.513	4.539					
		-.407	.666					
MGC-5	*Salix* spp.	.537	1.710	0.153	722.202	2.351	.657 .033 .000	.604 .048 .034
	Populus spp.	3.792	44.340					
	Betula spp.	.435	1.545					
	Amelanchier spp.	.610	1.841					
	Sorbus spp.	-3.217	.040					
	Acer spp.	1.571	4.812					
		-.463	.629					
MGC-6	*Salix* spp.	.538	1.713	0.153	723.972	5.699	.656 .033 .000	.594 .048 .056
	Prunus spp.	.120	1.128					
	Populus spp.	3.788	44.146					
	Betula spp.	.330	1.391					
	Amelanchier spp.	.610	1.841					
	Sorbus spp.	-3.165	.042					
	Acer spp.	1.582	4.865					
		-.475	.622					
Browse Density[9]	Total Density	.479	1.614	0.223	677.462	N/A[10]	.769 .028 .000	.736 .042 .000
		-.746	.474					

[1] Browse species are grouped by genus.
[2] Exp B is the odds-ratio from the logistic regression.
[3] Coefficient of determination from the logistic regression.
[4] AICc is Akaike's Information Criterion for small sample sizes.
[5] Evidence ratio from the AICc.
[6] Reciever Operating Characteristic Curve for both the development (Dvlp) data and the evaluation (Test) data sets.
[7] Area under the ROC curve.
[8] Standard error.
[9] Model constructed using total browse density irrespective of species.
[10] The evidence ratio is many orders of magnitude larger than the comparable model; if it were to be used as the benchmark value, the remaining models would not be as easy to interpret.

Table 3.5. Summary Statistics (mean, range, and standard deviation) of individual and total browse densities in core areas versus home range peripheries of 60 GPS-collared adult female moose in Northwestern Ontario between 1995-2000.

Variable	Core Area Mean	Core Area Range Min.-Max.	Core Area Std Dev.	Home Range Periphery Mean	Home Range Periphery Range Min.-Max.	Home Range Periphery Std Dev.
MGC[1]						
Salix spp,	.0927	.00 .91	.17279	.0815	.00 2.18	.21488
Prunus spp.	.1892	.00 5.50	.56249	.1679	.00 2.64	.40640
Populus spp.	.1630	.00 2.15	.32472	.0375	.00 .56	.08659
Corylus spp.	.2219	.00 5.67	.77633	.1339	.00 2.17	.38803
Betula spp.	.1100	.00 2.00	.27548	.1087	.00 1.18	.19530
Amelanchier spp.	.1350	.00 2.75	.35547	.0840	.00 1.93	.24767
Sorbus spp.	.011	.00 .45	.0450	.0155	.00 .40	.050999
Acer spp.	.1133	.00 4.33	.52684	.0255	.00 .72	.10247
Total Browse Density	2.2036	.00 18.67	2.40111	.9527	.02 4.09	.88496
PCC[2]						
Salix spp,	.0697	.00 1.00	.16333	.0450	.00 1.43	.14858
Prunus spp.	.1039	.00 2.67	.32563	.0663	.00 1.14	.16136
Populus spp.	.1047	.00 2.56	.31233	.0355	.00 .63	.09538
Corylus spp.	.3045	.00 7.50	1.01510	.1376	.00 6.50	.64507
Betula spp.	.1550	.00 2.70	.32377	.0759	.00 1.00	.14569
Amelanchier spp.	.0438	.00 1.27	.14336	.0624	.00 3.71	.36443
Sorbus spp.	.0204	.00 .50	.0630	.0116	.00 .30	.0383
Acer spp.	.2573	.00 4.29	.66467	.2253	.00 2.60	.52354
Total Browse Density	2.1338	.18 13.25	2.23736	1.0320	.05 9.25	1.20466

[1] Modified Guidelines Cut (MGC); Core Area n=141; Home Range Periphery n=138.
[2] Progressive Clear Cut (PCC); Core Area n=119; Home Range Periphery n=120.

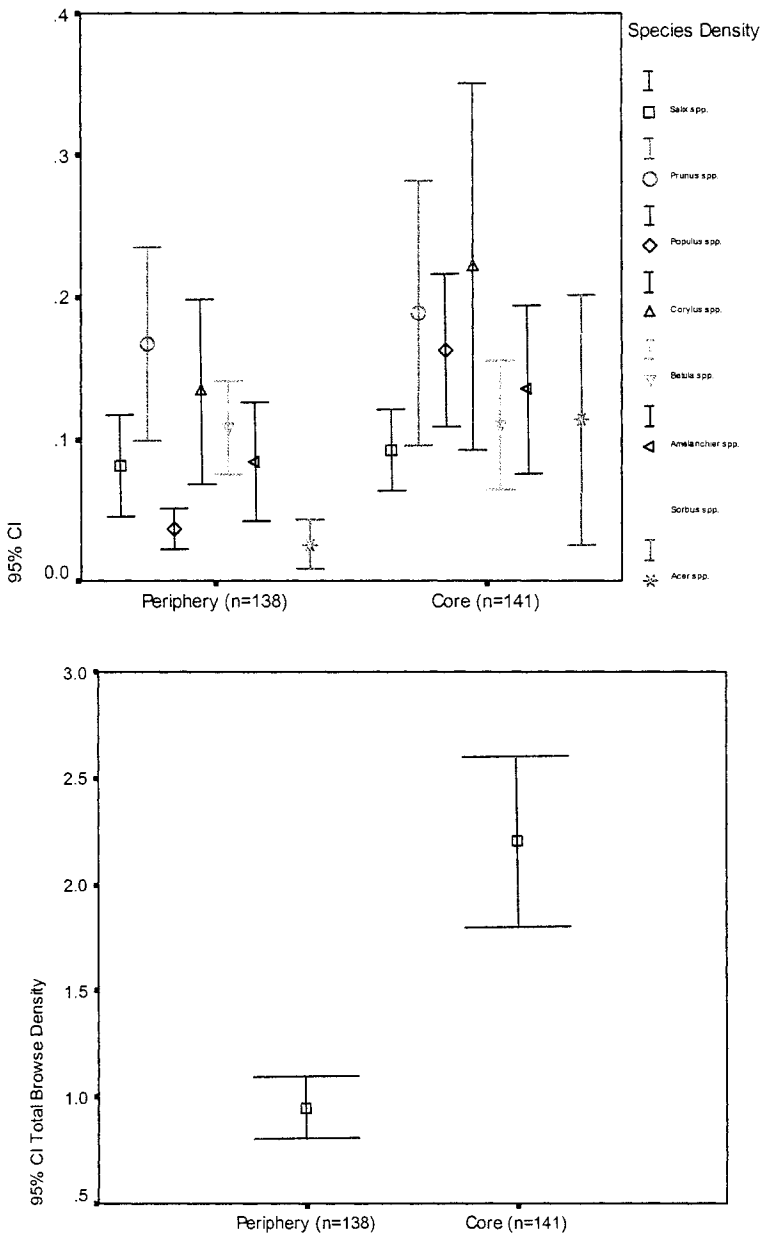

Figure 3.3. Mean and 95% confidence intervals of individual browse group densities as well as total browse density between home range peripheries and core areas in the MGC landscape from analyses of core area and home range periphery use of GPS-collared adult female moose in Northwestern Ontario between 1995-2000. Individual species densities for the 7 preferred species above: *Salix* spp., square; *Prunus* spp., circle; *Populus* spp., diamond; *Corylus* spp., up-facing triangle; *Betula* spp., down-facing triangle; *Amelanchier* spp., left-facing triangle; *Sorbus* spp., right-facing triangle; *Acer* spp., asterisk.

PCC Landscape

Similar to the above, the PCC landscape total browse density model was a better fit and discriminator than the individual models (7 orders of magnitude; Table 3.6). Compared to the MGC landscape total browse model, however, the PCC total browse model explained less variation (17%). The ROC curve on the test data occupied an area of 73%.

Five individual models were selected using the information-theoretic approach (AICc). Contrary to the MGC landscape, all species had a positive influence on the models in the PCC, particularly *Sorbus* spp., which had an odds-ratio >74 for all PCC models in which it occurred. *Betula* spp. and *Populus* spp. both had odds-ratios greater than 4 for all models, whereas, when present, *Prunus* spp., *Corylus* spp., *Acer* spp., and *Salix* spp. all had odds ratios less than 2.

Three PCC models had evidence ratios less than 2; 1 model (PCC-5) had an evidence ratio near 4 and the remaining model (PCC-1) an evidence ratio >7. The model with the smallest evidence ratio (PCC-3) consisted of: *Populus* spp, *Corylus* spp., *Betula* spp., *Sorbus* spp., and *Acer* spp. In ascending order of evidence ratios, PCC-2 without *Acer* spp. density had the next highest and PCC-4 was the same as PCC-3, but also included *Salix* spp. density. PCC-5 included the final variable *Prunus* spp. and the largest evidence ratio belonged to PCC-1, comprised of *Populus* spp., *Corylus* spp., and *Betula* spp. See Figure 3.4 and Table 3.5 for comparisons among individual densities and pooled density.

Table 3.6. Progressive Contiguous Clear Cut (PCC) Landscape Candidate Models for Browse Density in Core Areas versus Home Range Peripheries of GPS-collared adult female moose in Northwestern Ontario between 1995-2000 (n Dvlp=239; n Test=144).

Candidate Model	Variables[1]	Coefficients	Exp B[2]	R^2[3]	AICc[4]	Evidence Ratio[5]	ROCc[6] Dvlp (A[7], s[8], Sig)	ROCc Test (A, s, Sig)
PCC-1	*Populus* spp.	1.546	4.694	0.100	635.761	7.011	.630 .036 .001	.616 .052 .027
	Corylus spp.	.418	1.519					
	Betula spp.	1.770	5.873					
		-.388	.678					
PCC-2	*Populus* spp.	1.657	5.242	0.114	632.402	1.307	.638 .036 .000	.589 .052 .090
	Corylus spp.	.366	1.442					
	Betula spp.	1.753	5.770					
	Sorbus spp.	4.802	121.797					
		-.461	.631					
PCC-3	*Populus* spp.	1.682	5.378	0.120	631.866	1.000	.639 .036 .000	.579 .052 .134
	Corylus spp.	.359	1.432					
	Betula spp.	1.862	6.434					
	Sorbus spp.	4.465	86.939					
	Acer spp.	.243	1.274					
		-.532	.588					
PCC-4	*Salix* spp.	.630	1.877	0.123	633.002	1.765	.642 .036 .000	.609 .051 .038
	Populus spp.	1.698	5.462					
	Corylus spp.	.362	1.436					
	Betula spp.	1.853	6.380					
	Sorbus spp.	4.313	74.642					
	Acer spp.	.256	1.292					
		-.566	.568					
PCC-5	*Salix* spp.	.494	1.640	0.124	634.720	4.167	.639 .036 .000	.604 .051 .048
	Prunus spp.	.243	1.275					
	Populus spp.	1.582	4.864					
	Corylus spp.	.358	1.430					
	Betula spp.	1.797	6.032					
	Sorbus spp.	4.440	84.777					
	Acer spp.	.261	1.298					
		-.572	.565					
Browse Density[9]	Total Density	.849	2.338	0.173	602.199	N/A[10]	.710 .033 .000	.732 .046 .000
		-1.123	.325					

[1] Browse species are grouped by genus.
[2] Exp B is the odds-ratio from the logistic regression.
[3] Coefficient of determination from the logistic regression.
[4] AICc is Akaike's Information Criterion for small sample sizes.
[5] Evidence ratio from the AICc.
[6] Reciever Operating Characteristic curve for both the development (Dvlp) data and the evaluation (Test) data sets.
[7] Area under the ROC curve.
[8] Standard error.
[9] Model constructed using total browse density irrespective of species.
[10] The evidence ratio is many orders of magnitude larger than the comparable model; if it were to be used as the benchmark value, the remaining models would not be as easy to interpret.

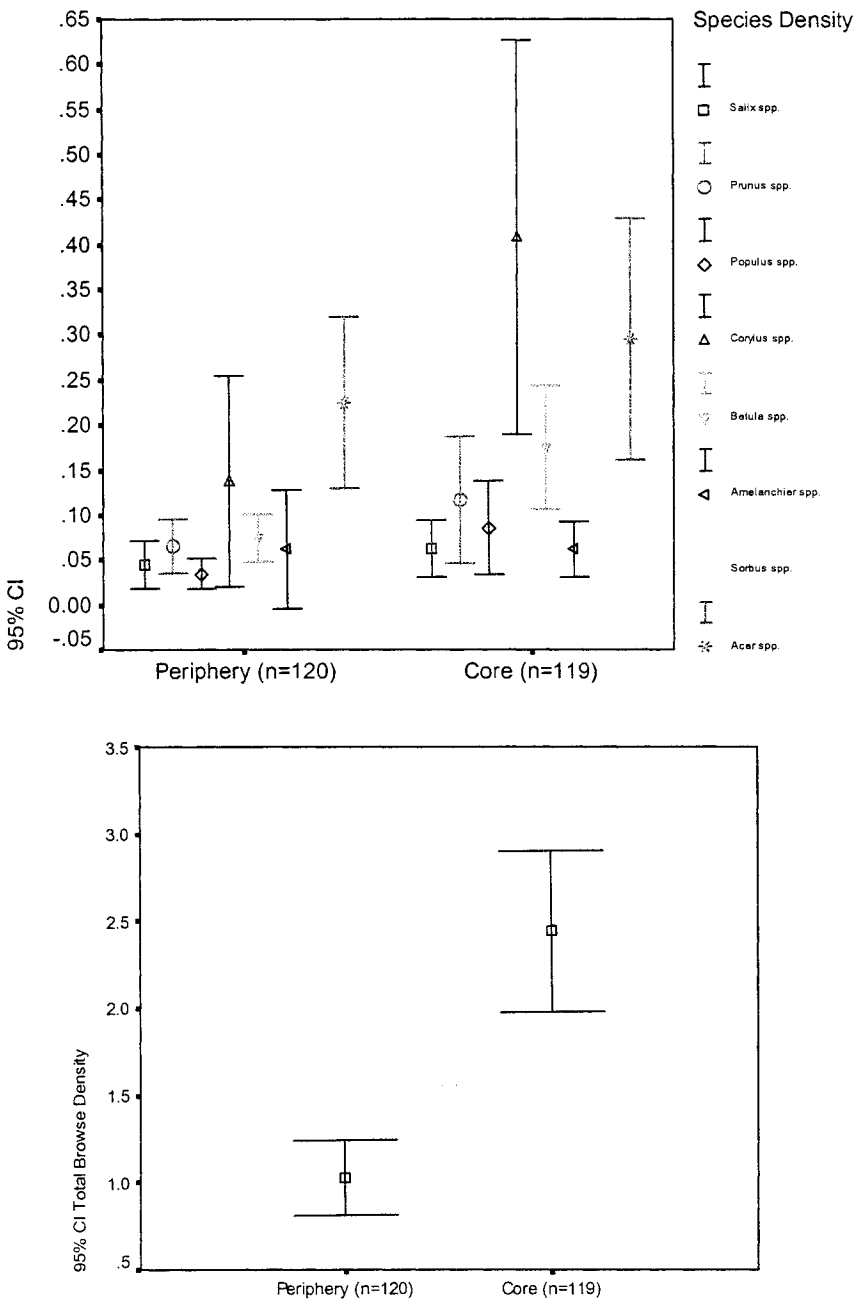

Figure 3.4. Mean and 95% confidence intervals of individual browse group densities as well as total browse density between home-range peripheries and core areas in the PCC landscape from analyses of core area and home range periphery use of GPS-collared adult female moose in Northwestern Ontario between 1995-2000. Individual species densities for the 7 preferred species above: *Salix* spp., square; *Prunus* spp., circle; *Populus* spp., diamond; *Corylus* spp., up-facing triangle; *Betula* spp., down-facing triangle; *Amelanchier* spp., left-facing triangle; *Sorbus* spp., right-facing triangle; *Acer* spp., asterisk.

Discussion

In this study, core areas averaged 8.63 km^2, representing only 26% of the total summer home range size of adult female moose (Chapter 2). Within-home-range habitat use by moose was not random; rather characteristics of core areas represented more suitable habitat than home range peripheries. The data suggest that areas consisting of multiple high use patches comprised a network of resources, spatially arranged to capitalize on the complementation or supplementation (Dunning et al. 1992) of type, shape, and size of forest stands comprising the landscape.

Spatial Approach

The spatial models were "reasonable discriminators" (Pearce and Ferrier 2000) between core areas and home range peripheries of female moose in both landscapes. The models reinforce much that is understood about moose biology, particularly the importance of young seral stages (Crête 1988; Courtois et al. 2002), which comprise 4 out of 6, and 3 out of 7 potential metrics in the MGC and PCC landscapes, respectively. Of the metrics that were selected, 30% pertained to young deciduous patches, which concurs with Courtois et al. (2002) who reported an increased preference for young deciduous patches by moose during the summer. What did not appear among the candidate models were edge metrics. To a certain degree other spatial metrics can act as proxies for edge; however, collinearity did not exist between the final metrics and edge metrics. Edge appears not to influence within-home-range habitat selection by female moose, as there was no appreciable

difference between edge densities in the core and home range periphery. That does not preclude edge playing a role in second order home range selection when compared to available habitat on the landscape (first order selection).

Although the MGC and PCC landscapes were disturbed differently, the model selection technique allowed identification of 2 variables that acted as discriminators between the core and home range in both landscapes. First, the variation in patch size of young mixed-wood stands was selected for both landscapes. In both landscapes, this metric negatively influenced the model: where relative to the mean patch size, the coefficient of variation was smaller in the core than in the home range periphery. Core areas, thus, have more uniform young mixed-wood patch sizes than the periphery. As a young seral class, these patches are likely used for feeding. As moose rarely enter beyond 80 m into a clear cut (Crête 1988), the relationship between patch use and size is probably not linear, where an optimally sized patch will have little to no inaccessible stand interior, yet will not be so small that it provides inadequate forage.

The second variable that was important in both landscapes was the interspersion and juxtaposition of young deciduous stands. Courtois et al. (2002) found that moose sought out landscapes with higher patch diversity and interspersion. At the core level, however, my study found that moose were selecting young deciduous stands that were less interspersed and juxtaposed to fewer patch types in the core area than the home range periphery, for both the MGC and PCC landscapes. Young deciduous patches are prime foraging areas for moose and need to be interspersed among patches suitable to fulfil other

life history requisites. Complementation among different patch types is important for habitat selection (Dunning et al. 1992). For instance, some patches may act as better predator refugia. Foraging under predation pressure is well studied (Lima and Dill 1990; Brown 1999). Females with young will choose to trade-off exploiting patches of high forage availability for patches in proximity to protective cover (Stringham 1974; Langley and Pletscher 1994; White and Berger 2001). Additionally, habitat structure affects thermal cover (Mysterud and Ostbyte 1999). Thermoregulation is vital for moose in the summer, due to their large body size (Peek et al. 1982; Schwab and Pitt 1991), and influences foraging decisions at the patch level (Dussault 2002). Moose show signs of heat stress at temperatures above 14 ° C (Renecker and Schwartz 1998) and avoid areas where the temperature exceeds 30 ° C (Schwab and Pitt 1991). To avoid heat stress, moose feed in open areas, in water or wallow (Renecker and Schwartz 1998). These behaviours lend themselves to specific subsets of habitats that could be juxtaposed or interspersed with foraging areas.

Young deciduous stands in the PCC landscape also had less complex morphology in the core areas than the home range periphery. The trend was similar for both young coniferous and middle-aged deciduous stands in the MGC landscape. Patch shape is a trade-off between available forage and predator safety (Mysterud and Ostbyte 1999). Cover has two impacts on predation: reduced detection and a means of prey evasion (e.g., structure for escape) (Mysterud and Ostbyte 1999). Cover that obstructs the view of an animal causes an increase in vigilance and consequently a decrease in time allotted to feeding (Lima and Dill 1990). Uniform shaped patches, though with less edge and likely less foraging

opportunities, offer the animal unobstructed spaces for increased vigilance against predators.

Young deciduous stands had another influence on core selection in the MGC landscape. Core areas tended to have larger stand interiors of young deciduous trees and shrubs. Stand interiors likely played a small role as a discriminator: it was a metric that was selected only in models for which there was weak and definitive evidence for their ultimate parsimony (Akaike's evidence ratios for these models were 2, 6 and 8); and the data (Figure 3.1; Table 3.2) had a small mean (~ 0.1 disjunct patches with stand interiors per 1 ha) and high degree of variation in the core areas. However, if stand interior did influence selection, perhaps this represents an increase in potential forage: large stand interiors do represent potential forage, given the trade-offs related to foraging in a clear-cut.

Stand interior size played a more obvious and influential role in the PCC landscape for discriminating between habitats selected in the core area versus the home range periphery. Core areas had a lower density of old conifer and old mixed-wood stand interiors (Figure 3.2; Table 3.2). Moose thus avoided using areas with a higher density of old-growth stands. Where old conifer stands did exist in the core areas they had less variation in their size compared to the home range periphery.

Browse Approach

Individual browse species' density did not act as good discriminators between the core area and the home range periphery and explained little variation between these areas. However,

independent of the models' discrimination ability, data indicated higher individual species' browse densities in the core than the home range periphery, with one exception: *Sorbus* spp. which was more abundant in the periphery of the MGC landscape home ranges. Peek et al. (1976), in a study from northern Minnesota, ranked *Sorbus* spp. as the second most preferred winter forage of moose. Perhaps the periphery of the summer range is more intensely used during the winter months, though a more holistic temporal approach would be required to test this hypothesis. Other genera that were absent in my analyses were *Cornus* spp. and *Fraxinus* spp., as they occurred at less than 5% of sites sampled.

Total browse density models, conversely, were better discriminators than individual species between the core area and home range periphery in both landscapes. Although the total browse density models were only "reasonable" estimators (Pearce and Ferrier 2000), they discriminated better than the individual species' models (Tables 3.4 and 3.5). Moreover, in combination with the individual models, it appears that moose were not selecting for individual browse species; rather there was a stronger affinity to selection for cumulative availability of forage. This is likely because each of the individual species sampled is a subset of suitable and preferred forage (Peek et al. 1976) so any combination of the above, given a minimum density, will fulfil the nutritional requirements of the animal in summer. Furthermore, this behaviour is consistent with moose being generalists and feeding on low quality foods (Peek 1998).

Scale

From the perspective of scale, the bulk of the evidence would indicate that available forage plays an important role in the selection of core areas. This is apparent to a lesser extent with the browse density models than with the spatial models. The physiognomic features of patches which produce forage, young seral stages in particular, influenced the models selected using an information-theoretic approach.

The browse density models developed in this study do suggest a relationship between spatial scale and optimal foraging for moose in summer. Typically an animal optimizes its foraging at Johnson's (1980) fourth order level of selection, where bite size and individual plants are chosen (Belovsky 1978; Saether and Andersen 1989). The two sets of browse data from this study, however, suggest that total browse density influences selection more than individual species. This implies that optimizing foraging, in summer, may occur at a larger spatial scale. One possible explanation is relative parity among low nutrient foods and that extra search effort is more expensive than exploiting readily available "preferred" foods; i.e., herbivores consume foods with low nutritional value, so perhaps among the 8 preferred genera there is nutritional equality such that even if one group has marginally higher energetic value it is not economical or appealing enough to motivate an animal to seek it out when some composite of the other 7 groups are readily available.

Regarding physiognomies, patch size and shape within the core area suggest that predator avoidance does impact habitat selection by moose while meeting the requirements of

feeding. This study supports the assertion that selecting patches that mediate the effects of predation occurs at a smaller scale, or is nested within selection for forage itself (Voigt et al. 2000). Dussault (2002) examined home range selection versus landscape availability and found the trade-off between predator avoidance and forage availability occurred at a coarse spatial scale; rather than a fine scale, which balanced energy gain and mitigated adverse effects from the environment. This observation is further supplemented by evidence from my study. If, according to Courtois et al. (2002), the spatial arrangement of a home range increases the ability to avoid predators, the use of core areas further enhances the differences in habitat physiognomies to minimize the effect of predation. Dussault's (2002) fine scale trade-off of energy gain and environmental inclemency thus occurs at the patch level within the core areas. The core area potentially also incorporates characteristics inherent to fine scale ecological processes, where increased forage is balanced by patch complementation that potentially mitigates environmental stresses.

By definition, spatial domains occur when the scale spectrum of ecological processes is discontinuous (Wiens 1989). Given the results of this study in combination with Courtois et al. (2002), it appears that the ecological factors influencing core-use behaviour by moose change monotonically with scale. Thus, the core area is not a distinct domain, or ecologically significant spatial scale, from the home range or patch. Rather, it exists in an ambiguous transition space (Figure 3.5). It is within the core area that critical thresholds (With and Crist 1995) occur, affecting ecological processes that influence habitat selection at multiple spatial scales for moose. Core areas do have greater forage availability and refined physiognomies that could reduce the effect of predation and environmental stresses.

These ecological interactions, however, also influence the selection of the home range and fine-scale patches individually, not exclusively, within the core area.

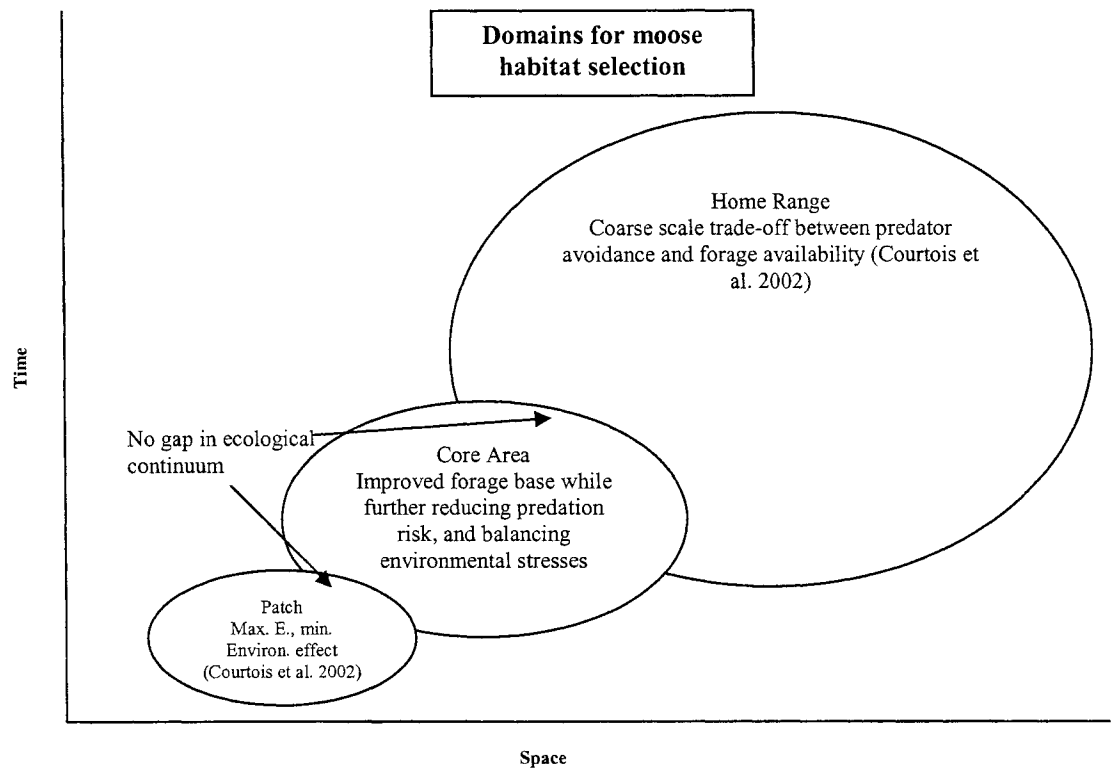

Figure 3.5. This figure is a hypothetical representation of domains for moose. The elements that influence habitat selection at the core area scale are a monotonic refinement of habitat selection at the home range level. Thus, core areas are both spatially and ecologically nested within the home range of moose.

Summary

Areas of intense use, or cores, where an animal devotes a disproportionate amount of time, are conspicuous features within the habitat of moose home ranges. For moose, core areas have superior qualities in comparison to home range peripheries. They have higher browse density and patch configurations that potentially complement or supplement the animal's life requisites such as predator avoidance or mitigating environmental stress. Core areas do not appear, however, to occur at an ecologically significant spatial scale wholly apart from either the home range or fine-scale patches, as they are influenced by ecological interactions which shape both scales of selection. Core areas are significant features within an animal's home range on the landscape and could potentially play an important role in understanding how to manage the landscape for particular species.

Management Implications

This study was based on data obtained from a management study (Moose Guidelines Evaluation Program): the prerogative of my study was not management. Though the study has broader biological implications, its management potential is narrow; i.e., it solely studied proximate factors of habitat selection, whereas a sophisticated management plan should include density dependent effects on moose habitat selection. Additionally, I would caution that although many of the spatial metrics (e.g., avoidance of late seral stage large stand interiors) favour the existing *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR 1988), a holistic approach including Rempel et al. (1997) on densities, predation, etc., Crouse (2003) on productivity, and Welch et al. (2000) on calving

site selection be employed for comparing the 2 landscape treatments. Nonetheless, my study yields several points pertinent to management. Spatially, there is merit in managing for moose at the core 'scale'. The findings on patch physiognomies, which potentially represent more suitable habitat than home range peripheries, could be used to further sculpt the landscape, post logging. Also, if future research distinguished the ways in which patches complement one another, some configurations could be recommended as guidelines to forest regeneration. Rather than defaulting to traditional habitat selection based systems for management, a more sophisticated approach is required. This approach would: (1) incorporate information from 'preferred' habitats, i.e., cores, rather than merely habitats 'used' from the traditional use versus availability argument; (2) include density dependent effects; and (3) equate habitats used with temporally explicit functional responses (i.e., rate of movement), to relate habitat used to moose condition and productivity. From this information managers could classify marginal habitats versus habitats that realize high fitness and in turn sustain vigorous wild populations.

Literature Cited

ADDICOT, J.F., J.M. AHO, M.F. ANTOLIN, D.K. PADILLA, J.S. RICHARDSON, AND D.A. SOLUK. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340-346.

ANDERSEN, R., AND B-E. SAETHER. 1992. Interactions between a generalist herbivore, the moose, and its winter food resources: a study of behavioural variation. Alces Supplement 1: 101-104.

BALLARD, W.B., AND V. VAN BALLENBERGHE. 1998. Predator/Prey relationships. Pages 247-273 in A.W. Franzmann and C.C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

BELOVSKY, G.E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Population Biology 14: 105-134.

BISSONETTE, J.A., D.J. HARRISON, C.D. HARGIS, AND T.G. CHAPIN. 1997. The influence of spatial scale and scale-sensitive properties on habitat selection by American marten. Pages 368-385 in J.A. Bissonette, editor. Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer-Verlag Inc., New York, New York, USA.

BOWYER, R.T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy 72: 138-145.

BOWYER, R.T., V. VAN BALLENBERGHE, AND J.G. KIE. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79: 1332-1344.

BRILLINGER, D.R., H.K. PREISLER, A.A. AGER, AND J.G. KIE. 2004. An exploratory analysis (EDA) of the paths of moving animals. Journal of Statistical Planning and Inference 122: 43-63.

BROWN, J.S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research 1: 49-71.

BOYCE, M.S., P.R. VERNIER, S.E. NIELSEN, AND F.K.A. SCHMIEGELOW. 2002. Evaluating resource selection functions. Ecological Modeling 157: 281-300.

BURNHAM, K.P., AND D.R. ANDERSON. 1998. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

BURT, W.H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24: 346-352.

CAMERON R.D., W.T. SMITH, S.G. FANCY, K.L. GERHART, AND R.G. WHITE. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71: 480-486.

CEDERHOLM, M. 2000. Random Points in Polygon. Extension for ArcView. ESRI Support Center, Redlands, California, USA.

CEDERLUND, G.N., AND H. OKARMA. 1988. Home range and habitat use of adult female moose. Journal of Wildlife Management 52: 336-343.

CHAMBERLAIN, M.J., C.D. LOVELL, AND B.D. LEOPOLD. 2000. Spatial-use patterns, movements, and interactions among adult coyotes in central Mississippi. Canadian Journal of Zoology 78: 2087-2095.

CHARNOV, E.L. 1976. Optimal foraging: attack strategy of a mantid. The American Naturalist 110: 141-151.

CHRISTIAN, K., W.P. PORTER, AND C. TRACEY. 1986. Core areas within the home ranges of land iguanas *Conolophus palidus*. Journal of Herpetology 20: 272-276.

COADY, J.W. 1974. Influence of snow on moose behaviour. Naturaliste Canadien 101: 417-436.

COCHRAN, W.G. 1977. Sampling Techniques. John Wiley and Sons Inc., New York, New York, USA.

COURTOIS, R., C. DUSSAULT, F. POTVIN, AND G. DAIGLE. 2002. Habitat selection by moose (*Alces alces*) in clear-cut landscapes. Alces 38: 177-192.

CRÊTE, M. 1988. Forestry practices in Quebec and Ontario in relation to moose population dynamics. The Forestry Chronicle 64: 246-250.

CROUSE J.A. 2003. Health, nutritional condition, and productivity of female moose (*Alces alces*) in Northwestern Ontario. M.Sc. Thesis, Lakehead University, Thunder Bay, Ontario, Canada.

DARWIN, C. 1871. The Descent of Man and Selection in Relation to Sex. Special contents © 1972. George Macy Companies Inc., The Heritage Press, New York, New York, USA.

DELAUNE, M.G. 2000. XTools ArcView Extension (Version 10/18/2000). Oregon Department of Forestry, Salem, Oregon, USA.

DONCASTER, C.P., AND D.W. MACDONALD. 1991. Drifiting territoriality in the red fox *Vulpes vulpes*. Journal of Animal Ecology 60: 423-439.

DUNNING, J.B., B.J. DANIELSON, AND H.R. PULLIAM. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-175.

DUSSAULT, C. 2002. Influence des contraintes environmentales sur la sélection de l'habitat de l'orignal (*Alces alces*). Ph.D. Thesis, Université Laval, Québec, Canada.

EDWARDS, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia 60: 185-189.

ELKIE, P.R., R.R. REMPEL, AND A.P. CARR. 1999. Patch Analyst user's manual. Northwest Science and Technology, Ontario Ministry of Natural Resources, Thunder Bay, Publication TM-002.

FIELDING, A.L., AND J.F. BELL. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24: 38-49.

FORD, R.G., AND D.K. KRUMME. 1979. The analysis of space use patterns. Journal of Theoretical Biology 76: 125-155.

FRETWELL, S.D., AND H.L. LUCAS JR. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheriologica 19: 16-36.

GASAWAY, W.C., AND J.W. COADY. 1974. Review of energy requirements and rumen fermentation in moose and other ruminants. Naturaliste Canadien 101: 227-262.

GITZEN, R.A., AND J.J. MILLSPAUGH. 2003. Comparison of least-squares cross-validation bandwidth options for kernel home-range estimation. Wildlife Society Bulletin 31: 823-831.

GITZEN, R.A., J.J. MILLSPAUGH, AND B.J. KERNOHAN. In press. Bandwidth selection for fixed-kernel analysis of home-range use. Ecological Modeling.

GLENN, E.M., M.C. HANSEN, AND R.G. ANTHONY. 2004. Spotted owl home-range and habitat use in young forest of western Oregon. Journal of Wildlife Management 68: 33-50.

HARRELL, F.E. 2001. Regression Modeling Strategies with Applications to Linear Models, Logistic Regression, and Survival Analysis. Springer, NewYork, New York, USA.

HAYNE, D.W. 1949. Calculation of size of home range. Journal of Mammalogy 30: 1-17.

HEIKKILA, R., K. NYGREN, S. HARKONEN, AND A. MYKKANEN. 1996. Characteristics of habitats used by female moose in the managed forest area. Acta Theriologica 41: 321-326.

HJELJORD, O., F. SUNDSTOL, AND H. HAAGENRUD. 1982. The nutritional value of browse to moose. Journal of Wildlife Management 46: 333-343.

HODDER, K.H., R.E. KENWARD, S.S. WALLS, AND R.T. CLARKE. 1998. Estimating core ranges: a comparison of techniques using the common buzzard (*Buteo buteo*). Journal of Raptor Research 32: 82-89.

HOOGE, P.N., AND B. EICHENLAUB. 2000. Animal movement extension to Arcview. ver. 2.0. Alaska Center - Biological Science Office, U.S. Geological Survey, Anchorage, Alaska, USA.

HOLLING, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European sawfly. Canadian Entomology 91: 293-320.

HOLLING, C.S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecological Monographs 62: 447-502.

HUBBS, A.H., AND R. BOONSTRA. 1998. Effects of food and predators on the home-range sizes of Arctic ground squirrels (*Spermophilus parryii*). Canadian Journal of Zoology 76: 592-596.

JACKSON, G.L., G.D. RACEY, J.G. MCNICOL, AND L.A. GODWIN. 1991. Moose habitat interpretation in Ontario. Ontario Ministry of Natural Resources, NOFTDU Technical Report 53. Thunder Bay, Ontario, Canada.

JAREMOVIC, R.V., AND D.B. CROFT. 1987. Comparison of techniques to determine eastern grey kangaroo home range. Journal of Wildlife Management 51: 921-930.

JOHNSON, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

KALMER, J.F., W.B. BALLARD, R.L. GILLILAND, AND K. MOTE. 2003. Spatial relationships between swift foxes and coyotes in northwestern Texas. Canadian Journal of Zoology 81: 168-172.

KAUFMANN, J.H. 1962. Ecology and social behavior of the coati *Nasua narica* on Barro Colorado Island, Panama. University of California Publications in Zoology 60: 95-222.

KERNOHAN, B.J., R.A. GITZEN, AND J.J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pages 125-165 in J.J. Millspaugh and J.M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, San Diego, California, USA.

KIE, J.G., R.T. BOWYER, M.C. NICHOLSON, B.B. BOROSKI, AND E.R. LOFT. 2002. Landscape heterogeneity at different scales: effects on spatial distribution of mule deer. Ecology 83: 530-544.

KILPATRICK, H.J., S.M. SPOR, AND K.K. LIMA. 2001. Effects of population reduction on home ranges of female white-tailed deer at high densities. Canadian Journal of Zoology 79: 949-954.

KITCHEN, A.M., E.M. GESE, AND E.R. SCHAUSTER. 2000. Long-term spatial stability of coyote (*Canis latrans*) home ranges in southeastern Colorado. Canadian Journal of Zoology 78: 458-464.

LANGLEY, M.A., AND D.H. PLETSCHER. 1994. Calving areas of moose in northwestern Montana and southeastern British Columbia. Alces 30: 127-135.

LI, H., AND J.F. REYNOLDS. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75: 2446-2455.

LIMA, S.L., AND L.M. DILL. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68: 619-640.

MCGARIGAL, K., AND B.J. MARKS. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service GTR-PNW-GTR-351.

MECH, L.D., R.E. MCROBERTS, R.O. PETERSON, AND R.E. PAGE. 1987. Relationship of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56: 615-627.

MENARD, S.W. 1995. Applied Logistic Regression. Sage Publications Inc., Thunder Oaks, California, USA.

MESSIER, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60: 377-393.

MICHENER, G.R. 1979. Spatial relationships and social organization of adult Richardson's ground squirrels. Canadian Journal of Zoology 57: 125-139.

MOEN, R., J. PASTOR, AND Y. COHEN. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78: 505-521.

MOLVAR, E.M., AND R.T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. Journal of Mammalogy 75:621-630.

MYSTERUD, A., AND E. OSTBYTE. 1999. Cover as a habitat element for temperate ungulates: effect on habitat selection demography. Wildlife Society Bulletin 27: 385-394.

NICHOLSON, M.C., R.T. BOWYER, AND J.G. KIE. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78: 483-504.

OEHLER, M.W., SR., R.T. BOWYER, AND V.C. BLEICH. 2003. Home ranges of female mountain sheep. Mammalia 67: 385-402.

(OMNR) Ontario Ministry of Natural Resources. 1988. Timber management guidelines for the provision of moose habitat. Ontario Ministry of Natural Resources, Toronto, Ontario, Canada.

(OMNR) Ontario Ministry of Natural Resources. 1999. Forest Resource Inventory for Wabigoon, Seine and Manitou Forest Management Areas. Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

(OMNR) Ontario Ministry of Natural Resources. Moose guidelines evaluation program. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

PASSINELLI, G., J. HEGELBACH, AND H.U. REYER. 2001. Spacing behaviour of the middle spotted woodpecker in central Europe. Journal of Wildlife Management 65: 432-441.

PEARCE, J., AND S. FERRIER. 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133: 225-245.

PEEK, J. 1998. Habitat relationships. Pages 351-375 in A.W. Franzmann and C.C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

PEEK, J.M., M.D. SCOTT, L.J. NELSON, D.J. PIERCE, AND L.L. IRWIN. 1982. Role of cover in habitat management for big game in northwestern United States. Forty-Seventh North American Wildlife Conference 47: 363-373.

PEEK, J.M., D.L. URICH, AND R.J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs 48.

PREISLER, H.K., A.A. AGER, B.K. JOHNSON, AND J.G. KIE. 2004. Modeling animal movements using stochastic differential equations. Environmetrics 15: 643-657.

PYKE, G.H., H.R. PULLIAM, AND E.L. CHARNOV. 1977. Optimal foraging: a selective review of theory and tests. The Quarterly Review of Biology 52: 137-154.

REMPEL, R.S., P.C. ELKIE, A.R. RODGERS, AND M.J. GLUCK. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. Journal of Wildlife Management 61: 517-524.

REMPEL, R.S., AND A.R. RODGERS. 1997. Effects of differential correction on accuracy of a GPS animal location system. Journal of Wildlife Management 61: 525-530.

RENECKER, L.A., AND R.J. HUDSON. 1985. Estimation of dry matter intake of free-ranging moose. Journal of Wildlife Management 49: 785-792.

RENECKER, L.A., AND R.J. HUDSON. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. Journal of Wildlife Management 53: 296-302.

RENECKER, L.A., AND C.C. SCHWARTZ. 1998. Food habits and feeding behaviour. Pages 403-439 in A.W. Franzmann and C.C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

RETTIE, W.J., AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23: 466-478.

RISENHOOVER, K.L. 1986. Winter activity patterns of moose in interior Alaska. Journal of Wildlife Management 50: 727-734.

RODGERS, A.R. 2001. Recent telemetry technology. Pages 79-121 in J.J. Millspaugh and J.M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, San Diego, California, USA.

RODGERS, A.R., AND A. P. CARR. 2002. HRE: the Home Range Extension for ArcView. Version 1.1c. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Thunder Bay, Ontario, Canada.

RODGERS, A.R., R.S. REMPEL, AND K.F. ABRAHAM. 1995. Field trials of a new GPS-based telemetry system. Pages 173-178 in C. Cristalli, C.J. Amlaner, Jr., and M.R. Neuman, editors. Proceedings of the Thirteenth International Symposium on Biotelemetry. Williamsburg, Virginia, USA.

ROSENZWEIG, M.L. 1981. A theory of habitat selection. Ecology 62: 327-335.

ROWE, J.S. 1972. Forest Regions of Canada. Department of the Environment, Canadian Forest Service, Publication 47-1300, Ottawa, Ontario.

SAETHER, B-E., AND R. ANDERSEN. 1989. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68: 993-999.

SAMSON, C., AND J. HUOT. 2001. Spatial and temporal interactions between female American black bears in mixed forests of eastern Canada. Canadian Journal of Zoology 79: 633-641.

SAMUEL, M.D., D.J. PIERCE, AND E.O. GARTON. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54: 711-719.

SCHOENER, T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369-404.

SCHWAB, F.E., AND M.D. PITT. 1991. Moose selection of canopy cover types related to operative temperature, forage and snow depth. Canadian Journal of Zoology 69: 3071-3077.

SCHWARTZ, C.C. 1992. Physiological adaptations of moose to northern environments. Alces Supplement 1: 139-155.

SCHWARTZ, C.C., AND K.J. HUNDERTMARK. 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57: 454-468.

SCHWARTZ, C.C., W.L. REGELIN, AND A.W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. Alces 20: 223-245.

SEAMAN, D.E., J.J. MILLSPAUGH, B.J. KERNOHAN, G.C. BRUNDIGE, K.J. RAEDEKE, AND R.A. GITZEN. 1991. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63: 739-747.

SENFT, R.L., M.B. COUGHENOUR, D.W. BAILEY, L.R. RITTENHOUSE, O.E. SALA, AND D.M. SWIFT. 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37: 769-799.

SHATLAND, E.S., K KLIENMANN, AND E.M. MCCAIN. 2003. Stepwise methods in using SAS proc logistic and SAS enterprise miner for prediction. SUGI'28 Proceedings paper 258-28. SAS Institute Inc., Cary, North Carolina, USA.

SILVERMAN, B.W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, U.K.

SPRINGER, J.T. 1982. Movement patterns of coyotes in south central Washington. Journal of Wildlife Management 46: 191-200.

STEWART, R.R., R.R. MCLENNAN, AND J.D. KINNEAR. 1977. The relationship of plant phenology to moose. Saskatchewan Department of Tourism and Renewable Resources, Technical Bulletin Number 3. Regina, Saskatchewan, Canada.

STEWART, K.M., R.T. BOWYER, J.G. KIE, N.J. CIMON, AND B.K. JOHNSON. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. Journal of Mammalogy 83: 229-244.

STRINGHAM, S.F. 1974. Mother-infant relations in moose. Naruraliste Canadien 101: 325-355.

SWIHART, R.K., AND SLADE, N.A. 1985. Testing for independence of observations in animal movements. Ecology 66: 1176-1184.

TESTA, J.W., E.F. BECKER, AND G.R. LEE. 2000. Movements of female moose in relation to birth and death of calves. Alces 36: 155-162.

THOMPSON, I.D. 2000. Forest vegetation in Ontario: factors influencing landscape change. Pages 30-53 in A.H. Perera, D.L. Euler, and I.D. Thompson, editors. Ecology Of A Managed Terrestrial Landscape. Patterns and Processes of Forest Landscapes in Ontario. UBC Press, Vancouver, British Columbia, Canada.

TIMMERMANN, H.R., AND J.G. MCNICOL. 1988. Moose habitat needs. Forestry Chronicle 64: 238-245.

TURCHIN, P. 1998. Quantitative Analysis of Movement. Sinauer Accociates Inc., Sunderland, Massachusetts, USA.

VIVAS, H.J., AND B-E. SAETHER. 1987. Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: an experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology 56: 509-520.

VOIGT, D.R., J.A. BAKER, R.S. REMPEL, AND I.D. THOMPSON. 2000. Forest vertebrate level responses to landscape-level changes in Ontario. Pages 198-233 in A.H. Perera, D.L. Euler, and I.D. Thompson, editors. Ecology Of A Managed Terrestrial Landscape. Patterns and processes of Forest Landscapes in Ontario. UBC Press, Vancouver, British Columbia, Canada.

WATKINS, L., AND R. DAVIS. 1999. SFMMTool 2.2: User Guide. Ontario Ministry of Natural Resources, Queens Printer, Toronto, Ontario, Canada.

WELCH, I.D. 2000. Calving site selection by GPS-collared moose in timber harvested areas of Northwestern Ontario. M.Sc. Thesis, University of Waterloo, Waterloo, Ontario, Canada.

WELCH, I.D., A.R. RODGERS, AND R.S. MCKINLEY. 2000. Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces 36: 93-103.

WHITE, K.S., AND J. BERGER. 2001. Anti-predator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? Canadian Journal of Zoology 79: 2055-2062.

WIENS, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

WILSON, P.J., S. GREWAL, A. RODGERS, R. REMPEL, J. SAQUET, H. HRISTIENKO, F. BURROWS, R. PETERSON, AND B.N. WHITE. 2003. Genetic variation and population structure of moose (*Alces alces*) at neutral and functional DNA loci. Canadian Journal of Zoology 81: 670-683.

WITH, K.A., AND T.O. CRIST. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446-2459.

WORTON, B.J. 1989. Kernel methods for estimating utilisation distribution in home-range studies. Ecology 70: 164-168.

WRAY, S., W.J. CRESSWELL, P.L.C. WHITE, AND S. HARRIS. 1992. What, if anything, is a core area? An analysis of the problems of describing internal range configurations. Pages 257-271 in I.G. Priede and S.M. Swift, editors. Wildlife Telemetry: Remote Monitoring and Tracking ofAnimals. Ellis Horwood, New York, New York, USA.

Appendix 1

SQL for habitat classification: DEC; MIX; CON; for year classes 20, 20-60, 60+.

DEC_20

([Sfu]="HrDom") or ([Sfu]="BwDom") or ([Sfu]="OthHd") or ([Sfu]="PoDee") or ([Sfu]="PoSha") and ([Age]<20)

DEC_20_60

([Sfu]="HrDom") or ([Sfu]="BwDom") or ([Sfu]="OthHd") or ([Sfu]="PoDee") or ([Sfu]="PoSha") and ([Age]>=20) and ([Age]<60)

Dec_60

([Sfu]="HrDom") or ([Sfu]="BwDom") or ([Sfu]="OthHd") or ([Sfu]="PoDee") or ([Sfu]="PoSha") and ([Age]>=60)

MIX_20

([Sfu]="HrdMx") or ([Sfu]="ConMx") or ([Sfu]="PjMx1") or ([Sfu]="SbMx1") and ([Age]<20)

MIX_20_60

([Sfu]="HrdMx") or ([Sfu]="ConMx") or ([Sfu]="PjMx1") or ([Sfu]="SbMx1") and ([Age]>=20) and ([Age]<60)

MIX_60

([Sfu]="HrdMx") or ([Sfu]="ConMx") or ([Sfu]="PjMx1") or ([Sfu]="SbMx1") and ([Age]>=60)

CON_20

([Sfu]="OcLow") or ([Sfu]="BfDom") or ([Sfu]="PjDee") or ([Sfu]="PjSha") or ([Sfu]="SbDee") or ([Sfu]="SbSha") or ([Sfu]="SbLow") or ([Sfu]="PwDom") or ([Sfu]="PrwMx") and ([Age]<20)

Con_20_60

([Sfu]="OcLow") or ([Sfu]="BfDom") or ([Sfu]="PjDee") or ([Sfu]="PjSha") or ([Sfu]="SbDee") or ([Sfu]="SbSha") or ([Sfu]="SbLow") or ([Sfu]="PwDom") or ([Sfu]="PrwMx") and ([Age]>=20) and ([Age]<60)

Con_60

([Sfu]="OcLow") or ([Sfu]="BfDom") or ([Sfu]="PjDee") or ([Sfu]="PjSha") or ([Sfu]="SbDee") or ([Sfu]="SbSha") or ([Sfu]="SbLow") or ([Sfu]="PwDom") or ([Sfu]="PrwMx") an

"Many of the views which have been advanced are highly speculative, and some no doubt will prove erroneous; but, I have in every case given the reasons which have led me to one view rather than to another....False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by evidence, do little harm, for every one takes a salutary pleasure in proving their falseness; and, when this is done, one path toward error is closed and the other road to truth is often at the same time opened."
--C. Darwin The Descent of Man pp. 315