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Integrated Modelling of Moose Habitat and Population: Preliminary Investigations Using an **Ontario Boreal Forest**

Peter Duinker Colin Daniel **Richard Morash** Will Stafford **Ron Plinte Chris Wedeles**



Natural Resources

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Final Report prepared under the Northern Ontario Development Agreement. Project cosponsored by the Canadian Forest Service, Sault Ste. Marie, under the Northern Forestry Program of NODA, by ESSA Technologies Ltd., Richmond Hill, and by the Chair in Forest Management and Policy, Faculty of Forestry, Lakehead University, Thunder Bay

Chair in Forest Management and Policy
Faculty of Forestry
Lakehead University
Thunder Bay, Ontario
P7B 5E1

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¹Chair in Forest Management and Policy Faculty of Forestry Lakehead University Thunder Bay, Ontario P7B 5E1

phone: 807-343-8508 fax: 807-343-8116

email: pduinker@lakeheadu.ca

²ESSA Technologies Ltd. 308-9555 Yonge St. Richmond Hill, Ontario L4C 9M5

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ABSTRACT

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Moose (Alces alces) is a wildlife species of major ecological and social importance in Ontario's boreal forest. To our knowledge for the Ontario situation, nowhere in the process of managing habitat via timber management guidelines and managing populations via harvest regulations are the two processes explicitly linked by specific consideration of relationships between habitat characteristics and population dynamics. Our main objective in the study was to develop and test an integrated set of simulation models that will predict effects of forest and population management on a moose population.

Our modelling approach was GIS-based simulation. The GIS was required to account for spatial relationships, and simulation was required for projecting moose habitats and populations into the future. The modelling framework included a forest-inventory projection model, a set of GIS programs to calculate moose food and cover across the landscape, and a moose population model for interpreting habitat values in terms of moose densities. The models were tested in this initial exploratory study on the Lake Abitibi Model Forest in Northeastern Ontario.

Four forest-management strategies were created as inputs to the forest-inventory projection model, one of which involved cessation of timber harvests. The moose-habitat models calculated food supplies in each of three seasons - spring/summer, autumn, and early winter. The early winter food supplies at each habitat location (based on grid points representing four hectares each) were adjusted based on proximity to good cover. Hunting of moose was adjusted in the moose population model based on a surrogate measure of road building and timber harvesting.

The models were able to predict moose densities (i.e., a range of 0.05 to 0.4 moose/km2) roughly similar to those found in the Model Forest (i.e., about 0.1 to 0.15 moose/km2). While the predictions are shrouded in much uncertainty, they indicate that (a) moose density is likely to be reduced under any of the forest-management strategies, and (b) hunting appears to have an appreciable effect on keeping the moose densities below what the habitat might support in the absence of hunting. Regarding the former, we believe that the strategies we created have features that do not resemble reality, and that future habitats would not actually turn out to be as bad for moose as our predictions indicate. Regarding the latter, our findings seem to corroborate what many biologists have been saying for some time about moose in Northern Ontario - control of hunting is a vital tool in trying to increase moose densities, and control of habitat manipulations through timber management, in many situations, may be relatively less important.

ABSTRACT ii

CONTENTS iii

LIST OF TABLES v

LIST OF FIGURES vi

ACKNOWLEDGEMENTS vii

- 1. INTRODUCTION 1
 - 1.1 The Problem 1
 - 1.2 Why Moose? 2
 - 1.3 Project Objectives 4
- 2. THE CASE STUDY FOREST 5
- 3. METHODS 7
 - 3.1 Approach 7
 - 3.2 Forest Management Strategies 8
 - 3.3 Forest Inventory Projection 11
 - 3.4 Moose Habitat Interpretations of Projected Inventories 13
 - 3.4.1 Reclassification of the Forest 14
 - 3.4.2 Food and Cover Values 14
 - 3.4.3 Food and Cover Calculations for Stands 19
 - 3.4.4 Food and Cover Calculations for Habitat Assessment Units 21
 - 3.4.5 Data Transfer to the Population Model 23
 - 3.5 Moose Population Modelling 23
 - 3.5.1 Population Structure 24
 - 3.5.2 Growth 25
 - 3.5.3 Starvation Mortality 27
 - 3.5.4 Other Mortality 28
 - 3.5.5 Hunting Mortality 28
 - 3.5.6 Births 31
 - 3.5.7 Input Parameters 33

ø

4. RESULTS AND DISCUSSION 42

- 4.1 Forest Inventory Projection and Wood Supply 42
 - 4.1.1 Age-class Structure 42
 - 4.1.2 Stocking Levels 43
- 4.2 Moose Habitat Forecasts 44
 - 4.2.1 Spring/Summer Food Responses 45
 - 4.2.2 Early-Winter Food Responses 46
- 4.3 Moose Population Forecasts 48
 - 4.3.1 Two Strategies without Hunting 49
 - 4.3.2 The Basic Strategy with and without Hunting 50
 - 4.3.3 The Three Timber-harvest Strategies with Hunting 50
- 4.4 Overall Interpretations 51
- 5. CONCLUSIONS 52
 - 5.1 Limitations of the Analysis 52
 - 5.1.1 Data Inadequacies 53
 - 5.1.2 Sensitivity Analysis 53
 - 5.1.3 Scenario Exploration 54
 - 5.2 Model Development, Testing and Research Needs 54
 - 5.3 Final Comments 56
- 6. LITERATURE CITED 57
- 7. APPENDICES 86

LIST OF TABLES

- 2.1 Summary of forest types and site classes in the Lake Abitibi Model Forest 60
- 3.1 The state table used as input to HSG in the forest-inventory projections 61
- 3.2. Forest reclassification scheme for moose habitat calculations 64
- 3.3. Variables used in the moose population model 65

LIST OF FIGURES

- 2.1 Location of the Lake Abitibi Model Forest 67
- 3.1 Overview of relationships of the models 68
- 3.2 Overview of the moose population model 69
- 3.3 Calculation sequence in the moose population model 70
- 3.4 Growth calculations 71.
- 3.5 Starvation mortality rates as a function of each cohort's mean weight per animal and the weight at which an individual dies 72
- 3.6 Cow harvest rate relationship 73
- 3.7 Relative hunting pressure relationship 74
- 3.8 Relationship between birth weight and mother's weight 75
- 4.1a Age-class structure evolution under the No-Harvest Strategy 76
- 4.1b Age-class structure evolution under the Basic Strategy 77
- 4.1c Age-class structure evolution under the Lower Strategy 78
- 4.1d Age-class structure evolution under the Spatial Strategy 79
- 4.2 HAU-average SS food values of the four scenarios 80
- 4.3 HAU-average EW food values of the four scenarios 81
- 4.4 HAU-average EW cover indices of the four scenarios 82
- 4.5 Predicted moose densities in April No-Harvest Strategy with no hunting, Basic Strategy with no hunting 83
- 4.6 Predicted moose densities in April Basic Strategy with no hunting, and Basic Strategy with hunting 84
- 4.7 Predicted moose densities in April Basic Strategy, Lower Strategy, and Spatial Strategy, all with hunting 85

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1. INTRODUCTION

1.1 The Problem

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Moose (Alces alces) is a wildlife species of major ecological and social importance in Ontario's boreal forest. Habitat management for moose takes place by attempting to accommodate habitat needs during forest management operations. To this end, provincial guidelines exist for moose (OMNR, 1988) to provide forest managers with information on key habitat characteristics and features so they may plan forest operations with minimum negative impacts (and foster positive impacts) on moose habitat.

The intent of the guidelines and their implementation is not just to protect and develop good habitat, but to foster and help maintain moose populations. A logical link exists, therefore, between objectives for habitat quality and objectives for moose populations. However, to our knowledge, nowhere in the process of managing habitat via timber management guidelines and managing populations via harvest regulations are the two processes explicitly linked by specific consideration of relationships between habitat characteristics and population dynamics. The integration between managing habitat and managing harvests (and populations) is incomplete, therefore, because no objective means exists to translate the effects of forest operations into population measures.

Surprisingly, few attempts have yet been made to translate the simulated effects on habitat to

effects on populations (see Duinker (1986) for an example). Most habitat models predict either a habitat suitability index that is translated in a very simple way into a population index, or a measure of habitat carrying capacity (Greig et al., 1991). We have developed a set of simulation tools that specifically address the missing links between the effects of forest management operations on population numbers of one vertebrate species, namely the moose. The integrated models will be suitable for use in an applied research manner or in a preliminary exploration of the effects of long-range forest management plans. Our approach has been to develop the integrated models with an eye towards "every-day" operational use in the near future. The present version has been completed with an applied research orientation.

1.2 Why Moose?

We have chosen moose as the species for attention in this study because:

- We have experience in building a habitat simulator for moose (Duinker et al., 1991;
 1993; Higgelke et al., 1992; Higgelke, 1994);
- 2. Moose is a featured species across the boreal forest of Ontario, and high in social and economic value. Moose populations in Ontario's forests are significant engines of the economy. For example, in 1991, 91,000 hunters spent over \$55 million in pursuit of moose in northern Ontario (H. Smith, pers. comm., 1995). The economic activity

generated from hunting in the province is directly related to the quotas set by OMNR biologists. The development of a means to assist in setting harvest quotas with greater confidence will have significant financial implications for the economy of the north.

- 3. Forest-management companies spend much money on forest planning, and the costs of arranging timber harvests according to guidelines to meet moose habitat needs can be substantial. Such costs need stronger justification for habitat protection, which can be provided by predicting moose population responses to habitat change caused by forest operations.
- 4. The clients, including mainly Northeast Science and Technology of OMNR and the Lake Abitibi Model Forest, requested the work to focus on moose.

Moose are also being studied in OMNR's Moose Guidelines Evaluation Project (MGEP) at the OMNR Centre for Northern Forest Ecosystem Research, Thunder Bay. MGEM is a long-term comprehensive study of moose populations and their relationships with habitat in Ontario's boreal forest. In this study we have tried to fill an immediate need for a planning tool for moose habitat and population management, expecting that the tool will be refined or even restructured over time with ongoing research such as that done by MGEM. This work can benefit other projects of a similar sort by identifying some of the pitfalls of linking habitat and population simulators. Also, development of alternative models for the same phenomena is a powerful approach to furthering the complex science of managing natural resources (Walters, 1986).

1.3 Project Objectives

Our main objective was to:

develop and test an integrated set of simulation models that will predict effects of forest and population management on a moose population.

Ancillary objectives, for moose in the Lake Abitibi Model Forest, were to:

- begin the process of developing computerized tools suitable for use by forest/wildlife
 managers in an operational context that will assist in developing and implementing
 integrated (i.e. habitat and population) management strategies;
- 2. develop tools to assist in identifying key habitat and population information needs for moose management; and
- develop tools to assist in evaluation/testing of hypotheses related to the relative importance of habitat and population management of moose.

2. THE CASE STUDY FOREST

The Lake Abitibi Model Forest (LAMF), of some 1.1 million hectares in total extent, is situated in northeastern Ontario, just to the east of Cochrane (Figure 2.1). The forest is part of the Northeastern Ontario claybelt, and lies mostly in the Lac Matagami Ecoregion (Wickware and Rubec, 1989). The territory has a relatively cool climate, with a total number of frost-free days of 120-160/yr. Of the annual precipitation of some 75 cm, about half falls as rain.

According to Wickware and Rubec (1989):

"The Lac Matagami Ecoregion is predominantly an imperfectly to poorly drained, very weakly to weakly broken, glacio-lacustrine clay plain. Surficial deposits were reworked during a late glacial re-advance and redeposited as a clay moraine. . . . Much of the area is covered by a blanket of peat with depths ranging from 3 to 4 meters.

"Soils of the ecoregion are predominantly poorly drained Organic soils or imperfectly drained peaty phase Gleysols. Humo-Ferric Podzols occur on the well drained sandy sites, while Gray and Brunisolic Gray Luvisols occur on the better drained, fine loamy to clayey textured soils.

"Extensive stands of black spruce occur on the thick deposits of peat which cover much of the ecoregion. On fresh, well drained, fine loamy an clayey deposits, white spruce,

balsam fir, black spruce, and eastern white cedar occur. Jack pine, and jack pine-black spruce stands are common on the drier, rapidly drained, coarse textured sandy sites.

Mixedwood stands of trembling aspen, white birch, black spruce, white spruce and balsam fir occur on a wide range of disturbed sites."

The forest inventory data made available to us for the study corroborate the above vegetation assessment. The Model Forest is dominated by lowland black spruce stands with surface organic soils and clay subsoils (Table 2.1). Other forest types, defined by dominant overstorey tree species, include poplar (11.1% of the forest area), balsam fir (3.7%), jack pine (3.5%), and white birch (2.0) (Table 2.1). Productivity, as indicated by site class, is moderate to good, with about 80% of the forest in site-class 2 or better (Table 2.1).

Most of the Model Forest is contained within the Iroquois Falls forest management unit, which is under a sustainable forest license, as prescribed by Ontario's Crown Forest Sustainability Act, to Abitibi Price Inc. The harvested timber goes mostly to Abitibi Price's pulp and paper mill in Iroquois Falls. Forest management plans have heretofore been prepared under Ontario's timber management planning manual (OMNR, 1986), but the next one will be developed under the new forest management planning manual (OMNR, 1995). Industrial timber harvesting has taken place in the Model Forest since 1915.

Land in the Model Forest not under sustainable forest licence includes two provincial parks, a First Nations reserve, and several small blocks of freehold land. Non-timber values in the area

include remote tourism, horticultural peat, fishing, Crown land camping, wildlife habitat, canoeing, trapping, mineral exploration, and cultural heritage.

3. METHODS

3.1 Approach

Our approach to the study had the following features.

- (a) GIS-based simulation modelling underlies the research framework. A GIS (geographic information system) is needed to account for proximities of food and cover habitat, and for variations of moose habitat quality across the landscape. Simulation is needed to track habitat and population responses through future time.
- (b) Models would be linked and used in a modular fashion. Each major set of required calculations would be made by a discrete model.
- (c) Peer review during study completion would be gained through small workshops of biologists knowledgeable about moose-habitat relationships, the study forest, and GIS-based simulation modelling.

The modelling framework involves three models or sets of models (Figure 3.1):

- the forest-inventory projection tool called HSG (Moore and Lockwood, 1990), which requires data on current forest inventory, management strategies, and successional pathways (among other data), and produces simulated future forest inventories;
- (b) a suite of GIS programs (mostly set up as ARC\INFO AML (ARC Macro Language)

 programs) which require forest inventories as input data, and interpret those inventories
 in terms of moose food and cover; and
- a moose population model, which requires data on moose food and cover and on forest age-class structure (along with a series of parameter values) and calculates cohort-specific moose population data (e.g., number of animals, weights of animals) in response to the habitat data.

3.2 Forest Management Strategies

For initial simulations using the moose habitat and population models, we created four forestmanagement strategies covering a 100-yr period into the future:

(a) The "No-Harvest" Strategy - here, no timber management takes place (i.e., no timber

harvest and no regeneration activities). For pragmatic reasons, we were able to account only for non-catastrophic stand succession in our depiction of forest development, which means that fires, insect and disease epidemics, and blowdowns are unaccounted for.

Indeed, these disturbance factors are not part of any of the four scenarios developed and tested. The No-Harvest Strategy was developed to provide a theoretical baseline for comparison with the timber-management strategies.

- (b) The "Basic" Strategy here we matched, in general terms, all the major assumptions from the management plan for the Iroquois Falls forest management unit (which comprises the overwhelming majority of the Model Forest territory). Thus, from the management plan we took annual harvest volumes (380,725 m3/yr of spruce, incidental volumes of associated species) and silvicultural ground rules, and used them throughout the 100-yr simulation. To simplify our study, we assumed that all timber harvests would use the clearcut method. The Basic Strategy was formulated to explore moose-population response to a long-term continuation of the current management strategy for the forest. In this and the following scenario, HSG was unconstrained with respect to the location and size of stands to be harvested.
- (c) The "Lower" Strategy in this case, we assumed that annual timber harvests would amount to 75% of those of the Basic Strategy (285,544 m3/yr of spruce and incidental volumes of associated species). Silvicultural ground rules remained the same, although annual areas treated would be lower, depending on forest types harvested in any time

period. The Lower Strategy was formulated to explore the general premise that relaxation of timber-harvest pressures might benefit some species of forest-dwelling wildlife.

(d) The "Spatial" Strategy - using harvest volumes and silvicultural ground rules of the Basic Strategy, we constrained the eligibility of harvestable stands according to their general location. Thus, for the first three 10-yr simulation periods (1994-2024), only stands in specific inventory mapsheets (we used 19 of a total of 85) where the management plan depicted the main harvesting activities for 30 yr would take place. For the next three 10-yr periods (2024-2054), harvestable stands had to be found within another subset of the forest inventory mapsheets (38 of 85 mapsheets). For the final four 10-yr periods (2054-2094), the locations of harvestable stands were unconstrained. This is based on the assumption that by 2054, the whole forest would have a well-developed road network. The Spatial Strategy was formulated to explore the notion, inherent in the design of the moose habitat guidelines (OMNR, 1988), that smaller and well-distributed clearcuts are better for moose habitat than are larger and more-concentrated cuts.

The following specifications were common to all the scenarios in which timber harvest took place:

all timber harvests were regulated on the annual yields of spruce; harvest of other species were incidental;

- a set of forest-specific yield curves which show wood volume trends over stand age for all combinations of stand type, stocking, and site class (Appendix I);
- timber harvest priority rule: minimize primary volume loss;
- minimum operable volume: 40 m3/ha;
- prohibition of timber harvest on site class 4; and
- silviculture programs unrestricted in areal extent, but set in priority according to a treatment priority table (Appendix II).

3.3 Forest Inventory Projection

We presume that readers requiring basic familiarity with stand-based forest-inventory projection in general, and HSG in particular, will consult appropriate literature (e.g., Moore and Lockwood, 1990). We used a 10-yr time step over a 100-yr horizon, expecting little to be gained by making the time step smaller and the horizon further into the future.

HSG's so-called "state" table is particularly important in determining the traits of simulated future forests. The state table (Table 3.1) describes all stand transformations as a result of

disturbance, whether natural (i.e., stand breakup and renewal) and human-caused (i.e., clearcut). Stand development following one disturbance and before another is governed by a set of timber yield curves (see Appendix I). For this study, we used the basic state table developed by Moore and Lockwood (1990) for their initial development and testing of HSG, which, fortunately for us, used the Iroquois Falls FMA. The state table was based mainly on the professional judgements of local foresters consulted by Moore and Lockwood (1990) during their study.

Forest-inventory input data for HSG, on a stand-by-stand basis, contain data on: (a) working group; (b) age; (c) species composition; (d) stocking by species; (e) site class; (f) area, and other variables (see Moore and Lockwood, 1990). HSG's periodic future inventories contain the same data. Thus, the simulation outputs from HSG in our study include ten structurally identical future forest inventories for each of four strategies, one for each 10-yr time step. The forest-inventory input data for each HSG run was the same 1994 dataset, thus anchoring all simulations to the same present forest.

With respect to the process of converting the received FRI dataset into a dataset ready for input into HSG, the following data are relevant:

- number of polygons in the received FRI dataset = 53,052
- area of the polygons in the received FRI dataset = 959,369 ha
- number of polygons in the HSG inventory input file (forest polygons only) = 28,408
- area of the polygons in the HSG inventory input file = 795,660 ha

main polygon types rejected from the HSG inventory input file = water bodies (including double-line rivers), bogs, rock, small polygons which straddled mapsheet boundaries, forest polygons with miscoded stand numbers

3.4 Moose Habitat Interpretations of Projected Inventories

The main function of the moose-habitat models is to interpret the future forest inventories in terms of moose food and cover values. Several steps are required in our modelling framework to accomplish this, including:

- (a) reclassification of the forest;
- (b) development of forest-type-specific, stocking-dependent and age-dependent curves for browse availability and cover values;
- (c) calculation of food and cover values for each stand (or part of stand) in the forest;
- (d) calculation of average food and cover values for habitat assessment units.

3.4.1 Reclassification of the Forest

As is often the case in strategic wildlife-habitat studies of this sort (e.g., Higgelke, 1994), the Ontario FRI working groups are too coarse for calculation of moose food and cover values, and the stand-composition data are too detailed. We therefore reclassified the forest for the specific purposes of this study. We followed a procedure similar to that of Higgelke (1994), where each major working group (as defined by the dominant overstorey species) was divided into subgroups depending on associated overstorey species and relative area in the forest (Table 3.2. This last factor was used to lump together classes whose area turned out to be only a few percent of the total forest area.

3.4.2 Food and Cover Values

Again following the protocol of Higgelke (1994), we established relationships depicting stocking-dependent, forest-type-dependent food and cover values over stand age. The following methods were used for each of food and cover.

3.4.2.1 Food

Food values were expressed in units of kilograms dry weight per hectare of total available moose browse. In the absence of actual measurements from the study forest, we used Higgelke's (1994) curves, developed originally for the Aulneau Peninsula in Lake of the Woods, northwestern Ontario, and based largely on professional judgements:

"The food supply curves depict the amount of available browse in a stand type at any stand age. Two curves showing available browse for each stand type were given - one for the stocking level of 10% and the other for the stocking level of 100%. The development of the curve sets was accomplished in consultation with a number of experts in the field of moose ecology. Food supply curves were generated with consideration of the following key points:

- Forage production peaks 5-20 years after timber harvesting (Vallée et al., 1976;
 Crête, 1977). Joyal (1987) stated that maximum browse production was achieved
 to 15 years after cutting. After this period browse production begins to diminish
 (Joyal, 1987). The food supply curves (thus) peak at 5 to 20 years.
- 2. Food supply curves were maintained below maximums indicated in the literature.

 For summer the maximum was set at 450kg/ha, below the value of 458 kg/ha as indicated by Cumming (1989). For early winter the maximum was set at 167

kg/ha which conformed with values found by Todesco (1988).

"The final curve sets were acceptable to each of the experts. Food supply for stands having stocking levels between these values are derived through linear interpolation between these extremes" (Higgelke, 1994).

Higgelke's (1994) curves were set up for a 170-day summer. Higgelke's early-winter curves were 40% of the summer curves, for a 105-day period. Thus, Higgelke had a total food supply of 140% of the summer curves for a period of 275 days. In our study, the seasons are different, as follows (also, see below in section 4.5):

- spring/summer is 155 days in length (mid April to mid September);
- autumn is 90 days (mid September to mid December); and
- early winter is 60 days (mid December to mid February).

Of the entire feeding year (i.e., these three seasons, and not late winter), these represent roughly the following percentages of the total length of time of 305 days:

- spring/summer 50%;
- autumn 30%; and
- early winter 20%.

We had to find a way to distribute the 140% over the three feeding seasons. If this were done strictly by proportion of days, we would get:

- spring/summer $50\% \times 140 = 70$
- autumn $-30\% \times 140 = 42$
- early winter $20\% \times 140 = 28$

Given that leaves are available with twiggy browse in spring/summer, but not in autumn and early winter, we adjusted these (spring/summer was raised to 60%, and 5% was taken off both autumn and early winter) to reflect both raw abundance of food biomass and the higher nutritional quality of spring/summer food. We set up four user-defined parameters:

- (a) one parameter "y" where: Curve Value * y = full-year food supply; and
- (b) three parameters as partitioning coefficients (PCs/s, PCaut, and PCew), each a percentage, the three adding up to 100, one for each feeding season, to be used to partition the full-year food supply to each feeding season.

Thus:

- S/S Food Supply = Curve Value * y * PCs/s;
- Aut. Food Supply = Curve Value * y * PCaut; and

- EW Food Supply = Curve Value * y * PCew.

For our first-round analyses, as presented in this report, we set:

- y = 1.4;
- PCs/s = 60%;
- PCaut = 25%; and
- PCew = 15%.

Our moose food-supply curves are depicted in Appendix III.

3.4.2.2 Cover

It had been our intention to deal with both early- and late-winter cover, as per the Higgelke (1994) study, but given the complications arising in the study, we were able to deal with early-winter cover only. We modified the Higgelke (1994) approach for generation of an early-winter cover index for each stand, for subsequent use in calculating cover-adjusted food values for early winter (see Appendix IV for the curves). To quote:

"McNicol and Gilbert (1980) found that stands most used by moose during the early winter period were moderately stocked with scattered conifers and deciduous trees. The

early winter cover curves . . . were developed to reflect this finding. It was assumed that stands with a stocking level of 50% would be consistent with the work of McNicol and Gilbert (1980). This stocking level provided the best early winter cover potential in each stand type. Stands that are more or less dense [i.e., with higher or lower densities] have lower early winter cover potential. Each stand type was assigned early winter cover curves for 10% stocking and 50% stocking levels. The 10% stocking curve is also the 100% stocking curve in this case. These curves are assumed to represent opposite extremes of early winter cover for moose. . . . interpolation is used to calculate early winter cover indices for stocking levels not equal to 10%, 50% or 100%" (Higgelke, 1994).

3.4.3 Food and Cover Calculations for Stands

A 200 m by 200 m point grid was laid over the stand map of the study forest for the purposes of calculating food and cover supplies. The grid was used in calculations of food supplies for all three seasons - spring/summer, autumn, and early winter - but it was actually only necessary for the special calculations of cover-adjusted food in early winter. Higgelke (1994) explained as follows:

"Hamilton et al. (1980) found that 95% of moose browsing occurred within 80 m of residual cover in severe winters. The work of Allen et al. (1987), which was based on the

results of a workshop of moose experts, used 100 m as the distance from cover that moose would travel for browse. The 200-m point grid used in M-HSAM would yield average proximity calculations between habitats of 100 m, which coincided with the work of these authors."

In describing the rationale behind calculating early winter food as function of proximity to cover, Higgelke (1994) wrote:

"This relationship has commonly been referred to as the edge effect . . . In addition to the food calculation made for all points, they were rated on a scale of 0 to 1 based on their suitability to provide cover to moose. The species composition, age and stocking of the stand represented by the point contributed toward the early winter cover index . . .

"Early winter MCC (moose carrying capacity) calculations accounted for the interspersion of habitat patches providing food and those providing cover. The food supply potential of each 200 m sampling point was multiplied by the cover index that was found to be the highest amongst itself and its eight nearest neighbours (each point lies in the centre of a 3-by-3 grid of points). . .

"The proximity calculation was an attempt to account for ecotones between stands. The early winter MCC of a grid point was adjusted upward if a neighbouring point had a higher early winter food supply value or a higher early winter cover index value. Grid

points in ecotones between a stand of high food supply and low cover index and one of low food supply and high cover would assume higher cover-adjusted browse potentials. This reflects the preference of moose to browse near cover as found by Hamilton *et al.* (1980)."

The resulting intermediate datasets for strategy-specific, period-specific moose food supplies thus consists of three food quantities (one for each season of spring/summer, autumn, and early winter), in kg/ha dry weight, for each grid point withing the entire forest.

3.4.4 Food and Cover Calculations for Habitat Assessment Units

Consistent with the work of Duinker (1986) and Higgelke (1994), we decided to capture spatial variation in moose carrying capacity across the whole study-forest landscape (on the order of 1 million hectares) using overlapping habitat assessment units (HAUs). The rationale for overlapping HAUs is given in detail by Duinker (1986) and Higgelke (1994). In summary, with stands on the order of tens of hectares, moose home ranges on the order of hundreds of hectares and of unknown locations, and a forest of a million hectares, some method must be found to quantify local moose population responses to local habitat change. Given our approach of modelling moose population response to habitat change, and a density of moose known to be roughly 0.1 moose/km2, we needed a habitat assessment unit of hundreds of square kilometres before a minimally acceptable size of moose population would be amenable to simulation. We

settled on a square HAU of ca. 50,000 ha (square for computational simplicity).

Each HAU has a unique associated set of 200 m by 200 m gridpoints. To calculate average food values per unit area (i.e., kg/ha dry weight) for each HAU, the gridpoint-specific values were multiplied by 4 (for the number of hectares represented by each cell), summed across the entire HAU, and divided by the HAU area (specifically, 50,172 ha).

In no position to base the boundaries of HAUs on any biophysical features of the forest (the landscape is very flat, and data on moose movement patterns are non-existent), we chose to overlap HAUs so that most locations in the forest could contribute several times to an HAU calculation of food supply or moose number. The HAUs were overlapped by 50% in each direction. This yielded just over 100 HAUs for the study forest, in a grid-like pattern. We removed HAUs at the edges of the forest when they represented territories just a small fraction of 50,000 ha, leaving us with about 85 HAUs for final calculations. In these final calculations, HAU-specific food values (in average kg/ha) and moose numbers (in average number/km2) were assigned ultimately to non-overlapping square spatial units (so-called Thiessen polygons) that represent zones of influence around the geographic centres of the original HAUs.

Before food-supply data can be used directly in the population model, we need to account for cropping rates. The food supplies are calculated as total moose-edible food supplies in the respective habitat types. Moose, however, will not find all potentially available food. Therefore, it is necessary to reduce the raw food data by some appropriate factor which we shall call the

cropping rate (actually, a proportion used to reduce the raw food data to available food data). In accord with Allen et al. (1987), we have applied a cropping rate of 0.2 for S/S and 0.6 for AU and EW.

3.4.5 Data Transfer to the Population Model

The population model requires the following data from the habitat models:

- (a) season-specific, HAU-specific food supplies for each future snapshot of the forest inventory (in our case, once every 10 years for 100 years); and
- (b) areas of forest in age classes 0-10, 11-20, 21-30, and 31-40.

The population model runs on an annual time step, but the habitat model provides data only for each tenth year. To create population model inputs for each year, we simply used each set of snapshot data from the habitat model to create ten years of population-model input data. To initialize the population model with sensible values for numbers and weights of animals in each sex-by-age cohort, we ran the model for 100 years using only the 1994 data.

3.5 Moose Population Modelling

Three elements of moose population dynamics represented in the model are mortality, reproduction, and weight change (Figure 3.2). Feeding occurs in spring/summer, fall and early winter, with changes in weight being a function of the food supply (as predicted by the habitat model). Mortality includes hunting mortality in the fall and other mortality (e.g. predation) in all seasons. Mortality due to starvation can also occur in any season if significant weight loss occurs (due to insufficient food supply). Reproduction is characterized by births occurring in the spring/summer season.

3.5.1 Population Structure

For modelling purposes, the moose population in each HAU is tracked independently over time. The population is divided into cohorts based upon sex (male, female) and age (11 classes, representing ages 0 - 10+). For each of these cohorts, the model tracks two state variables over time: the number of animals in the cohort, and the cohort's average weight per animal. The model divides the year into four seasons: spring/summer (April 15 - Sept. 15), fall (Sept. 15 - Dec. 15), early winter (Dec. 15 - Feb. 15), and late winter (Feb. 15 - Apr. 15). The model produces "census" data for each between-season enumeration by calculating the change in the number of animals and average weight per animal for each cohort (Figure 3.3).

The following sections provide a detailed description of the moose population submodel and its equations (see Table 3.4 for definitions of the variables used in the equations).

3.5.2 Growth

The growth of animals in the model is simulated through changes in average animal weights for each cohort. The change in weight of each cohort is calculated for each season by converting the food supply from each HAU into available energy, distributing this energy amongst the cohorts, and translating the energy available to each cohort into an average weight gain or loss (Figure 3.4).

The habitat model provides the population model with predictions of the available forage (kg dry weight/hectare), by decade and HAU, for each of three seasons: spring/summer, fall, early winter. The model assumes that no forage is available in late winter. Given a prediction for available forage by decade for each season and HAU, the model converts these into annual predictions by linearly interpolating between successive decadal output values.

The annual prediction of available forage in each of three seasons is then converted into available metabolizable energy, for each season, according to the following equation:

$$totalEnergy_{w,i} = availForage_{w,i} \times unitSize_{w} \times energyPerForage$$
 (1)

This total pool of metobolizable energy is then distributed amongst the various cohorts, for each season, according to the following equation:

$$availEnergy_{w,i,s,a} = \frac{totalEnergy_{w,i} \times animals_{w,i,s,a}}{\sum_{s=0}^{1} \sum_{a=0}^{10} animals_{w,i,s,a}}$$
(2)

The seasonal energy supply per animal is then used as the basis for calculating the change in average weight of each cohort over the season. First the metobolizable energy required for maintenance over the season is calculated for each cohort (for each window) using the following equation:

$$maintEnergy_{w,i,s,a} = dailyMaintEnergy_{n,s,a} \times weight_{w,i,s,a}^{0.75} \times seasonLen_n \times animals_{w,i,s,a}$$
 (3)

The surplus (or deficit) energy over and above maintenance requirements is then calculated as follows:

If the surplus energy is greater than zero, then it is converted to weight gain; otherwise, it is converted to a weight loss:

$$weight_{w,i,s,a} = weight_{w,i-1,s,a} + \frac{energySurplus_{w,i,s,a}}{growthEnergy_{s,a}}$$
 if $energySurplus_{w,i,s,a} \ge 0$

$$= weight_{w,i-1,s,a} + \frac{energySurplus_{w,i,s,a}}{lossEnergy_{s,a}}$$
 otherwise

Note that for the late winter season, in which the model assumes there is no energy supply $(availEnergy_{w,i,s,a} = 0)$, the energy deficit is equivalent to the maintenance energy requirement $(maintEnergy_{w,i,s,a})$ for the season.

Finally, weight gain is limited to an upper threshold value for each cohort:

$$weight_{w,i,s,a} = maxWeight_{n,s,a} \qquad if \ weight_{w,i,s,a} > maxWeight_{n,s,a} \qquad (6)$$

3.5.3 Starvation mortality

Mortality due to starvation is calculated by the model in all four seasons. For each cohort, the average weight of the cohort ($weight_{w,i,s,a}$) is compared to a threshold weight ($deathWeight_{n,s,a}$) below which individuals are assumed to die as a result of starvation. To calculate the proportion of the individuals in each cohort that would fall below this threshold, a distribution of weights for each cohort is generated using the mean cohort weight and an assumed standard deviation ($sdWeight_{n,s,a}$) expressed as a proportion of the mean weight. The weights of individual animals within a cohort are assumed to be normally distributed about the mean weight of the cohort (Figure 3.5). The proportion of individuals that would be expected to fall below the threshold weight are then calculated by the model; these individuals are then assumed to die due to starvation in this season. To reflect properly the change in mean weight of the cohort resulting

from the death of those individuals falling below the death weight, the post-starvation mean weight of the cohort is adjusted to account for their removal from the cohort.

death of these individuals.

3.5.4 Other Mortality

Mortality due to factors other than starvation and hunting is calculated by the model in all four seasons. For each cohort (and season), the proportion of animals that die due to other factors each season is specified as an input to the model. The equation for calculating other mortality is as follows:

$$other Mortality_{w,i,s,a} = other MortalityRate_{n,s,a} \times animals_{w,i,s,a}$$
 (7)

3.5.5 Hunting Mortality

Hunting mortality is calculated in the fall season each year. In calculating the hunting mortality for the each of the individual habitat windows, the model first determines a level of harvest for the entire forest (i.e. all HAUs combined). This calculation of harvest follows the tag allocation process currently used in Ontario for establishing harvest levels each year (Heyden et al., 1992;

Greenwood et al., 1982).

The first step in determining the annual harvest is to calculate a target harvest rate for cows. This is done by comparing the total density of animals over the entire forest to a user-supplied desired density (targetDensity), and using this ratio to determine the overall target harvest rate for cows (cowHarvestRate). The relationship between this ratio and the cow harvest rate is defined by the user as a series of points, between which the model interpolates linearly to define the entire curve (Figure 3.6).

Given the cow harvest rate, the target number of cows harvested (i.e. females with age>0) is calculated as:

$$targetCowHarvest_i = cowHarvestRate_i \times \sum_{all \ w} \sum_{a=1}^{10} animals_{w,i,1,a} \text{ if } i \in fall$$
 (8)

The target number of bulls harvested each year (i.e. males with age>0) is calculated as a function of the cows harvested and the user-supplied bull-to-cow harvest ratio (bullToCowHarvest):

$$targetBullHarvest_i = bullToCowHarvest \times targetCowHarvest_i$$
 if $i \in fall$ (9)

Similarly, the target number of calves harvested each year (i.e. male and females with age=0 and thus born in previous spring) is calculated using the user-supplied calf-to-cow harvest ratio

(calfToCowHarvest):

$$targetCalfHarvest_i = calfToCowHarvest \times targetCowHarvest_i$$
 if $i \in fall$ (10)

Given an overall target for the number of cows, bulls and calves to be harvested from the entire forest, the model then distributes this harvest across the HAUs as a function of the relative availability of animals and the hunting pressure in each HAU. The hunting pressure for each HAU is assumed to be a function of the road access, where road access is greatest in areas where timber has been most recently harvested.

The population model calculates a surrogate for the proportion of each HAU that is accessible each fall as follows:

$$propAccess_{w,i} = \frac{\sum_{f=0}^{3} accessFactor_{f} \times forestArea_{w,i,f}}{\sum_{f=0}^{3} forestArea_{w,i,f}}$$
 if $i \in fall$ (11)

This measure assumes that access is a function of the age since clearcut timber harvest, and that the younger the forest is, the greater the access will be. The user-supplied parameters in this relationship that weight each age-class of forested area (accessFactor_f) will generally range between 0 and 1, and be greatest for the age 0-10 class (i.e. recently cut forest will provide the greatest contribution to access) and lowest for the 31-40 age class; the model assumes that forested area that is 40 years of age or older will not contribute significantly to increasing the access.

The relative fall hunting pressure in each window ($huntingPressure_{w,i}$) is then calculated as a function of this surrogate for access ($propAccess_{w,i}$); the relationship between hunting pressure and access is defined by the user as a series of points, between which the model interpolates linearly to define the entire curve (Figure 3.7).

The model then distributes the total harvest of cows, bulls and calves across the forest in proportion to the relative abundance and hunting pressure of each habitat window:

$$huntingMortality_{w,i,s,a}^{\cdot} = \frac{targetCalfHarvest_i \times animals_{w,i,s,0} \times propAccess_{w,i}}{\sum_{all \ w} \sum_{s=0}^{1} (animals_{w,i,s,0} \times propAccess_{w,i})} \quad \text{if } a = 0$$

$$= \frac{targetBullHarvest_i \times animals_{w,i,0,a} \times propAccess_{w,i}}{\sum_{all \ w} \sum_{a=1}^{10} (animals_{w,i,0,a} \times propAccess_{w,i})} \quad \text{if } a > 0 \text{ and } s = 0$$

$$= \frac{targetCowHarvest_i \times animals_{w,i,1,a} \times propAccess_{w,i}}{\sum_{all \ w} \sum_{a=1}^{10} (animals_{w,i,1,a} \times propAccess_{w,i})} \quad \text{if } a > 0 \text{ and } s = 1$$

$$= \frac{\sum_{all \ w} \sum_{a=1}^{10} (animals_{w,i,1,a} \times propAccess_{w,i})}{\sum_{all \ w} \sum_{a=1}^{10} (animals_{w,i,1,a} \times propAccess_{w,i})} \quad \text{if } a > 0 \text{ and } s = 1$$

Note that the hunting mortality for each cohort is further constrained so as not to exceed the total number of animals in that cohort.

3.5.6 Births

The number of births for the population is calculated by the model each year in the spring season.

The number of calves born from each female cohort is calculated as a product of the number of females in the cohort (in spring/summer) and the cohort's average birth rate.

$$births_{w,i} = \sum_{a=0}^{10} animals_{w,i,1,a} \times fecundity_{w,i,a} \qquad \text{if } i \in \text{spring/summer}$$

$$= 0 \qquad \text{otherwise}$$
(13)

The birth rate ($fecundity_{w,i,a}$) in the model is defined as the average number of calves born in the spring/summer per female (also in the spring/summer); it is calculated each year as a function of the average weight of the female cohort in the previous fall. The relationship between the birth rate and weight of the mother is defined as a series of user-supplied birth rate-weight points, between which the model interpolates linearly to define the entire curve (Figure 3.8).

Each calf born into the model is assigned an initial (user-supplied) birth weight and a sex.

$$weight_{w,l,s,0} = birthWeight$$
 if $i \in spring/summer$ (14)

animals_{w,i,s,0} =
$$(1 - sexRatio) \times births_{w,i}$$
 for $i \in spring/summer$; $s = 0$
= $sexRatio \times births_{w,i}$ for $i \in spring/summer$; $s = 1$

33

3.5.7 Input Parameters

The moose population model requires users to specify a number of input parameters for each

model run. The following section provides some background on the values assigned to each of

these parameters for the Model Forest model runs. Included with each input parameter (in italics)

is the associated variable name used in the model description (see Table 3.4).

3.5.7.1 Initial moose density (animals)

The initial density of moose was set to match the estimated 1995 density for the LAMF area.

Population estimates are calculated across Ontario each year by the OMNR according to Wildlife

Management Units (WMUs). As the LAMF includes area from 3 different WMUs (26, 27, 28),

the density estimate for the LAMF was calculated using an area weighted average of the

provincial population estimates for these WMUs (H. Smith, pers. comm.). The resulting initial

density estimates were:

Calves: .039 moose.km⁻¹

Adult Females: .074 moose.km⁻¹

Adult Males: .027 moose.km⁻¹

Total Density: .14 moose.km⁻¹

3.5.7.2 Ideal weights (maxWeight)

The "ideal" weights of each cohort (i.e. weights when food is not limiting) were estimated from information provided in an OMNR report (OMNR, 1990); these estimates were based primarily on survey information gathered from 59 moose live-captured in Algonquin Park in the winters of 1985 and 1987:

Calves (5 months): 160-180 kg

Mature bulls: 400-542 kg (average of 483 kg)

Mature cows: 376-533 kg (average of 445 kg)

As the habitat in the LAMF is less productive than Algonquin Park, these weight estimates were assumed to represent approximate ideal weights for the LAMF. The ideal weights (in kg) for each cohort in the model were set as follows:

	Calf	Yearling	Young Adult (2-5)	Mature Adult (6+)
Male	170	300	450	485
Female	160	250	400	445

3.5.7.3 Initial weights (weight)

To initialize the model, weights for all cohorts were set at their "ideal" levels (as outlined above).

3.5.7.4 Weight at death (deathWeight)

This variable represents the weight, for each cohort, below which an individual animal will die due to starvation. Verne (1970), in Gasaway and Coady (1974), reported that a winter killed bull in Michigan had lost 33% of its body weight. Gasaway and Coady (1974) further report that moose in Alaska can be expected to lose approximately 24% of their weight between fall and spring (and survive).

Based upon this limited information, the weight below which an individual will die was set at 66% of the "ideal" weight for each cohort (as outlined above).

3.5.7.5 Distribution of weights (sdWeight)

The typical distribution of weights is represented in the model through a standard deviation about the mean weight of each cohort, where the standard deviation for each cohort is expressed as a proportion of the cohort's mean weight.

3.5.7.10 Energy requirement for weight gain (growthEnergy)

Based upon studies in Alaska, Gasaway and Coady (1974) calculated the energy requirements for weight gain in moose from the rate of tissue production; gross energy of tissue deposited amounted to a total of 7556 kcal per day (both fat and protein). Assuming a 70% efficiency for tissue production, they translated this into an average of 9800 kcal required to produce one kg of fat and protein. This value was used for all cohorts in the model to represent the energy required for weight gain.

3.5.7.11 Energy requirement for weight loss (lossEnergy)

Gasaway and Coady (1974) further determined that moose lost an average of 115 kg of body fat and protein over a 240 day period in mid to late winter in Alaska, and that fat and protein reserves were catabolized at an average rate of 3900 kcal per day. From these figures one can calculate that 8141 kcal are catabolized for every kg of body weight lost. A value of 8100 kcal per kg was therefore used for all cohorts in the model to represent the energy required for weight loss.

3.5.7.12 Fecundity (fecundity)

Heydon et al. (1992), in modelling the Ontario moose harvest, used reproductive rates of 30 calves per 100 cows for yearlings and 157 calves per 100 cows for 2-year olds and older; these values, which were originally reported in Greenwood et al. (1982), were also used in our initial study. Note that, for the purposes of these model runs, fecundity was not made to vary as a function of cow weight.

3.5.7.13 Target density for harvest (targetDensity)

As with the initial moose densities (as described above), the target density for moose was set to match the estimated 1995 density for the LAMF area. As part of the harvest quota calculation in Ontario each year, targets are set by the OMNR according to Wildlife Management Units (WMUs). As the LAMF includes area from 3 different WMUs (26, 27, 28), the target density for the LAMF was calculated using an area weighted average of the 1995 provincial targets for these WMUs (H. Smith, pers. comm.); the resulting target density was calculated as 0.27 moose.km⁻¹.

3.5.7.14 Cow harvest rate (cowHarvestRate)

In their guidelines for setting moose harvest levels in Ontario, Greenwood et al. (1982) suggested that a cow harvest rate of 4% should lead to a dramatic increase in the population size, a rate of 6% will lead to a moderate increase, while a rate of 8-9% should stabilize the population. Using

this information, the relationship between the cow harvest rate and the density of moose each year was defined in the model by the following points:

Actual Density / Target Density	Cow Harvest Rate
0	0
0.25	0.02
0.5	0.04
0.75	0.06
>= 1.0	0.085

3.5.7.15 Bull-to-cow harvest ratio (bullToCowHarvest)

In the guidelines for setting moose harvest levels in Ontario, the suggested target for the ratio of bulls to cows harvested is 3.5 (Greenwood et al. 1982); this value was used for all the model runs.

3.5.7.16 Calf-to-cow harvest ratio (calfToCowHarvest)

In the guidelines for setting moose harvest levels in Ontario, the suggested target for the ratio of

calves to cows harvested is 1.67 (Greenwood et al. 1982); this value was used for all the model runs.

3.5.7.17 Relative hunting pressure and access (huntingPressure, accessFactor)

For the model to distribute the moose harvest spatially, the relationship between the amount of forested area and the relative hunting pressure must be specified (as described previously in the section "Moose Population Modelling". In quantifying this relationship, it was assumed that the younger a particular hectare of forest is, the more road access there will be (due to the recent timber harvesting) and the greater the relative hunting pressure. The relative contribution of each age class of forest to determining the total proportion of each HAU that was accessed (i.e. the variable accessFactor) was assumed to decrease exponentially as a function of the time since last harvest, with access being negligible 40 years harvesting. This was represented as follows in the model:

Forest Age Class	Relative Contribution to Access (accessFactor)
0-10	1
11-20	0.5
21-30	0.25
31-40	0.125

Finally, in translating the effect of access into relative hunting pressure in the model, a 1:1 relationship was assumed between the relative hunting pressure (huntingPressure) and the proportion of access in each habitat window.

4. RESULTS AND DISCUSSION

4.1 Forest Inventory Projection and Wood Supply

Except for one time step in one of the simulations (specifically, the second step (2004-2014) under the Spatial Strategy), all timber-harvest targets could be met, and therefore can be judged to be sustainable over the 100-yr simulation period. Regarding developments in the forest inventory under the four strategies, the following observations can be made.

4.1.1 Age-Class Structure

Age-class structure is important in determining moose food supplies according to our models because young stands (and, to some degree, very old stands) provide the highest per-unit-area food supplies. Like the other strategies, the No-Harvest Strategy has substantial area in young age classes in 1994 (see Figure 4.1), but as time progresses the strategy has little or no area in these age classes. This will, predictably, have the effect of lowering the moose food supplies of

the No-Harvest Strategy as time passes in the simulation.

The three timber-harvest strategies have age-class structures similar to each other. These age-class structures are roughly balanced over the 100-yr simulation, with the Lower Strategy having higher area of very old forest, likely the outcome of old, site-class-3 black-spruce stands missing harvest and becoming self-perpetuating old stands with harvestable wood volumes less than the operable minimum (i.e., less than 40 m3/ha).

4.1.2 Stocking Levels

In 1994, the average stocking per hectare across the forest is 74.5%. By the end of the 100-yr simulation, the average stocking under each strategy has increased: (a) under the No-Harvest Strategy, to 86.6%; (b) under the Basic, to 87.9%; (c) under the Lower, to 85.4%; and (d) under the Spatial, to 88.2%.

To understand the trends observed above, we need to examine the state table used to depict stand response to clearcut harvest and old-age breakup (Table 3.2). We noted earlier that the state table is the overriding controlling influence of the characteristics of the future forest in response to stand disturbance, whether harvested or naturally disturbed. We used a state table generated by Moore and Lockwood (1990) when HSG was first developed. In hindsight, we believe that the state table is responsible for forcing a general shift in stand stocking from a variably stocked

forest in 1994 to a well-stocked forest through the simulation (see Tables 3.2). Interestingly, the left side of each statement in the state table does not include data on stocking, but the right side does. This means that regardless what stocking the stand has at the moment of transformation due to disturbance, it will assume the right-side stocking as indicated. These numbers are overwhelmingly 0.8 and higher.

The shift from variable to moderate stocking will have two main effects upon moose habitat characteristics. On one hand, since the relationships to calculate food supplies are most generous to poorly stocked stands (food is inversely proportional to stocking), the average food supplies will shift downward over time as the average stocking shifts upward. On the other hand, EW cover is favoured by mid-range stocking, and its value too goes down as stocking move from mid-range to high range. Thus, moose habitat is taking a double downward pressure as the forest stocking increases over time. We are skeptical as to whether the state table accurately reflects the actual stocking changes that will occur over time as the forest is harvested for timber and regenerated. Perhaps the reality will be that future stocking will be much more similar to present stocking than we have simulated.

4.2 Moose Habitat Forecasts

Because of the manner of calculation, spring/summer and autumn food supplies respond in exactly the same manner to changes in forest structure, so the following discussions will focus on

spring/summer (SS) and early winter (EW) food responses. To be reminded, the SS food response in any particular HAU is solely a function of the sum of raw location-specific food supplies, but the EW food response is conditioned by the proximity of food supplies to good seasonal cover.

4.2.1 Spring/Summer Food Responses

- In 1994, the average SS food value (calculated as an average among HAU averages) for the whole Model Forest is roughly 24 kg/ha dry weight of browse (Figure 4.2). This value makes intuitive sense given that the Model Forest is not considered prime moose habitat compared with other areas of Ontario's boreal forest. For example, for the Aulneau Peninsula, Higgelke (1994) predicted average per-hectare food quantities of some xx kg.
- (b) The average SS food value plummets by 2004, and then rises for most of the scenarios, particularly the timber-harvest scenarios (Figure 4.2). The plummet is explained by the anomaly in the 1994 inventory that there are about 120,000 ha of 8-year-old stands (these are in the 0-10 age class). This area is of an age critical to the provision of relatively high site-specific food values (the peaks of food value in the browse curves occurs at ages 5-15). However, in 2004, all these stands are 18 years old, and food supplies per unit area, as demonstated by the food-supply curves (see Appendix xx) go down demonstrably.

- (c) The average SS food value declines over the 100-yr simulation for all scenarios (Figure 4.2). Indeed, this is the case for most individual HAUs in the forest. We explain this with the reminder that food values are dependent on stocking, and age class. For all scenarios, stocking is going up (rendering lower per-hectare food values), and the age-class structure contains a smaller proportion of stands in break-up age classes.
- (d) The scenarios are all remarkably similar to each other except at time steps 2014-2034 and 2084-2094. The earlier differences are explained by the differences in harvest area among the scenarios (more area harvested produces more browse overall). This must be overwhelmed by the abundance of area in well-stocked developing stands which produce the lower overall browse values in the middle of the 100-yr simulation. The superior performance of the No-Harvest Strategy at 2094 is explained by the huge area of old stands, all of which, according to the food-supply curves, would be relative rich in perunit-area food supplies.

Overall, we conclude that the habitat models as constructed and parameterized in this study are unable to distinguish, for the Model Forest as a whole, significant differences among the four strategies in terms of the predicted variable of SS food supply response.

4.2.2 Early-Winter Food Responses

- (a) EW food supplies, as an average across the whole Model Forest (Figure 4.3), decline steadily in all scenarios, from a 1994 high of almost 3 kg/ha, to a 2094 range of about 1 to 1.5 kg/ha. Again we observe that this is a low value, consistent with the general assumption that the Model Forest is poor quality moose habitat. The declines are, of course, partly related to the reasons for decline in SS food values, as discussed above (the raw food values for both seasons come from the same basic food-supply curve sets). However, the adjustment of EW food supply using EW cover (Figure 4.4) clearly dampens the patterns seen in SS food supplies. Indeed, the superior performance of the No-Harvest Strategy with respect to EW cover indices (Figure 4.4) moves it well ahead of the timber-harvest strategies.
- (b) The relative differences among the scenarios is much more pronounced for EW than SS food supplies. The EW food supply under the No-Harvest Strategy is roughly twice as good as under the Basic and Spatial Strategies, with the Lower Strategy between. As expected, the No-Harvest Strategy retains a superior level of EW cover, which otherwise gets harvested or does not develop at all in some areas in the timber-harvest scenarios.

Overall, we conclude that the habitat models as constructed and parameterized are able to distinguish, for the Model Forest as a whole, significant differences among the four strategies in terms of the predicted variable of EW food supply response.

4.3 Moose Population Forecasts

We implemented five sets of simulations with the moose population model using the four sets of outputs from the habitat models:

- (a) No-Harvest Strategy with no moose hunting;
- (b) Basic Strategy with no moose hunting;
- (c) Basic Strategy with moose hunting;
- (d) Lower Strategy with moose hunting; and
- (e) Spatial Strategy with moose hunting.

We did not make a run of the No-Harvest Strategy with hunting because we expected roads to become impassible for hunters over time, and the hunting opportunities in new and recent clearcuts to diminish rapidly. Thus, under a No-Harvest Strategy, the moose-hunting opportunities would rapidly erode.

With the five runs made we were able to make three comparisons of overall moose population response to changing habitat on the Model Forest:

- (a) two scenarios with no hunting (Figure 4.5;
- (b) two Basic scenarios, one without and one with hunting (Figure 4.6); and
- (c) three timber-harvest scenarios with hunting (Figure 4.7).

In initializing each simulation for each HAU under each scenario, we ran the population model for 100 yr using the 1994 habitat input values. This was done to allow the starting population data to come to equilibrium with the habitat data before feeding the population model the projected time-stream of dynamic food and cover data.

4.3.1 Two Strategies without Hunting

The current moose population density in the Model Forest is roughly 0.14 moose/km2. The moose populations are, in reality, responding to both their habitat and their predators, which include non-human vertebrates such as wolves and bear as well as humans. As evident in Figure 4.5, when the populations are allowed to come to equilibrium with the simulated habitat alone, i.e., without hunting, the model shows that the density of moose as determined by habitat would be just under 0.4 moose/km2 in 1994. This may indicate that hunting is responsible for holding the current population several times lower than it would be if the population were constrained by habitat alone.

Over time, given the evolution of the two simulated habitats, both scenarios result in reduced moose population densities, a finding which is consistent with the food and cover projections discussed earlier. By year 100, the No-Harvest Strategy (without hunting) results in a moose density of just over 0.2 moose/km2, while the Basic Strategy (without hunting) results in just over 0.1 moose/km2.

4.3.2 The Basic Strategy With and Without Hunting

The moose density of 1994 under the Basic Strategy with hunting is just under 0.1 moose/km2, which is a rough match with actual densities. This is certainly no cause for uncritical jubilation that the model is right, but it does give us a sense that we are on the right track. This scenario results in an eventual decline of the moose density over time, too, but a much less dramatic one than that when moose hunting does not occur. This suggests that, under the conditions modelled, moose respond more strongly to habitat change when the population is nearer the habitat's capacity for moose than when held well below that level by hunting.

4.3.3 The Three Timber-harvest Strategies with Hunting

Moose density responses under the three scenarios of timber harvest with hunting have relatively few differences among them (Figure 4.7). Those differences evident have a reasonable resemblance to those of the food-supply responses, as expected. The degree of difference among the timber-harvest strategies tested here was insufficient to elicit strong differences in moose density response. In addition, our approach to modelling sex- and age-specific harvest rates, the lack of habitat-induced variability in fecundity, and our equilibration period of 100 yr may also be playing a role in masking the moose-population effects of the timber-harvest strategies. These findings, of course, are specific to the strategies, forest, and moose populations examined - they

are thus not generalizable with any confidence.

4.4 Overall Interpretations

With considerable uncertainty yet remaining, the few simulations we have run using our suite of models lead us to the following tentative conclusions:

- (a) In the Model Forest, hunting seems to play an important role in keeping moose population densities at their current levels. If hunting were to cease entirely, the habitat could probably carry significantly higher densities of moose.
- (b) Spatial variability of moose population densities is high across the Model Forest landscape. In some areas there are very few moose, while in other areas the densities could be approaching 0.5 to 1.0 moose/km2. The numbers reported here are averages by HAU across the whole million-hectare forest.
- (c) Forest simulations driven by assumptions oriented toward timber production (e.g., successful plantation silviculture) are likely to lead to lower moose population densities than would be the case if nature and foresters shaped the real forest together over the next centuries. In particular, timber-minded foresters tend to seek timber-oriented rotations and stocking levels, whereas nature might keep more lower-stocked and older stands in

the landscape. Simulation analysts in forest-management planning must work diligently to prepare realistic forest-inventory projections for use in interpreting wildlife habitat and other biodiversity-oriented values.

(d) If current hunting pressures on moose in the Model Forest continue, then the kind of forest-management strategy implemented (i.e., how timber is harvested) may have relatively minor impacts on moose densities.

5. CONCLUSIONS

5.1 Limitations of the Analysis

We are unaware of any other attempts to model the effects of long-term future timber management on moose habitat and moose populations on a million-hectare landscape using a simulation modelling approach such as we have used. There is rather limited experience among forest modellers using such an approach. Our venture required enormous amounts of time and analytical energy, indeed much more than we had originally anticipated. We have in large part met our objective of developing an integrated set of models, but we certainly have been unable, within the limits of the present study, to test them in any thorough way. We caution that the habitat and population models are not, in their condition at the time of writing, ready for routine application in forest-management planning exercises. They are in shape, however, for further

development and research-oriented use by people with expertise in forest simulation, vertebrate population simulation, and GIS. Shortcomings in our analysis include the following.

5.1.1 Data Inadequacies

It had been our intention in this study to build and apply the models using only extant data - we were not prepared, given our time and budget, to gather new data to parameterize the models and build specific relationships. To gain a reasonable comfort level with the predictions, data should be assembled for improvement of: (a) HSG state table; (b) the HSG yield curves; (c) the moose food-supply curves; (d) the population parameter estimates; and (e) the influence of habitat structure (roads and age classes) on hunting success.

5.1.2 Sensitivity Analyses

Complex simulation modelling exercises such as this must include some effort to explore the relative importance of uncertainties in specific model components. The standard approach is sensitivity analysis, where model components are systematically altered and the effects of the alterations on model outcomes determined (Duinker and Baskerville, 1986). Sensitive model components, which require urgent research, are those where small changes in the components result in large changes in model outcomes. Unfortunately, we simply could not implement such

an analysis while trying to develop the first set of results reported here.

5.1.3 Scenario Exploration

We tried to develop four alternative forest-management strategies that would simultaneously be at least somewhat realistic and sufficiently different from each other for response differences to be significant. We missed this mark to some degree. The No-Harvest Strategy failed to incorporate natural disturbances such as fire and insect infestations, and the timber-harvest strategies were too similar.

At least three obstacles must be overcome if simulation analysts are to develop and test a useful array of forest-management strategies: (a) the uncertainties over what kinds of strategies would elicit sufficiently different responses in moose habitat and populations; (b) the burden of data and model manipulation to implement the alternative strategies; and (c) the potential for other people (forest managers, experts, the public) to dismiss specific strategies as foolish or unimplementable.

5.2 Model Development, Testing and Research Needs

Our work, as reported here, is just a beginning. We are firmly convinced that further

developments building on our progress so far is fully warranted - the need to understand the implications of alternative approaches to forest management on populations of important wildlife species is growing rapidly, as apparent in so many contemporary forest management and policy initiatives. Examples of such initiatives include the criteria and indicators of the Canadian Council of Forest Ministers (1995), the principles and criteria of the Forest Stewardship Council (1995), and the indicators of forest sustainability in the Ontario forest management planning manual (OMNR, 1995).

We have laid a firm foundation for further work. In our view, the following tasks would now prove useful:

- development of wider range of forest-management strategies;
- development of mechanisms to incorporate natural disturbances realistically into forest projection;
- implementation of a full sensitivity analysis of the models, particularly our population model;
- development of relationships for food and cover in late winter, a critical time of year for moose;
- development of methods to account for potential immigration and emigration of animals among habitat assessment units, and between the study area and neighbouring forests;

- development of relationships between cow weight and birth rate (i.e., habitat and fecundity);
- collection of field data for moose food and cover relationships, as well as demographic data on moose populations.

5.3 Final Comments

Integrated simulation modelling of moose habitats and populations (and, for that matter, for any forest-dwelling vertebrate) is yet in its infancy and scarcely ready for broad application in forest-management planning. We feel our accomplishments in this project, while not entirely as we had hoped, have been substantial and important. Additional progress building on our efforts will require much more substantial efforts than we were able to put in place for this project.

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Table 2.1. Summary of forest types and site classes in the Lake Abitibi Model Forest.

WORKING GROUP	,	PERCEN	PERCENT TOTAL AREA BY SITE CLASS							
	x	1	2	3	4	тот				
Sb	1.0	24.6	36.0	13.3	4.0	78.9				
Po	0.2	1.9	7.9	1.0	0.1	11.1				
В	1.5	1.6	0.5	0.1	****	3.7				
Pj		0.3	2.1	1.0		3.5				
Bw		0.3	0.8	0.7	0.1	2.0				
Sw	0.1	0.2				0.3				
Ce			0.1	0.1	~~~	0.2				
Pb		0.2	0.1			0.3				
TOTAL	2.9	29.0	47.5	16.3	4.3	100.0				

Total area of the forest included above is 795,660 ha. Numbers may not add properly due to rounding. "----" means less than 0.05%. Other minor working groups include larch and black ash. Sb = black spruce, Po = trembling aspen, B = balsam fir, Pj = jack pine, Bw = white birch, Sw = white spruce, Ce = eastern white cedar, Pb = balsam poplar.

Table 3.1. The state table used as input to HSG in the forest-inventory projections.

Speci	Sit	Age	%Po	dstrb	Treatmen		Spl	Stl	Agel	Stkl	Sp2	S12	Age2	Stk2
es Sb	e M	•	•	clearcut	intensive	,	Sp	мх	0	0.8				
	×	•	•	clearcut	intensive	,	Sb	x	0	0.8				
Sp Sp	×		0	clearcut	basic	,	Sb	x	0	0.8				
Sb	x	•	0	clearcut	extensive	1	Sb	x	0	0.3				
Sb	×	•	>0&<30	clearcut	basic	,	Sb	x	0	0.5	Po	1	0	0.5
Sb	×	•	>0&<30	clearcut	extensive	1	Po	1	0	1				
Sb	x	•	>30	clearcut	basic	1	Po	ı	0	0.65	Sb	x	0	0.4
Sb	×	•	>30	clearcut	extensive	,	Po	1	0	1				
Sb	×	>120		none	natural	,	Sb	х	20	0.8				
Sp	×	>120	>0&<30	none	natural	,	Sb	x	10	0.3	Po	1	15	0.7
Sb	×	>120	>30	nona	natural	,	Ро	1	15	0.8	Sb	х	10	0.2
Sb	1			clearcut	intensive	,	Sb	ı	0	0.8				
Sb			0	clearcut	basic	1	Sb	1	0	0.8				
Sb	1		0	clearcut	extensive	,	Sb	1	0	0.3				
Sb			>0&<30	clearcut	basic	,	Sb	1	0	0.65	Po	2	0	0.4
Sb	1		>0&<30	clearcut	extensive	1	Po	2	0	1	Sb	1	0	0.2
Sb	1		>30	clearcut	basic	1	Po	1	0	0.6	Sb	ı	0	0.5
Sb	1	•	>30	clearcut	extensive	7	Po	ī	0	1	Sb	1	0	0.1
Sb	1.	>170	,	none	natural	,	Sb	1	20	1				
Sb	1.	>170	>0&<30	none	natural	7	Po	1	30	0.6	Sb	1	20	0.5
Sb	1,	>170	>30	none	natural	7	Po	1	40	0.8	Sb	1	20	0.3
Sb	1 2	1.	0	clearcut	extensive	7	Sb	2	0	0.7				
Sb	2	•	0	clearcut	basic	1,	Sb	2	0	0.8				
Sb	2	•	0	clearcut	intensive	7	Sb	2	0	1				
Sb	2	1.	×	clearcut	extensive	1	Po	3	20	0.7	Sb	2	0	0.5
Sb	2	•	>0	clearcut	intensive	,	Sb	2	0	1				
Sb	2	>190	0	none	naturel	,	Sb	2	55	1				
Sb	2	>190	ж	none	natural	,	Sb	2	50	0.7	Po	3	20	0.5
Sb	2	•		clearcut	extensive	1	Sb	2	0	0.8				
Sb	2	1.	•	clearcut	basic	1	Sb	2	0	0.9				
Sb	2	•	•	clearcut	intensive	1	Sb	2	0	1				
Sb	2	>220	•	none	natural	1	Sb	2	60	1				
Sb	1,	1.	•	clearcut	basic	,	Sb	3	0	1				
Sp	3	>170	1.	none	natural	7	Sb	3	180	•				

Sw	M X	•	•	clearcut	intensive	′	Sw	мх	0	0.8				
Sw	x	•	•	clearcut	intensive	,	Sw	x	0	0.8				
Sw	х	•	0	clearcut	basic	1	Sw	x	0	0.8				
Sw	х	•	0	clearcut	extensive	,	S₩	x	0	0.3				
Sw	х	•	>0&<30	clearcut	basic	,	Sw	x	0	0.5	Po	1	0	0.5
Sw	x	•	>0.4c<30	clearcut	extensive	1	Po	1	0	ı				
Sw	х	•	>30	clearcut	basic	,	Po	1	0	0.65	Sw	х	0	0.4
Sw	x	•	>30	clearcut	extensive	1	Po	ı	0	1				
Sw	x	>120	0	none	natural	,	Sw	×	20	0.8				
Sw	x	>120	>0&<30	none	natural	,	Sw	x	10	0.3	Po	1	15	0.7
Sw	×	>120	>30	none	natural	,	Po	1	15	0.8	Sw	×	10	0.2
Sw	1	•		clearcut	intensive	7	Sw	ī	0	0.8				
S₩	 			clearcut	basic	7	S₩	1	0	0.8				
Sw	1		0	clearcut	extensive	,	Sw	ı	0	0.3				
Sw	1		>0&<30	clearcut	basic	,	Sw	1	0	0.65	Po	2	0	0.4
Sw	1		>0&<30	clearcut	extensive	,	Po	2		1	Sw	1	0	0.2
	+		>30	clearcut	basic	,	Po	1	0	0.6	Sw	1	0	0.5
Sw	╁		>30	clearcut	extensive	1,	Po	1.	1.	1	Sw	1	0	0.1
Sw	<u> </u>	 	0	none	natural	1	Sw	1.	20	0.8	1			
Sw	+	>170	>0&<30	none	natural	1	Ро	1	30	0.6	Sw	1	20	0.5
Sw	+-	>170	+		natural	1,	Po	1	40	0.8	Sw	1	20	0.3
Sw	1	>170	>30	clearcut	extensive	1,	Sw	1 2	10	0.7	1	\vdash		
Sw	2	 •	•		 	Ι,	Sw	1,	10	0.8	+	1	1	1
Sw	12	<u> • </u>	0	clearcut	basic	+	Sw	1;	1.	+-	+	+	+	1
Sw	12	 • 	0	clearcut	intensive	†	Po	1,	20	0.7	Sw	1,	0	0.5
Sw	2	 	 **	clearcut	extensive	+	+	1/2	1.	0.9	╅	+	\top	1
Sw	12	 •	>0	clearcut	basic	+	Sw	+	1:	1	+	+-	 	1
Sw	2	 	×0	clearcut	intensive	+	Sw	12	55	1	+	+	+	1
Sw	2	>190	0	none	natural	+	Sw	2 2	50	0.7	Po	1,	20	0.5
Sw	12	>190	×0	none	natural	+	+	_	60	1				
Sw	2	>220	·	none	natural	+	Sw	+-	\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\\	+				
Sw	_ 3	<u> </u>		clearcut	basic	+	Sw	╅	+-	+;				
Sw	3	>170	 - -	none	natural	+	+		180					
Po	×	>100	·-	none	naturel	+	╅	╅	15	+-				
Po	1	>100	<u> -</u> -	none	natural	+	╅	╌┼╌	15	+				
Ро	2	>100	<u> • </u>	none	natural	+	Po		15					
Po	3	>100	<u> -</u>	none	natural	+	Po	- 3	15					
Po		· _	<u> -</u>	clearcut	extensive	4	Po		- 0	+-				
Pj	J	>110	<u> </u>	none	natural	1	Pj	×	15					

Pj	1	>110	•	none	natural	1	Pj	ŀ	15	1
Pj	2	>110	•	none	natural	1	Pj	2	15	1
Pj	3	>110	•	none	naturai	1	Pj	3	15	1
Pj	•	•	•	clearcut	basic	1	Pj	1	0	1.2
В	×	>80	•	none	natural	1	В	×	20	1
В	1	>80	•	none	netural	1	В	1	20	1
В	2	>80	•	none	natural	′_	В	2	20	1
В	3	>80	•	none	natural	′	В	3	20	1
В	•	•	•	clearcut	extensive	1	В	•	20	1
В	•	•	•	clearcut	intensive	/	Sb	х	0	1

How to read the table: At each time period, each stand in the inventory dataset is checked against this table to determine whether it should be transformed into another stand type. If a stand finds a match on the left side of the table (to the left of the /, then its area assumes new characteristics as defined by the right side of the statement.

Table 3.2. Reclassification scheme for the Lake Abitibi Model Forest.

COVER TYPE DEFINITION	NEW COVER TYPE
all stands in the working group	1
> 70% spruce, or	2
non-working group species comprised more than half by conifer	
non-working group species comprised more than half by non-conifer	3
all stands in the working group	4
> 70% poplar, or	5
non-working group species comprised more than half by non-conifer	
non-working group species comprised more than half by conifer	6
all stands	7
	all stands in the working group > 70% spruce, or non-working group species comprised more than half by conifer non-working group species comprised more than half by non-conifer all stands in the working group > 70% poplar, or non-working group species comprised more than half by non-conifer non-working group species comprised more than half by conifer

Table 3.3. Variables used in the moose population model.

Variable	Description of variable	
s	index representing sex (0=male, 1=female);	
а	index representing moose age class (11 classes: ages 0 - 10+)	
I	index representing seasonal model time step (4 census periods for each year of simulation, corresponding to the seasons spring/summer, fall, early winter, late winter)	
n	index representing season (0=spring/summer, 1=fall, 2=early winter, 3=late winter)	
ſ	index representing forest age class (0= ages 0-10, 1= ages 11-20, 2= ages 21-30, 3= ages 31-40)	
w	index representing habitat window	
totalEnergy _{w,i}	total metabolizable energy supply for the population in period i and window w (kcal)	
availForage,	density of available forage (dry weight) in period i and window w (kg ha ⁻¹)	
unitSize_	total area of the habitat window w (ha)	
energyPerForage	metabolizable energy per unit of available forage (kcal kg ⁻¹)	
availEnergy _{w.i.i.a}	metabolizable energy available, in period i and window w , for cohort with sex s and age a (kcal)	
animals _{w.i.s.a}	number of animals, in period i and window w , for cohort with sex s and age a (# animals)	
weight _{w,i,i,a}	mean animal weight, in period i and window w , for cohort with sex s and age a (kg)	
maintEnergy _{w.i.s.a}	total metabolizable energy required for maintenance, in period i and window w , for cohort with sex s and age a (kcal)	
dailyMaintEnergy _{nsa}	daily maintenance metabolizable energy requirement per unit of metabolic body weight, in season n , for cohort with sex s and age a (kcal kg ^{-0.75} days ⁻¹)	
seasonLen"	duration of season n (days)	
energySurplus _{w.i.s.a}	total surplus metabolizable energy over and above maintenance requirements, in period i and window w , for cohort with sex s and age a (kcal)	
growthEnergy _{s.a}	metabolizable energy required for a unit increase in average weight of an animal in cohort with sex s and age a (kcal kg ⁻¹)	
lossEnergy	metabolizable energy required for a unit decrease in average weight of an animal in cohort with sex s and age a (kcal kg.)	
maxWeight _{ns.a}	ideal weight of an animal, in season n , for cohort with sex s and age a (kg)	
deathWeight _{n.a}	weight below which individual animals will die due to starvation, in season n , for cohort with sex s and age a (kg)	

Variable	Description of variable	
sdWeight _{n.s.a}	standard deviation of the weight distribution expressed as a proportion of the cohort's mean weight, in season n , for cohort with sex s and age a (>0)	
otherMortality _{w.i.s.a}	mortality due to factors other than starvation and hunting, in period i and window w , for cohort with sex s and age a (# of animals)	
predationRate _{nsa}	mortality rate due to factors other than starvation and hunting, for season n , for cohort with sex s and age a (0-1)	
targetDensity	target animal density used in calculation of harvest rate (# of animals / km2)	
cowHarvestRate,	overall target harvest rate for cows in period i (0-1)	
targetCowHarvest,	target for total cows harvested in period i (# of animals)	
targetBullHarvest,	target for total bulls harvested in period i (# of animals)	
bullToCowHarvest	target ratio of bull harvest to cow harvest (>=0)	
targetCalfHarvest,	target for total calves harvested in period i (# of animals)	
calfToCowHarvesi	target ratio of calf harvest to cow harvest (>=0)	
propAccess _{w.i}	proportion of habitat window w that is accessible in period i (0-1)	
accessFactor _f	weighting factor specifying the relative contribution of forest class f in the calculation of the proportion access (0-1)	
forestArea _{w,if}	area of the habitat window w in forest class f for period i (ha)	
huntingPressure,	relative hunting pressure for habitat window w in period i (>0)	
huntingMortality _{w,i,t,a}	mortality due to hunting, in period i and window w , for cohort with sex s and age a (# of animals)	
births _{w,i}	births in period i and window w (# of animals)	
fecundity _{w,s,a}	average number of calves born, in period i and window w , per female of age a (>=0)	
birthWeight	average birth weight of calves (kg)	
sexRatio	proportion of calves born as males (0-1)	

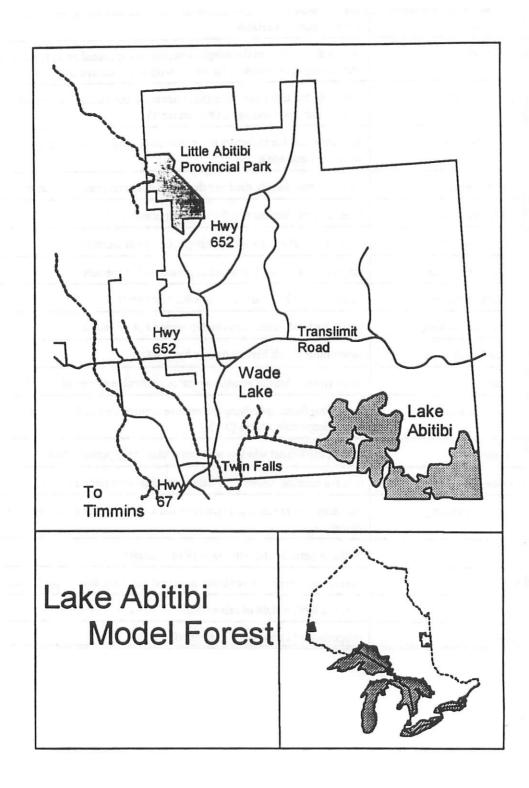


Figure 2.1 Location of the Lake Abitibi Model Forest.

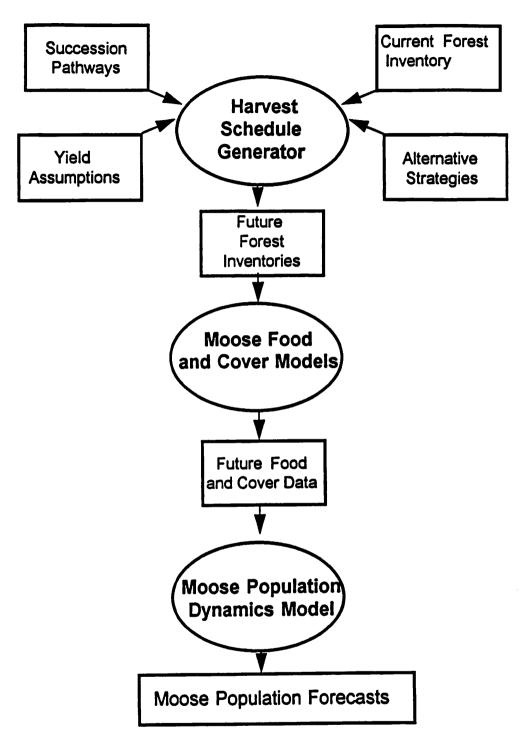


Figure 3.1 Overview of relationships of the models.

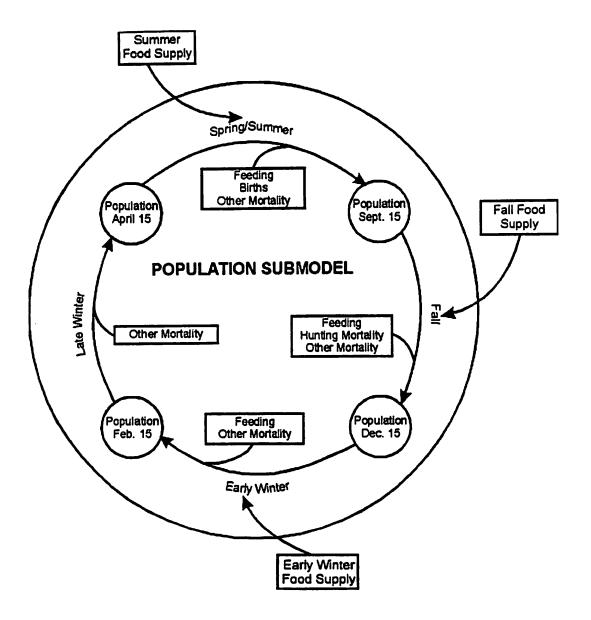


Figure 3.2 Overview of the moose population model.

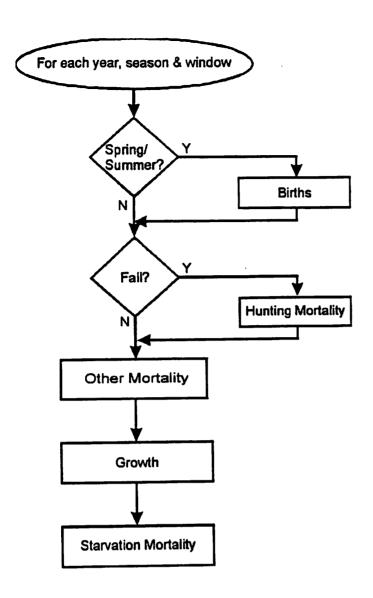


Figure 3.3 Calculation sequence in the moose population model.

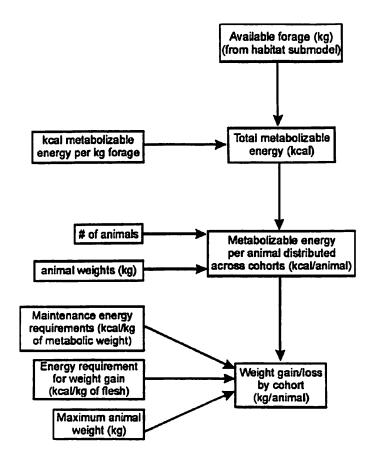


Figure 3.4 Growth calculations.

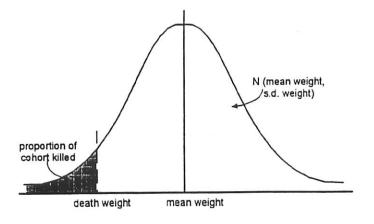


Figure 3.5 Conceptual representation of starvation mortality rates as a function of each cohort's mean weight per animal and the weight at which an individual dies.

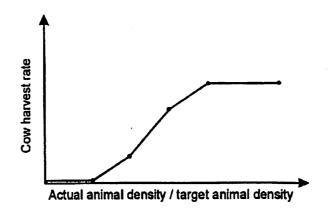


Figure 3.6 Conceptual representation of cow harvest rate relationship.

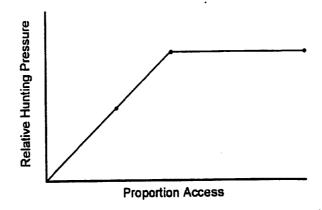


Figure 3.7 Conceptual representation of relative hunting pressure relationship.

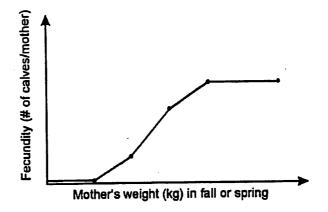


Figure 3.8 Conceptual representation of relationship between fecundity and mother's weight.

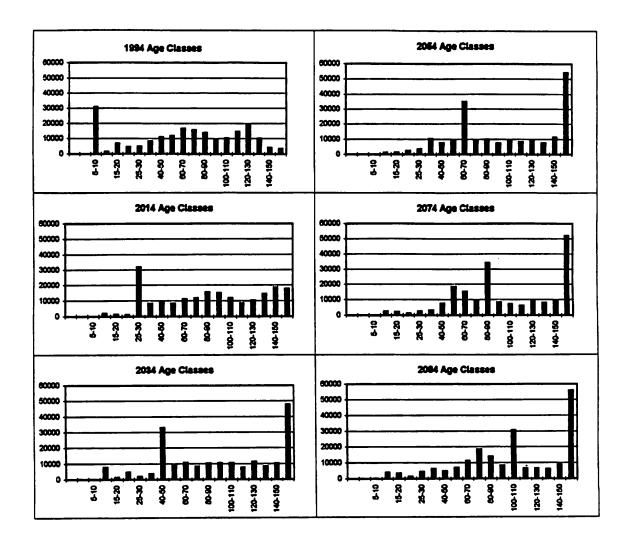


Figure 4.1a. Age-class structure evolution under the No-Harvest Strategy. X-axis units are age classes in years, y-axis units are hectares.

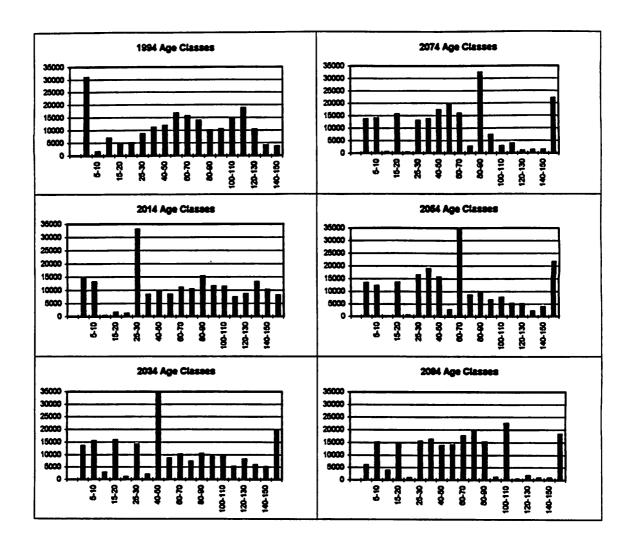


Figure 4.1b. Age-class structure evolution under the Basic Strategy. X-axis units are age classes in years, y-axis units are hectares.

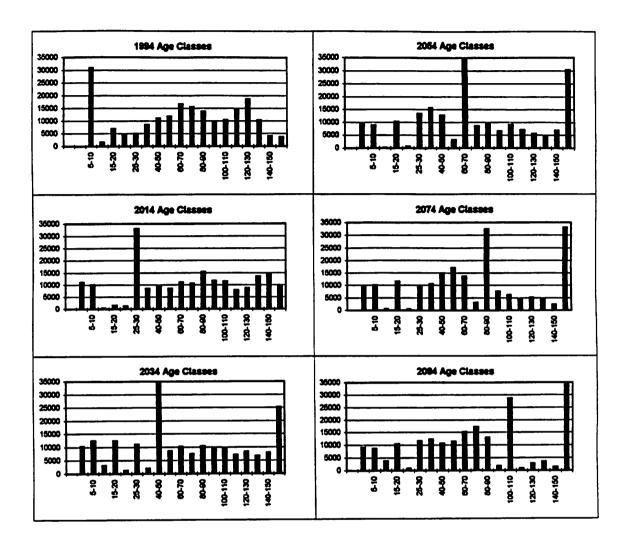


Figure 4.1c. Age-class structure evolution under the Lower Strategy. X-axis units are age classes in years, y-axis units are hectares.

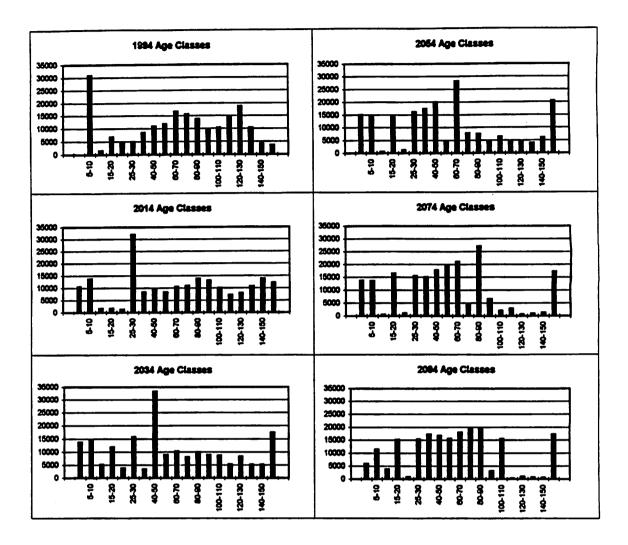


Figure 4.1d. Age-class structure evolution under the Spatial Strategy. X-axis units are age classes in years, y-axis units are hectares.



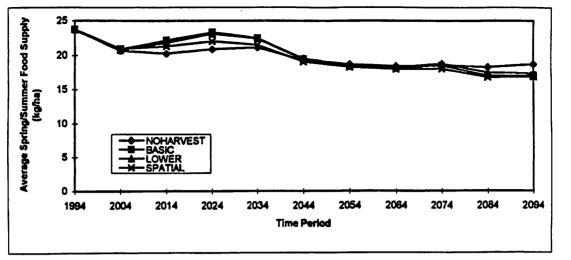


Figure 4.2 HAU-average SS food values of the four scenarios.

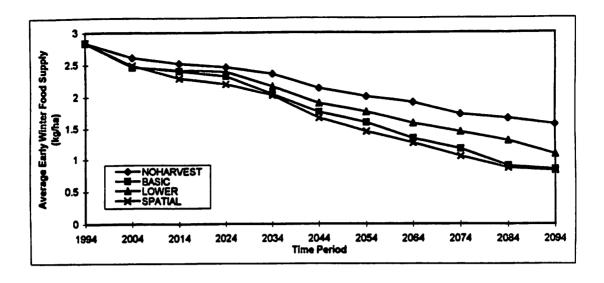


Figure 4.3 HAU-average EW food values of the four scenarios.

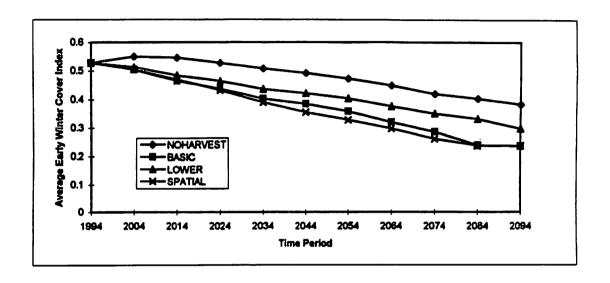


Figure 4.4 HAU-average EW cover indices of the four scenarios.

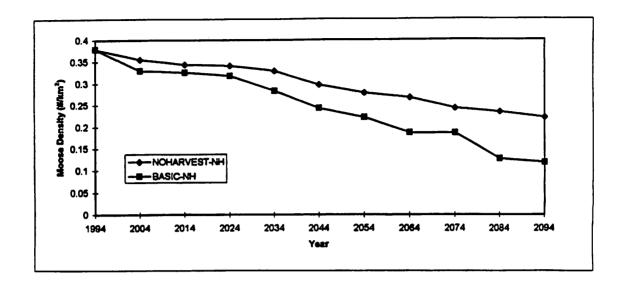


Figure 4.5. HAU-average simulated moose densities in April under two scenarios without hunting: (a) No-Harvest Strategy; and (b) Basic Strategy.

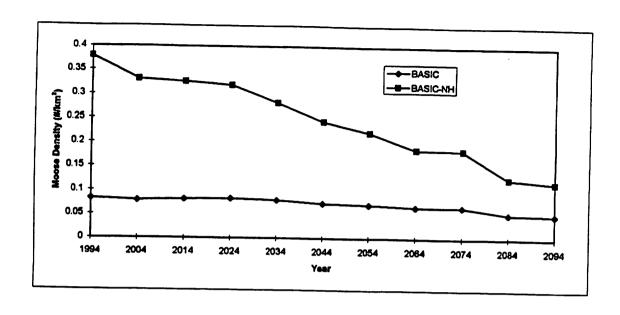


Figure 4.6. HAU-average simulated moose densities in April under the Basic Strategy with and without hunting.

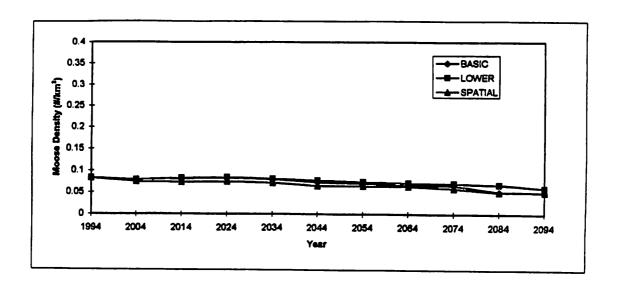


Figure 4.7. HAU-average simulated moose densities in April under three scenarios with hunting: (a) Basic Strategy; (b) Lower Strategy; and (c) Spatial Strategy.

7. APPENDICES

Appendix I - Timber yield curve sets used in forest simulation using HSG.

Appendix II - Silvicultural treatment priority table used in forest simulation using HSG.

Appendix III - Food-supply curve sets.

Appendix IV - Early-winter cover index curve sets.

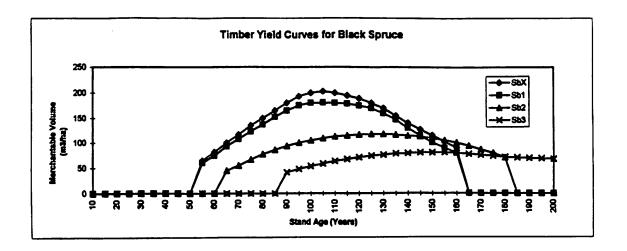
(Incorporate this into the Appendix)

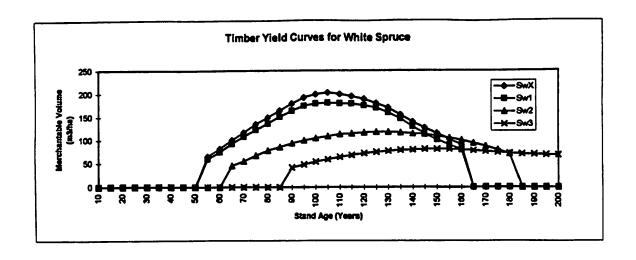
Regarding early winter cover, we use the same system as Higgelke did, with the following use of his curves for our types:

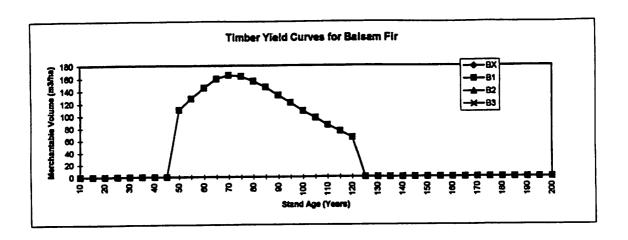
OUR TYPE	HIGGELKE CURVE
Pj	23
Sb, other Conif	23
Sb, other Hdwd	20
Bf	22
Po, other Hdwd	19
Po, other Conif	20

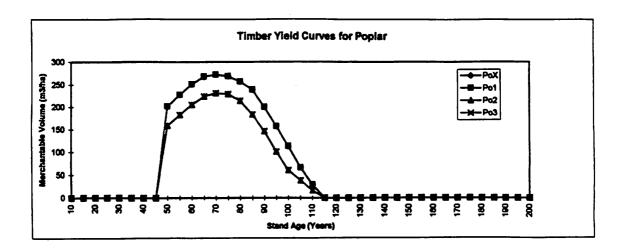
Appendix I

Timber yield curve sets used in forest simulation using HSG

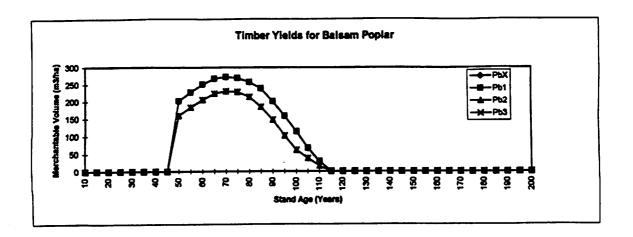


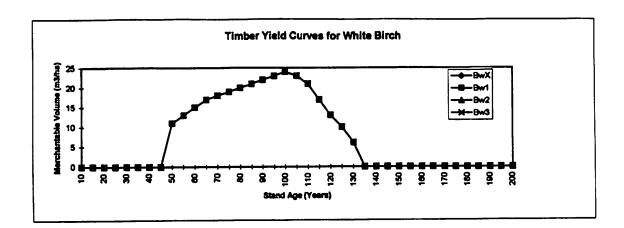






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Appendix II

Silvicultural treatment priority table used in forest simulation using HSG

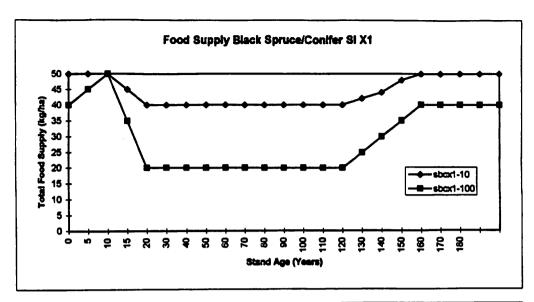
Treatment Priority List

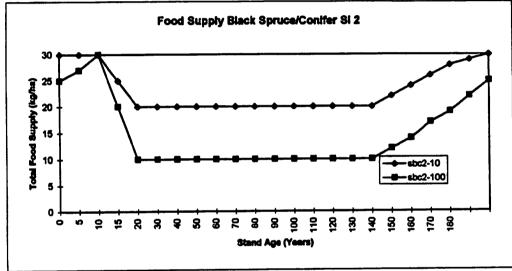
4

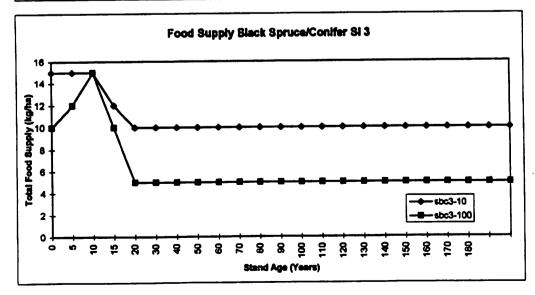
X	intensive
1	intensive
2	intensive
2	basic
3	basic
X	intensive
1	intensive
2	intensive
3	basic
X	basic
•	basic
	basic
3	basic
	1 2 2 3 X 1 2 3 X,1 2

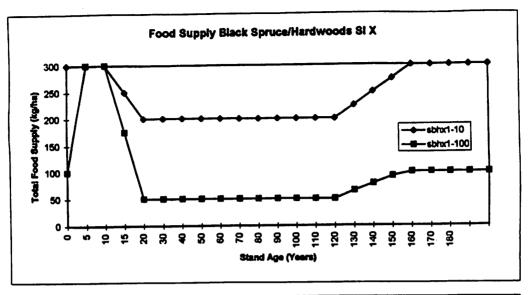
Appendix III

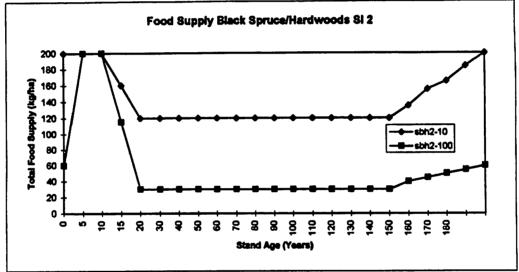
Food-supply curve sets

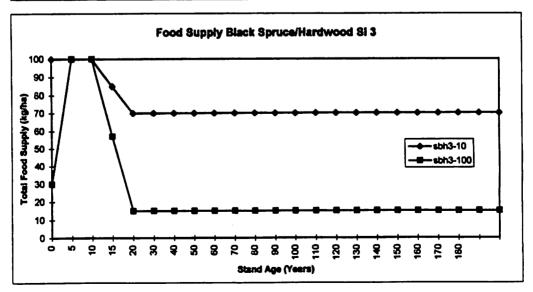


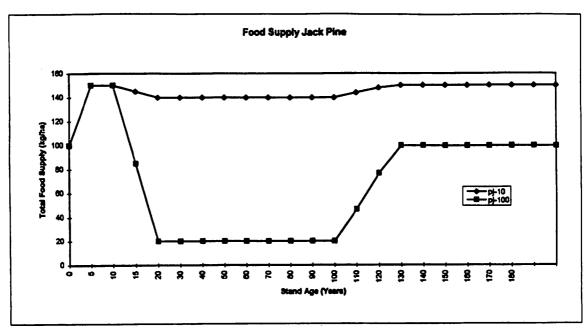


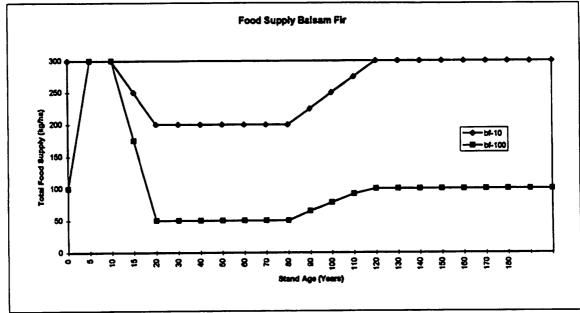


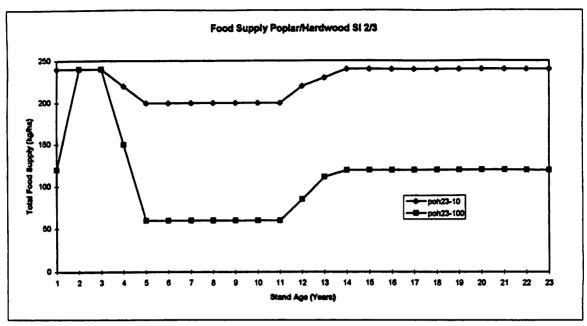


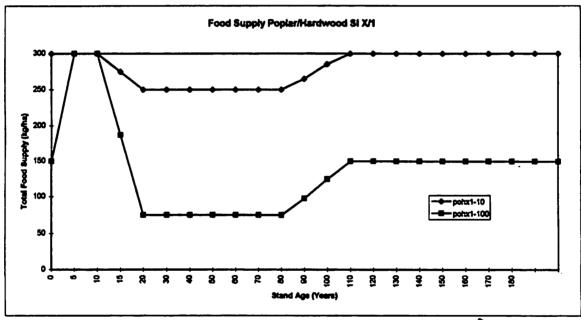


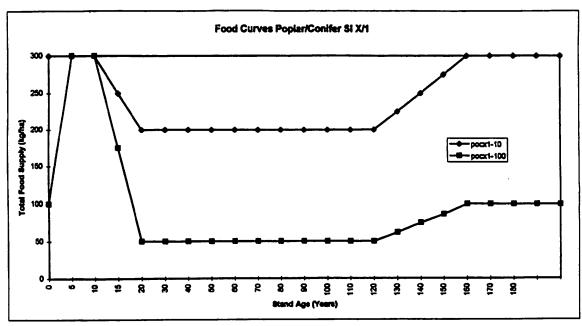


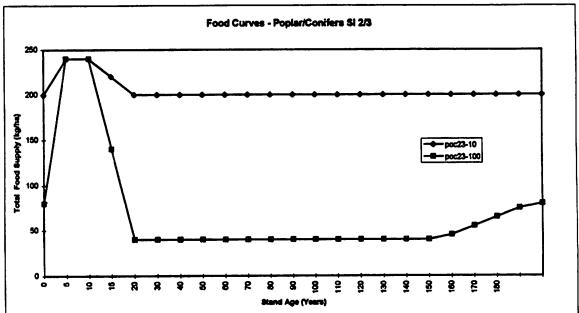












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Appendix IV

Early-winter cover index curve sets

