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A WHOLE-FOREST MANAGEMENT APPROACH INTEGRATING FOREST STRUCTURE, TIMBER HARVEST AND WILDLIFE DYNAMICS

by

Jitendra Kumar Das

A thesis submitted in conformity with the requirements
for the degree of Doctor of Philosophy
Graduate Department of Forestry
University of Toronto

0-612-41419-1

Thesis Title: **A WHOLE-FOREST MANAGEMENT APPROACH INTEGRATING FOREST STRUCTURE, TIMBER HARVEST AND WILDLIFE DYNAMICS**

Degree: **Doctor of Philosophy**
Year of Convocation: **1998**
Name: **Jitendra Kumar Das**
Department: **Forestry**
University: **University of Toronto**

ABSTRACT

A whole-forest management plan must consider timber as well as nontimber benefits of the forest. Difficulties in quantifying nontimber benefits have led to ignoring nontimber benefits in the formulation of forest management plans. Joint determination of two forest products (timber and wildlife) on a sustainable basis while maintaining certain characteristics of the forest desired by society is a useful approach.

A vector of forest variability, consisting of forest stand diversity index and compactness index, has been defined. Forest stand diversity depends on the unevenness of the forest. The unevenness of a forest is characterized as a continuum from an even-aged forest with only one patch to a perfectly uneven-aged forest with infinite number of patches. A method elaborated to quantify the point at which a forest may fall on this continuum leads to construction of a forest stand diversity index. A measure of the shape and fragmentation of a forest through compactness index has also been analyzed. Forest stand diversity and compactness both affect the potential of a forest to support wildlife. Analytical relationship between compactness index and the closeness of the wildlife population to its potential helps perform trade-off analysis. Quantification of forest structure through forest maturity index (which is a measure of timber yielding capacity) and forest stand diversity index is shown to be a useful tool for decisions in forestry.

Interactions among timber harvest, prey and predator have been analyzed using a simulation model technique. The basic premise of the model is that a timber harvest that alters the forest structure will also affect wildlife habitat. A combination of modified logistic equations and difference equations has been used to simulate deterministic and stochastic moose (*Alces alces*) populations.

Forest management scenarios depicting a timber harvest that achieves a certain wildlife population density, and a desired forest maturity have been generated. More scenarios can be developed easily. Thus, long run moose population density for different long-term timber harvests has been obtained. This is the timber-moose product transformation curve and can be used for management decisions. The forest manager can thus select the best scenario that fits her/his selection criteria.

Acknowledgement

I express my gratitude to my supervisor Dr. J. C. Nautiyal for his consistent support and guidance throughout this work. I especially thank him for his exceptional patience and constant encouragement. His unsurpassed analytical wisdom and knowledge of forestry provided me the impetus to complete this work. I truly appreciate that he has given me the foundation and the opportunity to broaden my knowledge and contribute to the science of forest management. He is an excellent role model for dedication to research.

I also extend special thanks to my thesis supervisory committee members, Professors R. B. Bryan, G. F. D. Duff, D. Krass, J. R. Malcolm, and S. M. Smith, for their valuable comments and suggestions on my work. I appreciate the careful review, questions and comments by Professors D. C. F. Fayle and D. L. Martell, which were of immense help. I am also thankful to Dr. S. Kant for providing very useful comments on my work.

I am thankful and indebted to Dr. G. D. Puttock for initiating and showing the way in the beginning, in this research area. I gratefully acknowledge the help and assistance provided by Mr. C. M. Corbett, Mr. J. Mihell, Mr. G. E. Martelle of the Algonquin Forestry Authority and Dr. M. L. Wilton of the Ontario Ministry of Natural Resources during my field visit to the Algonquin Park.

I cannot adequately express my deep appreciation to my parents and my wife for their unwavering support to allow me to complete this work. My very special appreciation is due my daughter, Ritu, and my son, Akshay, who willingly and patiently accepted my preoccupation with this work.

Financial support provided from research grants of Dr. Puttock and Dr. Nautiyal is gratefully acknowledged.

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CHAPTER 1

Introduction

The issues

Forests provide a multitude of products. Indeed, it is difficult to imagine a resource that provides more benefits for humans than do forests (Kittredge 1948). From the forest management perspective, forest products can be classified as timber and nontimber. Nontimber products can be fruits, flowers, resins, animals, water and many other tangible products. Also, there are many intangible nontimber products such as the amenities flowing from preservation of natural forest environments, wildlife habitat and opportunities for outdoor recreation.

Consideration of nontimber products is crucial for comprehensive forest management planning. For example, Rezende (1982) discussed and analyzed in detail the effect consideration of nontimber products can have on the rotation age of the forest. Godoy (1992), and Godoy and Lubowski (1992) contend that the value of nontimber products is a conservative proxy for the opportunity cost of the forest, or the value of the forest before it is put to new uses. However, from a revenue perspective, timber output of a forest is considered more important in comparison to nontimber outputs (Dove 1983, Hecht et al. 1988) because most nontimber products, especially the intangibles, are difficult to value. In a forest management plan that focuses on monetary returns, nontimber benefits are either ignored or considered with *ad hoc* assumptions about their contribution to forest value. As a result, much of the forestry of the past, and some of today's, has failed to achieve the objective of sustaining various social and environmental values. Nevertheless, in contrast to the popular notion in some quarters that forestry means exploitative logging, forestry is founded on the concept of sustainability (e.g., see Redclift 1987, Gale and Cordray 1991). However, as Repetto and Gillis (1988) contend, many countries with rich forest resources have adopted policies that encourage the conversion of forest land to agricultural and other uses. This stimulates rapid depletion of forest (timber) resources. Repetto and Gillis (1988) mention under-emphasis on foregone nontimber benefits of the forests as among the reasons that lead to rapid conversion of forest lands and ultimately environmental degradation. In essence, difficulties in quantifying nontimber benefits of the forest and near total absence of direct revenue have contributed to ignoring multiple values of the forests. No wonder that sustainable forestry has been difficult to achieve without appropriately considering nontimber benefits of the forest.

Adding further to this difficulty are the sustainable development definitions for a sub-sector such as forestry. These attempt to "maintain" the resource base as an end in itself. They do not consider sustainable development as a means to the ultimate goal of improving, on a sustainable basis, the quality of life of humankind. For a better understanding of sustainable development, the long-term benefits of forests must be expressed appropriately. It is understood that forests provide relief from environmental stress caused by economic development that requires using energy and raw materials. This, in turn, creates industrial waste that the environment must absorb. One of the major wastes polluting the atmosphere is carbon. Forests are natural carbon sinks as they withdraw carbon from the atmosphere and release oxygen (Salisbury and Ross 1992). The forest is also home to many plants and wildlife. A variety of plant species in a forest provides suitable conditions for most of the wildlife species to coexist. In addition, the ecological and environmental benefits of forests are enormous, and are better achieved by a diverse forest than a monoculture (Kimmins 1992). Further, a disturbance in a forest, such as timber harvesting or forest fire, leads to a change in the distribution of trees as well as the understorey (Carleton and MacLellan 1992). Management of trees can thus be seen to affect distribution and population of other flora and much of the fauna. This further means that any sustainable forest management must aim to maintain a certain kind of forest structure while deriving timber and nontimber products from the forest.

The practice and the challenge

Forest managers desire a harmonious and coordinated management of various resources, but face operational difficulties (Behan 1990). A desirable approach is to have a forest management strategy responsive to the increasingly diverse set of demands by society, and at the same time be environmentally, economically and silviculturally sound (Mather 1990, Kimmins 1992). The favored approach (Behan 1990) was multiple use by adjacency: in a given forest, timber is harvested at one place, recreational services provided somewhere else, and multiple-use is claimed overall. Reidel (1975) stated that this approach cannot be a functional concept. He further maintained that this is a flawed concept, which collapses, when intangibles are assigned values. Gregory (1972) and Nautiyal (1988) have also discussed the theory of using the same area for two or more purposes, and they elaborate on what to do if joint production function and prices of the products are known. Further, these approaches are considered in static contexts while production from forests is dynamic—it changes with time, as trees become older and the age structure of the forest changes. The decision process is further complicated by various circumstances that prevent normal market operations from determining the value of nontimber resources, such as wildlife habitats, through price-quantity relationships (McCollum and Bergstrom 1992). These circumstances are referred to as market failures and, in a market economy if not adjusted for, will result in an inefficient allocation of resources (Boadway and Bruce 1984).

Heilman (1990) and Kimmins (1992) advocated an integrated approach to forest-level management that would provide for multiple outputs and benefits to society while maintaining the ecological integrity and productive capacity of the forest. Also, public opinion for truly integrated forest management is reflected in the many ways the public is involved in forest management planning efforts. But the growing demand, and the public feelings for forests to provide recreational opportunity, clean environment and wildlife, as well as wood fiber, pose significant challenges.

Ideally, if specific relationships among all known products of the forest were available then a forest manager would be in a good situation to choose the best combination of products to harvest. This, however, is not quite achievable at the current level of understanding in which the knowledge of quantifiable relationships among various forest products is quite limited. Frequently, for want of such relationships, *ad hoc* assumptions are made about the contribution of a forest product, mostly nontimber, in an optimization model (e.g., see Davis and Johnson 1987). Therefore, attempts to develop quantifiable relationships, static or dynamic, among various outputs of the forest are essential for providing a framework to compare different combinations of forest outputs amongst which choice must be made (Gregory 1972, Nautiyal 1988). This thesis addresses such quantification.

The approach

Forest management practices that would produce the maximum timber harvest may not be the same as those that would provide the best wildlife populations or other environmental values of the forest. These management goals are often in conflict with each other (Thompson et al. 1994). Integrated forest management that provides for sustained yield of forest products, is now widely accepted as a requirement to maintain the ecological integrity and productive capacity of the forest while providing multiple outputs and benefits to society (Kimmins 1992). Two aspects of decision making must be known to develop an integrated approach. First and foremost is the dependency relationship among the multiple products of the forest (e.g., see Gregory 1972), that is, the interaction among various outputs of the forest must be known. Such an idea provides a significant challenge to forest managers because it requires joint production of timber and nontimber values, and an understanding of relative trade-off in the production process. Second, the price-quantity relationship of forest products must also be known. However, to keep the focus on interactions among the timber and nontimber outputs of the forest, the issue of price-quantity relationships will not be touched in this thesis.

With the ability to quantitatively consider various forest products, including forest structure—meaning age class distribution—a forest management plan will be able to better address the social and ecological role of forests. Managing for a wildlife species largely dependent on age class structure of the forest, and integrating it with timber management and a desirable forest structure would be a good starting point. This will indirectly help in managing for many other species as well as other intangible benefits of the forests, so that a clean environment and recreational opportunities may become available. To be able to keep track of and maintain a desirable forest that is environmentally and silviculturally sound, a method to quantify forest structure needs to be developed. A given forest structure determines the quantity of timber and nontimber products from it and is, in turn, determined by the products removed from it. Knowledge of the forest structure and interrelationships between products must form the basis of a sustainable forest management plan.

Objectives and organization of thesis

The main objective of this research is to develop a methodology that can measure the state of the forest and wildlife population resulting at various points in time due to any given pattern of timber harvest. This is achieved by developing indices for forest stand diversity, forest compactness and forest maturity, and relating forest age class structure resulting from timber harvest to quality of habitat for wildlife.

Given that a certain wildlife population and a forest structure are to be maintained with timber harvest, the research objectives of the study and organization of the thesis are as follows:

i. To develop a forest variability index, a vector, that quantifies forest stand diversity—a measure of the tree species and age class variability—and compactness of a forest. A step-by-step development of this vector is discussed in Chapter 2;

ii. To develop a model showing the impact of compactness index value on the potential of a forest to support a wildlife population. Considering shape and fragmentation in a forest, a measure of compactness index is developed in Chapter 3;

iii. To quantify forest structure considering forest maturity—a measure of timber yielding capacity and average age maturity—and forest stand diversity. Chapter 4 develops a method to quantify the state of a forest by defining a forest maturity index. Together with the forest stand diversity index developed in Chapter 2 a quantitative representation of the forest is obtained;

iv. To develop a dynamic simulation model relating a wildlife population density with age class structure of the forest. Chapter 5 elaborates upon an empirical static model of wildlife habitat by developing a dynamic simulation model that provides alternative scenarios of timber harvest and wildlife population. This model considers the interactions of moose, a large ungulate, found in southern Great Lakes-St. Lawrence Forest Region, and its predator in determining population density; and

v. To develop scenarios meeting the forest management objectives. A summary of forest management scenarios that meet the forest management objectives is discussed in Chapter 6. A scenario from among many scenarios can be selected based on criteria considered significant. Finally, limitations, outline of the applications of the proposed forest management methodology and suggested future research are presented.

CHAPTER 2

Forest variability index: A vector quantifying forest stand diversity and forest compactness

Introduction

Forest variability index may be defined as a vector consisting of two components: (i) forest stand diversity composed of tree species and age classes; and (ii) compactness of fragments in a forest. Forest stand diversity can be defined by the tree species and the age class variation among the stands of a forest. A stand is defined as a community of trees that has sufficient uniformity as regards composition, constitution, or age, and is distinguishable from adjacent communities (Ford-Robertson 1971). Compactness index is a measure of the shape of the forest as well as of the fragmentation within. Thus, the forest variability index has the ability to capture the variety of tree species and age classes in a forest, and its geographical configuration.

Existence of many tree species in a forest provides a variety of food and water sources for the wildlife species to survive and reproduce. Porter (1986) classified vegetation, the primary resource for wildlife, into that providing energy (food) and that providing for the conservation of energy (cover). Plant material is either a direct source of food as in foliage or seeds, or is host to other organisms that provide food for wildlife populations. Variety in plants provides different kinds of structural cover essential for survival of a wildlife population in a forest. The size of a stand, and its location relative to other stands, can determine whether wildlife habitat needs are met within the home range. Unsuitable habitat will restrain reproduction and long term survival, keeping the population low. Without variations in plant species and age classes many wildlife species, if not all, would find it hard to survive. For example, moose (*Alces alces*) require a variety of plant types and ages with both mature conifer stands for cover and open areas for food (Peek et al. 1976, Leptich and Gilbert 1989). Further, as a response to food availability, escape cover, predation, and environmental conditions, a wildlife species would alter its habitat use pattern (e.g., see Peek et al. 1976). Thus, a diverse forest, with many different stands, is more able to meet the varying needs of many wildlife species than a uniform monoculture forest.

Appropriate timber harvesting, a major forest activity and disturbance, can be applied to improve diversity relative to some set of wildlife species in a forest. For example, Carleton and MacLellan (1992) concluded that any disturbance in a boreal forest such as timber harvesting or forest fire, would lead to a change in the distribution of trees as well as the understorey. A forest with a specific plant and age class diversity will support a certain minimum wildlife population, and that can be taken as a proxy for the state of the forest (Hunter 1990). Further, the amount of habitat and its dispersion in a forest (i.e., configuration of patches) determines the population (Fahrig 1992). Gurd (1997) discusses the effect of patch size—created by timber harvest or forest fire—on wildlife population. He contends further that the habitat quality is affected by the spatial configuration of disturbance patches in a forest. For example, timber harvesting may create a large or a small patch, or fragment a forest. A patch is a spatially contiguous area of relatively homogeneous attributes. Patch boundaries are identified by discontinuities in surrounding environmental characteristics. Thus, a patch can be considered homogeneous in species and age class. Management of trees is, thus, seen to affect distribution and population of the entire flora and fauna in a forest. It is this fact that makes the development of a measure for "forest stand diversity", incorporating species and age class variation, useful.

Nevertheless, forest variability depends not only on forest stand diversity but also on the geographical distribution of forest stands. The spatial configuration of a forest, size and proximity of forest areas in a locality, vitally affect the movement and genetic variation in wildlife species. Many studies on wildlife populations in large geographical regions, in islands or patches (e.g., see Shapcott 1994), indicate the importance of genetic variation within species for their survival and expansion. If wildlife has an opportunity to move considerable distances in various directions then, as indicated by Ibrahim et al. (1996), population expansion will be relatively easy. It is therefore, useful to know whether a forest, for example, exists in one large compact block, or has the shape of a long but narrow strip, or is disjointed in the form of large or small fragments separated from each other. Recognizing this fact, Otto (1996) maintained that the shape of a forest or landscape plays an important role in forest and wildlife management. This concept provides a lead for the evolution of a "forest compactness index" and its development should be of practical use to forest managers. This chapter attempts to develop a relatively comprehensive measure of forest variability in the form of a vector, the two components of which are forest stand diversity and forest compactness.

In the following section some of the diversity indices discussed in the literature are reviewed to provide an understanding of the utility of the proposed forest variability index. Next, a methodology for developing this vector is discussed, followed by an example of its use. The utility of the forest variability index in making forest management decisions is also shown.

Landscape pattern and indices

In a forest, spatial heterogeneity is a universal feature of communities. It is a common observation that the spatial distribution of a similar age class or species of plants in a forest is seldom random; they often exist as clusters or patches (Zahl 1974). A forest stand can be viewed as an aggregation of patches of trees without any loss of generality. Describing such patches or non-random distributions of trees, in accurate terms is difficult. Recognizing the occurrence of non-randomly distributed plant populations, models expressing patterns of patches and the relationships of causal factors of such patterns have been proposed (Payandeh 1970). Non-random patterns reflect many environmental patterns as well as demographic processes of plants within the community. The term "pattern" can mean spatial arrangement of the plants on the ground or the arrangement of the members of one species relative to those of other species (Pielou 1965). Schaffer and Leigh (1976) asserted that lack of concise and interpretable description of patterns hampers mathematical modeling of spatial patterns. To determine the spatial patterns, fineness of scale (resolution) used to observe the parameter of interest is important (Levin 1992, Mladenoff et al. 1993). For a better understanding of ecosystems across scales, Risser (1995) emphasized the need for identifying critical structuring processes, and associated spatial and temporal scales. According to Pielou (1981), to learn more about the complexities of spatial pattern, intense empirical investigation is required.

Turner (1989) and Wiens et al. (1993) hypothesized a theoretical relationship between spatial patterns of forest landscape and ecological processes. However, Otto (1996) presented empirical evidence that such a relationship was not necessarily demonstrated and provided a possible explanation for the ambiguous results. He used fractal dimension (Lovejoy 1982) as the criterion to distinguish two landscapes across five scales. It is, however, quite possible that two landscapes have different values of fractal dimension but both meet most of the wildlife habitat needs within the species' home range. In such a case, landscape spatial pattern (as measured by fractal dimension alone) may not be able to differentiate between the two areas in terms of wildlife population. This perhaps was the case for Otto (1996).

Landscape patterns have intensity and grain as two basic components (Pielou 1977). Intensity, in general, is defined as the extent to which density of species changes from place to place. Several indices of intensity have been defined (Pielou 1977); Goodall and West (1979) provide a very useful comparison. Grain can be defined as the scale of patch size within a community. Grain may reflect the essential biological and environmental factors of spatial pattern. In a forestry context, where trees are evenly distributed (randomly or in clusters), intensity (Pielou 1977) may not be crucial for pattern analysis. Grain, on the other hand, would be a deciding factor in identifying a patch. Various analytical methods to measure patch size have been proposed (e.g., see Fowler and Antonovics 1981, Carpenter and Chaney 1983, Cullinan and Thomas 1992). These methods are very informative, but determining patch size is not a focus of this chapter.

To develop an understanding of patch distribution in a forest, a closer look at various species diversity indices is useful to help in conceptualizing the “forest stand diversity index”. An inspection of species diversity indices reveals that no particular formula has a pre-eminent advantage (Hill 1973). Many of the indices proposed apply only to counts of individuals and not to continuous measures. MacArthur and Wilson (1967) proposed that the number of species encountered is proportional to a fractional exponent of the area sampled. Thus, an index characterizing some feature of a hypothetically infinite community should allow for an infinitely large number of species. This indicates that such an index is scale dependent. At different scales of measurement, Whittaker (1977) distinguished four levels of inventory diversity. He defined diversity of a microhabitat or a homogeneous habitat as point diversity. This was also referred to as the "within-habitat" diversity or alpha (α) diversity – a term very commonly used. The diversity at the landscape level was defined as the gamma (γ) diversity which is the overall diversity of a group of areas of alpha diversity. The term beta (β) diversity was also coined by Whittaker (1977) as a 'differentiation diversity'. Beta diversity is essentially a measure of the degree of change in diversity. For example, β diversity will be high if few species are common in different communities. Beta diversity is a widely used diversity measure (Magurran 1988) particularly for forest landscapes. The fourth, the epsilon (ε) diversity, was defined as the total diversity of a group of areas of gamma diversity.

Different indices measure distinct aspects of the abundance of species. For example, the abundance of the more plentiful species in a sample is well represented by Simpson's index. Simpson's index is defined as the sum of squares of the proportional abundance (Hill 1973). Whittaker (1965) has referred to Simpson's index as a measure of "dominance concentration". Lloyd and Ghelardi (1964) have defined "evenness," which is a comparison of the diversity as measured by the total number of species against the diversity as measured by some other statistic. Evenness is then re-defined as the ratio of two such evaluations. A standard definition of evenness as stated by Pielou (1969) is a ratio of Shannon's current and maximum entropy.

Simpson's index, Shannon's entropy and "evenness" indices are evaluations of the number of species present in the sample. A reciprocal of Simpson's index, for example, is a measure of how many species are present. These indices differ in terms of their bias to include or exclude the relatively rarer species in the sample. Shannon's entropy being logarithmic is difficult to visualize and is not a good measure of evenness according to Hill (1973). The distribution of patches in a forest, however, is not captured by any of the above indices. Nonetheless, the principles used to define the above indices are useful in devising a simple and useful forest stand diversity index. A forest stand diversity index will be a measure of the patch distribution in a forest.

A measure of forest stand diversity

A forest stand diversity index, as discussed earlier, should logically be visualized as being higher if the number of age classes increases. Also, more tree species in the forest should result in higher forest stand diversity index. One might think that if trees in a forest had random distribution then no part of the forest would have homogeneity—species or age class wise—and forest stand diversity in such cases might be maximum. Such a forest might be an ideal uneven-aged forest.

An uneven-aged forest or stand is defined as composed of trees that markedly differ in age and an even-aged forest or stand is defined as composed of trees having no, or relatively small, differences in age (Ford-Robertson 1971). That is to say that in an "ideal" uneven-aged forest there are no patches, whatsoever, and all trees are randomly placed. This, however, does not happen in nature and it would be useful to accept that there may be varying degrees of unevenness. In even-aged forest management, even-aged stands that range from regenerating stands to stands more than 100 years old have been considered as a management unit (Davis and Johnson 1987), the logic being that the silvicultural operation is always at the stand level—which remains even-aged over time. In order to define a forest stand diversity index; the definition of an uneven-aged forest can be extended: an uneven-aged forest can be defined as consisting of patches of trees; the measure of the unevenness of the forest will be a continuum from an even-aged forest with only one patch to a perfectly uneven-aged forest with infinite number of patches. Thus, the classical even-aged forest or stand consists of one patch only and its measure of unevenness is set at zero. When the number of patches in a forest is equal to the number of age classes in the forest, then this forest can be considered as a unit for even-aged forest management. Thus, a forest with more than one patch can be classified as an uneven-aged forest with quantifiable measure of unevenness. This essentially means that with an increase in number of patches, the forest will become more uneven-aged even if the number of species or age classes remain unchanged. Thus, for a given forest, as the number of patches (and so the forest stand diversity) increases, the average patch size will decrease. This would also mean that as the average patch size becomes very small, forest stand diversity will tend to reach a high value. It can also be argued that for a given forest area, as the average patch size decreases the unevenness of trees in the forest increases, ultimately making it uneven-aged. Thus, the extent of unevenness of different-aged trees in a forest can be a direct measure of forest stand diversity. Tree species diversity has so far been ignored in this discussion of forest stand diversity as various species diversity indices already in existence can be appropriately used.

Let us now define forest stand diversity, λ, that is dependent on the forest structure which, in turn, is defined by the species and the age classes. By definition, a patch is homogeneous in species or species mixture and age class. That is, any variation in species, species mixture or age class would mean it becomes a different patch. Also, similar patches are disjointed from each other, or they will become one patch. Therefore, λ can be said to be a function of the number of patches in a forest. The range of λ, without any loss of generality, can be limited from 0 to λ_{max}, where λ_{max} is some maximum value of forest stand diversity. Therefore, as the number of patches, n, in the forest increases, forest stand diversity will increase. This can be mathematically expressed as:

$$\frac{d\lambda}{dn} \geq 0 \qquad [2.1]$$

It is also reasonable to assume that there will be diminishing contribution to forest stand diversity by an additional patch. Thus, the tenth patch, for example, should increase forest stand diversity more than the eleventh. This means that as n increases, growth in λ should be at a decreasing rate. This can be expressed as:

$$\frac{d^2\lambda}{dn^2} < 0 \qquad [2.2]$$

It can be assumed that $d\lambda/dn$, the rate of change in forest stand diversity with n, will have a maximum value C when $\lambda = 0$, and zero when λ equals λ_{max}. The reduction in $d\lambda/dn$ as λ increases from zero to λ_{max} can be approximated as a convex, concave, or straight line function as shown in Figure 2.1. Approximation of $d\lambda/dn$ as a convex or a concave function of λ results in more complex solutions for λ than the assumption of a straight line function[1]. For the sake of simplicity the reduction in $d\lambda/dn$ is assumed to be a straight-line function of λ. In view of condition [2.2], $d\lambda/dn$ can be written in the following form:

$$\frac{d\lambda}{dn} = C - K\lambda \qquad [2.3]$$

where K is a positive constant. Substituting equation [2.1] in equation [2.3] results in: $C-K\lambda \geq 0$ or $C/K \geq \lambda$. Also, choosing C/K to equal λ_{max} at the margin gives $K = C/\lambda_{max}$, the negative slope of the straight line in Figure 2.1. Substituting this in equation [2.3] results in:

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[1] See footnote 2

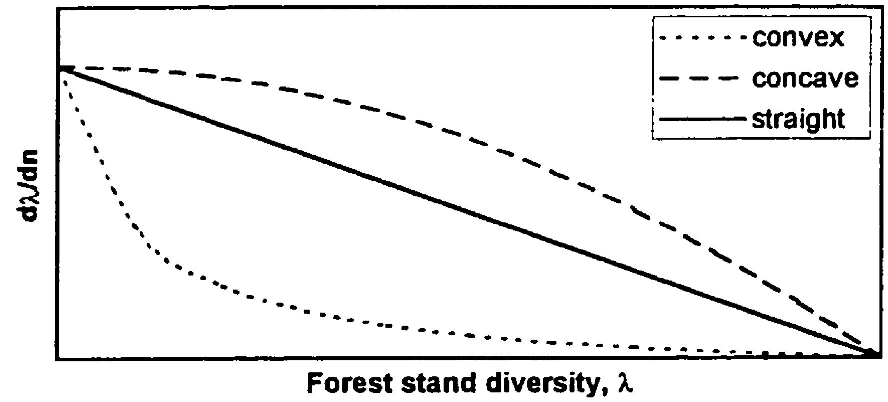

Figure 2.1. Rate of change in forest stand diversity with number of patches

$$\frac{d\lambda}{dn} = K(\lambda_{max} - \lambda) \qquad [2.4]$$

If forest stand diversity at n=1 equals λ_0, then equation [2.4] can be solved to yield:

$$\lambda = \lambda_{max} (1 - e^{-K(n-1)}) + \lambda_0 e^{-K(n-1)} \qquad [2.5]$$

It is reasonable to set $\lambda_0 = 0$. Equation [2.5] then reduces to:

$$\lambda = \lambda_{max} (1 - e^{-K(n-1)}) \qquad [2.6]$$

For convenience a 'forest stand diversity index, v' expressed by (λ/λ_{max}) can also be written as:

$$v = (1 - e^{-K(n-1)}) \qquad [2.7]$$

The value of v has a range 0 to 1. A value of zero for v indicates that n = 1 or the forest is a single stand. Also, v = 1 indicates that n → ∞, or the forest is uneven-aged with a single or a very small number of trees forming a patch. Thus, v is also a measure of unevenness of the forest[2].

Typically, in a forest patches will have varying sizes. For the same total number of patches, varying patch sizes will affect forest stand diversity differently. Therefore, the weighted average of proportional patch sizes as the effective size of a patch in the forest can be considered. If a_i is denoted as the area of patch i and A as the total area of the forest, then p_i can be defined as the proportional area of the i^{th} patch. Total number of patches equals n. Thus,

$$\sum_{i=1}^{n} a_i = A \qquad [2.8]$$

$$p_i = a_i / A \text{ and } \sum_{i=1}^{n} p_i = 1 \qquad [2.9]$$

Similar to the development of weighted Simpson's index for species diversity proposed by Hill (1973), if the weight of the i^{th} patch is denoted by x_i, then, $\sum x_i = 1$. Therefore, the weighted proportional area will be $q = \dfrac{x_1.p_1 + x_2.p_2 + \ldots + x_n p_n}{x_1 + x_2 + \ldots x_n}$ [2.10]

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[2] The equation for $d\lambda/dn$ as a convex function in λ, can have many forms. Assuming a simple form, one such equation can be written as $\dfrac{d\lambda}{dn} = b/(\lambda + x_1) - y_1$, where b, x_1, and y_1 are constants. The constant x_1 and y_1 are dependent on b, C, and λ_{max}. Similarly, equation for $d\lambda/dn$ as a concave function in λ, can have many forms. One such concave function in λ can be written as $\dfrac{d\lambda}{dn} = \dfrac{C}{\lambda^2_{max}}(\lambda^2_{max} - \lambda^2)$. In terms of forest stand diversity index, v, one obtains, for the convex function, $(1 - v)^{-b.y_1^2} = e^{v.K_2(n-1)}$ [i]

where K_2 is a constant and dependent on b, C, and λ_{max}. For the concave function, v can be expressed as: $v = \dfrac{1 - e^{-2C(n-1)/\lambda_{max}}}{1 + e^{-2C(n-1)/\lambda_{max}}}$ [ii]

The weight given to the i^{th} patch signifies the proportional contribution of this patch to the index being developed. If the weight to the i^{th} patch equals its proportion to the total area, then $x_i=p_i$, and thus, the following is obtained:

$$q = \sum_i p_i^{\,2} \qquad [2.11]$$

If p_i's were defined as the ratio of the mass of the i^{th} species to the total mass of the sample then, q is the Simpson's index for species diversity (Ludwig and Reynolds 1988). In the context of the whole forest, q becomes Simpson's index for forest stand diversity.

If all p_i's are equal then $q = 1/n$. Also, $1/q$ may be considered as the weighted number of patches when all p_i's are not equal. Thus, denoting the weighted number of patches by n_w, produces $n_w = 1/q$. If a patch in a forest is significantly small in comparison to others, then its contribution to forest stand diversity is expected to be insignificant relative to other patches and *vice versa*. This aspect is not represented if total number of patches, n, is considered in equation [2.7]. However, this difficulty is removed by considering the weighted number of patches, n_w. Thus, equation [2.7] can be modified using n_w for n as follows:

$$\nu = (1 - e^{-K(n_w - 1)}) \qquad [2.12]$$

Also, $n_w < n$ for p_i's not equal to each other and $n_w = n$ for the case when all p_i's are equal. Thus, the maximum value of n_w will be n. Obviously, then, if all patch sizes are known, forest stand diversity index, ν, can be determined using equation [2.12].

A forest with a large number of patches could have very few age classes and tree species. This is possible if similar patches are repeated many times. In such cases a high forest stand diversity must be adjusted to reflect the low number of age classes and tree species. It is logical to think that a repeated patch of different area but of same species and age class will contribute less to forest stand diversity than a patch of the same size but of different age class or species. Thus, giving a reduced weight to a patch that is similar to an existing patch of the same species and age class may be considered. Similarly, patches of different species are expected to contribute more to forest stand diversity than patches of the same species. A scheme can be developed to give more weight to the second, the third and so on, species. For example, the weight given to the species with the lowest number of patches can be highest; species with the next higher number of patches can be a "step" lower and so on. However, such a scheme to weigh may appear arbitrary. Therefore, as an alternative, v in equation [2.12] can be redefined as v_p signifying stand diversity due to patches alone. Also, using equation [2.12] and replacing n_w with counts of number of age classes and species, v_a and v_s (age class and species variation respectively) can be determined. Values of v_a and v_s would depend on the value of K as indicated in equation [2.12]. Ratios v_a/v_p and v_s/v_p will be less than or equal to 1 and would reflect the extent of repetition of patches with the same age class or species. That is, the ratios will equal 1 if all patches were of different age class and species. Now, the forest stand diversity can be re-defined as $v = \{v_p, v_a/v_p, v_s/v_p\}$. However for the sake of clarity and to keep the focus on forest stand diversity *per se*, this aspect will be ignored temporarily and equation [2.12] as the expression for forest stand diversity will be considered.

Figure 2.2 depicts v as a function of n_w for K values in the range 0.05 - 1.0 using equation [2.12]. Higher values of K would mean that as n_w increases v would tend to attain a value of 1 faster than when K is lower. So, how is a value of K selected? To some extent selection may appear arbitrary. However, there is one approach that can reduce the arbitrariness in the selection of a K value. From equation [2.12] for a given

K, irrespective of the size of the forest study area, n_w alone will determine the ν value. But, if two forest areas of different sizes are to be compared, then there is a problem. A large forest area having the same n_w as in a small forest area will have larger patch sizes on an average and, therefore, should have a lower forest stand diversity. For example, consider a forest of 100 ha with n_w equal to 40, and another forest of 1000 ha with n_w also equal to 40. The second forest can be considered to have less diversity than the first forest purely because of size of the forest or scale. Equation [2.12] does not consider this fact as its application results in the same ν value for these two forests. This means that equation [2.12] must be modified to accommodate scale. Only two parameters, n_w and K can be focused on to accommodate scale. Modification in equation [2.12] by fixing n_w is one approach but it is not robust.[3]

If different values of K were used for the two forests discussed above, then different ν values will be obtained even if n_w was same. This indicates that K could be dependent on the size of the forest area. Therefore, it is appropriate to refer to K as a 'scaling constant', which is in accordance with Greg-Smith (1983) who reported that all

---

[3] The weighted n_w in equation [2.12] can be 'normalized' by scaling down the forest area to some standardized size. Let this area be 100 ha. If the total area of the forest is A ha, then the normalized weighted number of patches, n_n, will become:

$$n_n = n_w.(100/A) \qquad [iii]$$

K can be given some arbitrary value. Denoting ν_n as the modified forest stand diversity index using the normalized weighted number of patches n_n, equation [2.12] becomes:

$$\nu_n = (1 - e^{-K(n_n - 1)}) \qquad [iv]$$

There is a problem though. Consider a forest stand of say, 5 ha ($n = n_w = 1$). Normalized weighted number of patches n_n for this forest would work out to 20 using equation [iii]. Thus, a stand becomes equivalent to a forest with twenty patches. This cannot be acceptable. To restrict this from happening a condition on n_n can be imposed by restricting normalization only to cases of $A > 100$ ha. For cases of $A < 100$ ha, equation [2.13] with weighted n_w can be used. That is, scaling up is not permitted while scaling down is allowed. If two forest areas both less than 100 ha are to be compared, there will be ambiguity due to different forest sizes. One way to overcome this difficulty is to limit the estimation of ν_n only for cases of forest areas greater than 100 ha. There are too many compromises in this method and thus, it is not a robust method.

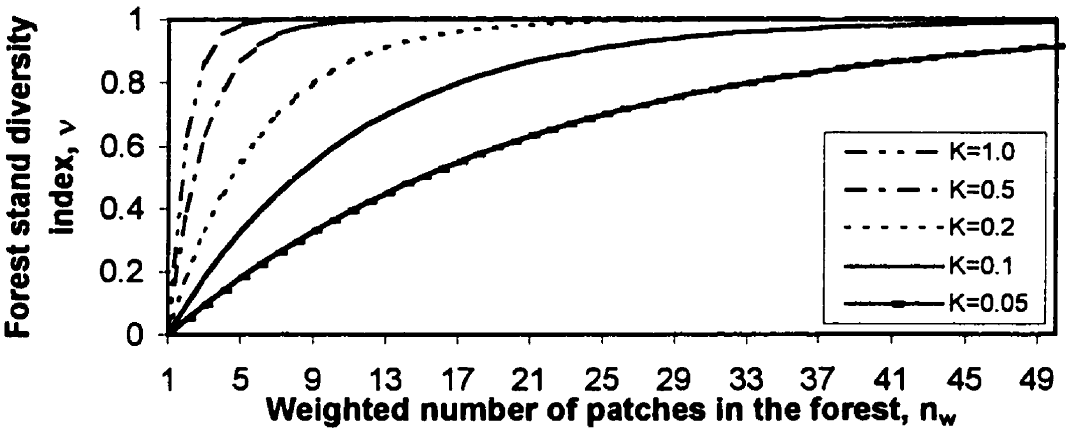


Figure 2.2. Forest stand diversity index for different values of K

methods for detecting non-randomness depend on the size and shape of the study area used.

Thus, it is acceptable to state that a larger forest area and a smaller forest area may have the same forest stand diversity index only if the larger forest area has a higher number of patches than the smaller forest. From Figure 2.2 it can be seen that for larger forest areas that are expected to have relatively higher n_w, K should be small to adjust for the scale of the forest. Alternatively, for smaller forest areas K should be relatively large. With this understanding, the arbitrariness in K can be restricted, and it can be defined as the inverse of the forest area in hectares (K = 1/A). Substituting this in equation [2.12] and rewriting, results in:

$$n_w = 1 - A \cdot \ln(1 - v) \qquad [2.13]$$

For a given v, equation [2.13] is a straight line on the n_w-A axes. The n_w-A plot for different v values is shown in Figure 2.3. Thus, if the total forest area and the weighted number of patches are known, the forest stand diversity index can be read off Figure

2.3. The measurement unit of forest areas under comparison must be of the same unit but not necessarily in hectares. It will, however, be useful to be cognizant that ν of a forest before and after timber harvest can be considered more robust for comparison than ν of different forests due to topographical and geographical differences among different forests. Forest stand diversity index, ν, is a measure of spatial variation of patches in a forest; values of ν that suit a wildlife or a group of wildlife species can be determined. For example, a large clearcut that reduces the number of patches may lead to a decrease in habitat availability over time for early successional species and an increase in habitat for late successional species. Also, in this case, the occurrence of forest interior species may increase and shrub species may decrease over time (Gurd 1997). Forest diversity index, ν, is able to capture variation in patch sizes in a forest. In the same way, one must also consider tree species diversity, providing number of species present in a forest, in a management plan.

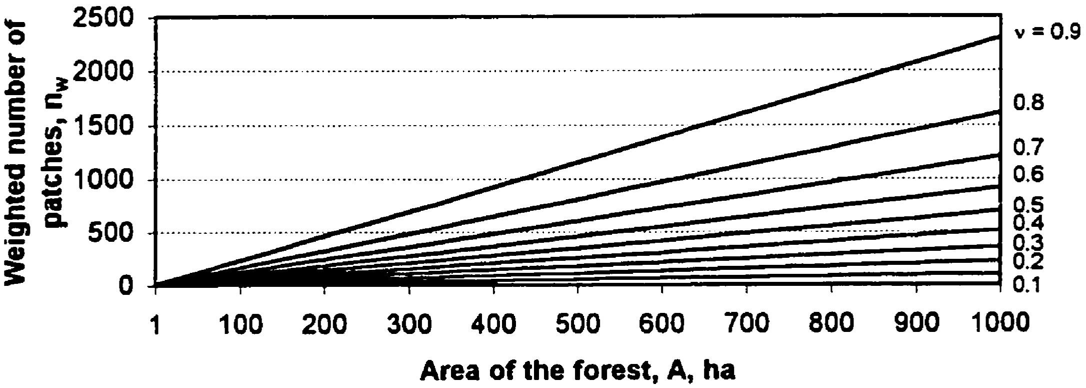


Figure 2.3. Weighted number of patches with ν as a parameter

A measure of forest compactness

Forests come in all shapes and sizes but the forest stand diversity index provides no clue about spatial form. A forest in the shape of a long narrow strip, for example, is less suitable to wildlife species, assuming that width of this forest constricts the home range, due to relatively increased edges and reduced core area, than a large circular forest. In such forests the availability of adequate cover, food, or reproduction opportunities may be restricted. Similarly a fragmented forest is less suitable from a wildlife perspective as fragmentation results in habitat loss and is a threat to the stability of landscape structure (e.g., biodiversity) (Saunders et al. 1991). Fragmentation can be described as a function of the mosaic of the patches. Thus, the number of smaller patches, isolation of patches, degree of spatial dispersion, amount of relative edge and core area, and spatial association of patches together constitute fragmentation (Li et. al. 1993). A measure of the spatial structure of the forest would be able to bring out the spatial suitability of the landscape to a wildlife or a group of wildlife species. Baskent (1997) discusses and summarizes various measurements as indicators of fragmentation. These measures represent different aspects of spatial landscape structure. A core area measure, for example, considers size and shape of a forest or forest fragment, and the nature of immediately surrounding conditions. Thus, it presupposes the core area suitability and availability for a specific wildlife species. A measure of the shape of the forest, instead, will be more general because the core area available to wildlife or a group of wildlife species will be specific for a given shape and can be estimated. However, shapes that, for example, inter-twine on themselves have a high shape distortion and small relative core area, though they may be quite compact and thus relatively more suitable to wildlife species. This shows that when wildlife species is a consideration, a measure of closeness of patches in a forest—that is compactness—

may be useful. Compactness in this context means closeness of a forest to a circle. Therefore, a compactness index, as will be defined later, along with the forest stand diversity index is necessary in quantifying the spatial structure of the forest.

Lovejoy (1982), and Cullinan and Thomas (1992) introduced fractal dimension, D, as a measure to study and compare shapes across different scales. O'Neill et al. (1988) used fractal dimension in studies to quantify patterns. Fractals allow direct comparison of pattern across scales without correcting for scale dependent changes in pattern. Turner (1989) states that difference in the scale of processes that affect patterns is most likely to influence differences in fractal dimension values. Such difference in fractal values, however, does not mean different processes. Denoting area by A and perimeter by P, relationship of fractal dimension, D, to area and perimeter has been expressed as follows:

$$P \propto \sqrt{A}^{D} \qquad [2.14]$$

For a circular or a square forest D will equal 1. As the perimeter becomes more and more contorted, the value of D will increase. D is a better measure of shape than of the compactness. For example, for a shape that doubles back on itself the value of D is close to 2.0, indicating a distorted shape, but the spread may still be relatively compact. Otto (1996) estimated values of D for patches in a forest and identified two landscapes having minimum and maximum D values. The results obtained by Otto (1996) did not agree with the landscape distinction made on the basis of these fractal values. This corroborates the point that D may not be a good measure of the spread or compactness of a forest area.

For a given forest that is contiguous or fragmented, the smallest circle can be found that completely encompasses the entire forest. Also, it is assumed that area outside the forest boundary is generally not available to wildlife species. A ratio of the area of the forest and the area of this circle can be estimated (Forman 1995). The value of this ratio that will range from 0 to 1 will be a measure of forest compactness, that is, how densely the forest is arranged or grouped. Also, this becomes a measure of the deviation of a forest area from circularity. That is, a circular forest is considered a standard shape against which any other shape can be compared with. This ratio is not a good measure of the extent of the forest edge, as it does not consider the perimeter of the forest. The objective of defining this ratio as a compactness index is to analytically study the impact of spread or fragmentation in a forest on the potential of wildlife population. It is expected that the home range size of the wildlife species and the area of the forest will be critical to such a study. This is based on the assumption that if the forest area is not very large compared to the home range size of the wildlife species, then a change in the compactness of the forest will affect wildlife population. Similarly, for a forest that is infinitely large in comparison to the home range, a change in compactness index will not affect its wildlife population. Thus, to study the sensitivity of compactness index to home range, a 'compactness factor of population' has been developed and is discussed in the next chapter. A value of 1 for the compactness index would mean that the forest is circular and there is no fragmentation or perforation. Thus:

$$\gamma = \frac{A}{C_a} \qquad [2.15]$$

where, γ = compactness index

A = area of the forest

C_a = area of the smallest circle encompassing the forest.

Thus, γ is an aggregate measure at the whole forest level. It is possible that a forest may be fragmented. Let there be m fragments and their proportions to the total forest be $x_1, x_2, \ldots, x_m$. Let the compactness indices of each of the fragments be $\gamma_1, \gamma_2, \ldots, \gamma_m$. Also, let the compactness index considering all the fragments together as a unit be γ_0. Now, the overall compactness index of this fragmented forest is the geometric mean (weighted by the proportion of total forest area occupied by each fragment) of the compactness index of the individual fragments multiplied with γ_0.

$$\gamma=\gamma_0\cdot\left(\gamma_1^{x_1}\cdot\gamma_2^{x_2}\cdots\gamma_m^{x_m}\right) \qquad [2.16]$$

Also, $\sum_{i}^{m} x_i = 1$.

For a forest γ will remain constant over time unless new areas are added, or there is loss of forested areas due to land degradation or land use change. For example, by adding new area if γ decreases, then it means that the modified forest is now less compact than the earlier one at the whole forest level.

The two indices v and γ can be put together as a vector to describe forest

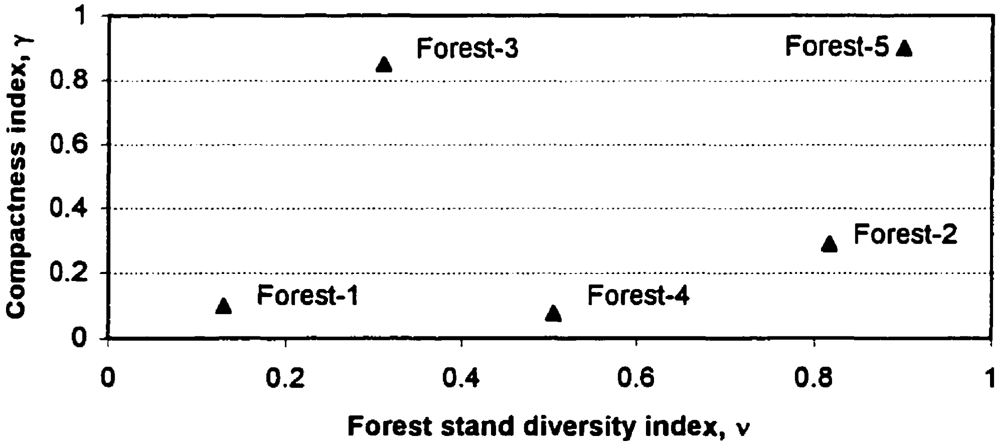


Figure 2.4. Forest variability index, F, of five forests

variability index F{ν, γ}. For comparison of two forests, and as ν and γ are in different units, a concept of distance can be introduced on a ν—γ plot (Figure 2.4). Such comparisons, however, must be considered with caution. The plot must be appropriately scaled, arbitrarily though, for better resolution. The scaling can be also done based on the relative importance of ν and γ. For example, if γ is considered twice as important as ν then γ values will have a multiplying factor of 2. The objective of this plot is only to provide relative comparison, therefore, the scale factors for both ν and γ in Figure 2.4 have been kept at 1. Figure 2.4 depicts that a forest can be represented in this space as a point. The separation between two points on this space will reflect how much one forest is different from the other in terms of ν and γ. Also, with relative importance of the two indices known for a decision process, two forests can be compared on this plot through their distances from a third—a standard—forest. Further, on this plot, a non-dominated forest as explained later, considering ν and γ as the criteria, can be identified.

An example considering sample forests

Consider five surveyed forests. The geographical layout of each forest as well as the areas of all patches have been estimated. Based on patch areas and their proportion in the forest, the weighted number of patches, n_w, has also been estimated for each of the forests. The spatial layouts of these forests are as in Figure 2.5a. The forest stand diversity and compactness indices have been estimated as shown in Table 2.1a. Forest-1 is a strip and has fifteen patches with n_w also equal to fifteen. The forest variability index for this forest is {0.13, 0.10}. For Forest-2 the forest stand diversity and compactness indices are equal to 0.82 and 0.29, respectively. Forest-3 has the same geographical area as Forest-2, but has a lower ν due to a lower n_w, and a higher γ.

Table 2.1a. Sample forests, with calculated indices

	Forest Number				
	1	2	3	4	5
Forest area, A, ha	100	580	580	1400	260
Number of patches, n	15	1055	251	1205	650
Weighted number of patches, n_w	15	985	216	985	600
Forest stand diversity index, ν	0.13	0.82	0.31	0.50	0.90
Forest compactness index, γ	0.10	0.29	0.85	0.08	0.90
Forest variability, $F\{\nu, \gamma\}$	{0.13, 0.10}	{0.82, 0.29}	{0.31, 0.85}	{0.50, 0.08}	{0.90, 0.90}

Forest-4, which is composed of ten fragments, has the same n_w value as Forest-2 (985), but a lower ν (0.50) indicating less stand diversity than Forest-2. This is expected because Forest-4 is geographically larger than Forest-2. For Forest-4, the forest survey indicated that the compactness index of the forest as a whole is 0.2; the ten individual fragments have compactness index of 0.35, 0.8, 0.35, 0.2, 0.35, 0.55, 0.2, 0.65, 0.7 and 0.35, respectively. The proportional area occupied by these fragments is 0.065, 0.071, 0.023, 0.057, 0.064, 0.071, 0.196, 0.106, 0.118 and 0.229, respectively. Therefore, the compactness index for Forest-4, using equation [2.16], can be estimated as:

$0.2(0.35^{0.065})(0.8^{0.071})(0.35^{0.023})(0.2^{0.057})(0.35^{0.064})(0.55^{0.071})(0.2^{0.196})(0.65^{0.106})(0.7^{0.118})(0.35^{0.229})$.

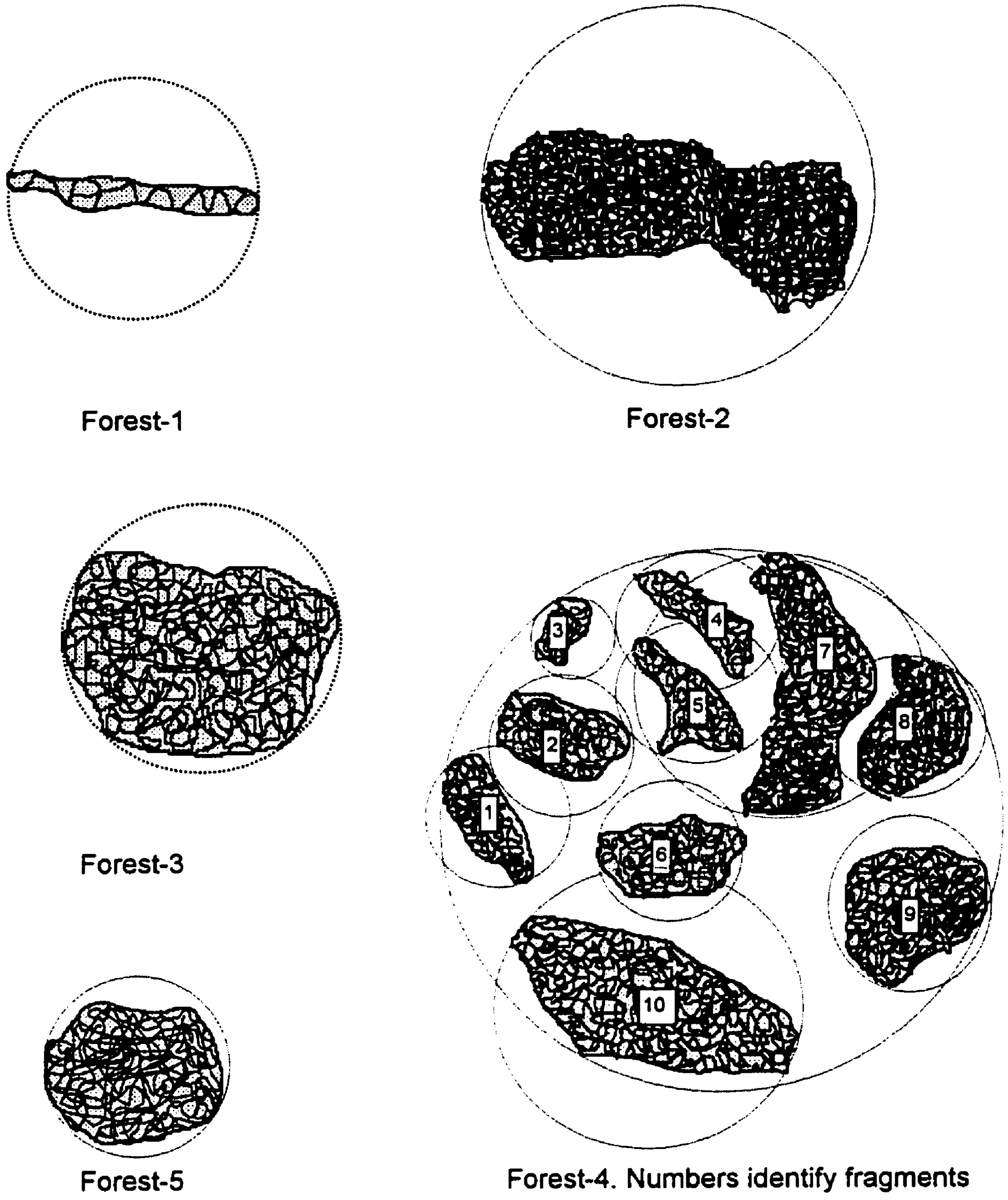
This is equal to 0.08, substantially lower than any other γ of the five forests considered, due to the combined effect of the ten forest fragments considered. Forest-5 is close to being ideal from the forest variability index perspective, because the value of this index is {0.90, 0.90}. Also, this forest appears to be very similar to Forest-3 because γ for these two sample forests, 0.90 and 0.85, respectively, are very close to each other. However, Forest-5 is much more diverse (ν=0.90) than Forest-3 (ν=0.31). Areas of the five forests considered so far are different, and so the comparative effects of ν and γ is not visually clear in Figure 2.5a. Therefore, for illustration purpose, four additional hypothetical forests—forest-6, forest-7, forest-8 and forest-9—with areas equal to that of forest-1 have been considered. These four additional forests have one to one correspondence with forest-2, forest-3, forest-4 and forest-5, respectively, in respect of their ν and γ values as can be seen in Table 2.1b. Spatial layouts of these forests are shown in Figure 2.5b. A very low value of γ may indicate that the forest area is either of elongated shape or is fragmented. 'Low values' for γ may be defined in a normative sense; a value of 0.1 or less, for example, would typically hint at fragmentation in the forest.

Timber harvesting affects the number of patches in a forest, with the impact depending on the size of the forest area. On the one hand, a small harvested area in comparison to the total forest area will not affect ν significantly. On the other hand, a relatively large clear-cut will affect ν appreciably. It is also possible to harvest timber in such a way as to increase the number of patches in the forest. This is possible in large or small clear-cuts. Large clear-cuts result in lowering the number of patches. For example, consider Forest-1 with different harvesting alternatives. In alternative-1 (Table 2.2) the harvest is done in a contiguous (single) clear-cut. In the other harvesting alternatives, the total area to be harvested remains the same, but the size of clear-cut

Table 2.1b. Sample forests of same area, with calculated indices

	Forest Number				
	1	6	7	8	9
Forest area, A, ha	100	100	100	100	100
Number of patches, n	15	185	51	83	250
Weighted number of patches, n_w	15	172	37	70	231
Forest stand diversity index, v	0.13	0.82	0.31	0.50	0.90
Forest compactness index, γ	0.10	0.29	0.85	0.08	0.90
Forest variability, $F\{v, \gamma\}$	{0.13, 0.10}	{0.82, 0.29}	{0.31, 0.85}	{0.50, 0.08}	{0.90, 0.90}

is reduced successively as the number of areas increases, thereby moving towards selection cutting in alternative-8. The weighted number of patches, n_w, after timber harvest can be estimated and, therefore, the effect of harvesting alternatives on forest stand diversity can be evaluated. Table 2.2 provides a summary of the impact of harvesting alternatives on weighted number of patches. Thus, for large clear-cuts as profits increase due to reduced cost of harvesting, forest stand diversity decreases. If, for example, by using short-term economic criteria, alternative-1 is judged to be the best, then this decision can be compromised by either reducing the harvested area or harvesting in more than one block to increase forest stand diversity. Thus, a trade-off relationship between harvesting cost and forest stand diversity can be established for a given forest area that must be harvested.



Forest-1

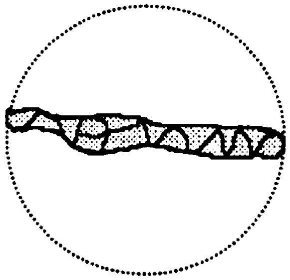
Forest-2

Forest-3

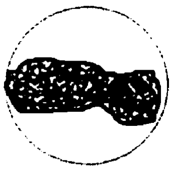
Forest-5

Forest-4. Numbers identify fragments

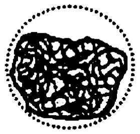
Figure 2.5a. Spatial layout of forests with patches outlined in the shaded areas



Forest-1

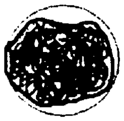


Forest-6



Forest-7

Forest-8 (ten patches)



Forest-9

Figure 2.5b. Spatial layout of forests of same area with patches outlined in the shaded areas

Discussion

An even-aged stand or forest by definition has only one age class. If there is only one tree species present then by applying equation [2.13] forest stand diversity index, v, for this case will be zero. Consider a forest with, say, fifteen age classes and having fifteen patches. If one patch is very large and rest of the fourteen patches are significantly small then the weighted number of patches, n_w, will be slightly more than one. Therefore, v will be marginally different from zero. As the average patch size increases the weighted number of patches, n_w, will increase and thus, v will also increase. When all patches are of the same size then the weighted number of patches will equal fifteen. This forest is a normal forest in which all age classes occupy equal areas (Allison 1985). Thus, applying equation [2.13], for a 100 ha normal forest with, say, fifteen age classes, the forest stand diversity index, v, can be determined to be equal to 0.13. Similarly, v for any other normal forest can be determined. Also, if the weighted number of patches is more than fifteen, the forest stand diversity index, v, will be more than 0.13. For $n_w \rightarrow \infty$ the forest stand diversity index, v, will tend to reach 1. It is comprehensible, now, to say that the higher the value of v, the more uneven-aged the forest is. The value of v, in this sense, becomes a measure of unevenness of the forest.

The examples considered show that there can be a forest with high stand diversity index but low compactness (Forest-2) and *vice versa* (Forest-3). It can be surmised that a forest with high stand diversity and high compactness indices will address ecological needs in the same way as a large—in relation to home range—uneven-aged forest does. The method proposed is different from most of the cluster

Table 2.2. Impact of timber harvest on forest stand diversity index

	Total area, ha	Harvested area, ha	Weighted number of patches after timber harvest, n_w	Forest stand diversity index, v
Initial forest	100	-	12	0.10
Alternative-1	100	20	10	0.086
Alternative-2	100	20	20	0.17
Alternative-3	100	20	30	0.25
Alternative-4	100	20	80	0.55
Alternative-5	100	20	130	0.72
Alternative-6	100	20	180	0.83
Alternative-7	100	20	230	0.90
Alternative-8	100	20	290	0.94

analysis approaches where the focus is to identify clusters *per se*. The method based on patches, as discussed in this chapter, a perspective to the whole forest is given, although there is no consideration of the relative placement of patches in the forest. This is an acceptable compromise as the forest area under study is taken as a unit. If wildlife is the focus then this area must at least equal the home range of the wildlife. Availability, and not the placement, of the habitat characteristics within this forest will be of importance. However, for better understanding of availability and needs of a wildlife species in a forest, more specific analyses need to be done. The focus here is to identify a diverse forest with many different stands.

The measures of forest stand diversity and the compactness indices are always finite with a minimum and a maximum. Hence, a value of these indices will help visualize the diversity of a forest. A low value of forest compactness may raise some concerns warranting a closer look at the forest. For distinguishing one forest from another, both these indices defined together as a forest variability index, must be compared. Suppose two forests have forest variability index as $F_1 \{\nu_1, \gamma_1\}$ and $F_2 \{\nu_2, \gamma_2\}$, then by the Pareto criterion F_2 dominates F_1 if the following condition is satisfied:

$$\left.\begin{array}{l} \nu_2 > \nu_1 \text{ and } \gamma_2 \geq \gamma_1 \\ \qquad\quad \text{or} \\ \nu_2 \geq \nu_1 \text{ and } \gamma_2 > \gamma_1 \end{array}\right\} \qquad [2.17]$$

and neither F_1 dominates F_2, nor F_2 dominates F_1 if

$$\left.\begin{array}{l} \nu_2 < \nu_1 \text{ and } \gamma_2 > \gamma_1 \\ \qquad\quad \text{or} \\ \nu_2 > \nu_1 \text{ and } \gamma_2 < \gamma_1 \end{array}\right\} \qquad [2.18]$$

In Figure 2.4 Forest-3 has higher values of both ν and γ in comparison to Forest-1. Therefore, Forest-3 is better than, or dominates, Forest-1 by this criterion. The same cannot be said for Forests-3 and 4, as the condition in equation [2.17] is not satisfied. Simply stated, a forest on this vector plot to the upper right of another forest, is the dominating forest from forest variability index, F, perspective. Reciprocally, a forest to the lower left of another forest is the dominated forest. In all other cases, dominance of a forest over another cannot be determined, as indicated by condition [2.18].

Conclusion

The forest stand diversity index provides a quantifiable measure of unevenness of a forest from even-aged to uneven-aged. Thus, a forest can be easily compared with the likeness of a normal forest of the same number of age classes by determining the value of this index. One of the major spin-off benefits of the forest stand diversity index is to have a quantifiable control over the size of clear-cut. This can be achieved by assessing the value of the forest stand diversity index in a would be clear-cut situation and comparing it with other possible timber harvesting alternatives as shown in the example discussed.

Further, the forest stand diversity index will reflect any change in a forested area due to change in land use. The forest variability index will reflect changes in forest structure due to forest growth or damage caused by timber harvest, forest fire, or pest infestations. Also, based on these indices that are scale independent, different forests can be easily compared.

CHAPTER 3

Effect of compactness index on wildlife population density

Introduction

Geographical shapes of forest fragments and landscapes are important ecologically, especially in affecting movements and flows of flora and fauna (Forman 1995). Ibrahim et al. (1996) and Otto (1996), among others, implied that shape and the extent of a forest area are important determinants in the process of growth of wildlife populations. Calish et al. (1978) suggested that a regulated forest with a mix of age classes close to each other provided suitable conditions, such as cover and browse, for wildlife. This may be true at the whole-forest level. This condition is theoretically best met when a forest meeting habitat requirements is circular. Also, a circular forest area has the highest amount of relative core area available. Therefore, it is reasonable to assume that forests in compact form, that is, as circular as possible, are effective in conserving resources and hence, important for wildlife preservation. In the absence of any contrary empirical evidence, a circular forest can be considered a standard for comparison. Therefore, the Compactness Index, γ, discussed in the previous chapter may conceivably be a determinant of wildlife population density in the long run and figure explicitly in any attempts to estimate the expected population density of the species.

Wildlife ecologists (Hunter 1990, Forman 1995) have discussed the concept of "home range" of any wildlife species, which is considered to be the minimum extent of area of a habitat that must be freely available to a species for day-to-day movements for food, shelter and reproduction. A forest that is perfect from a wildlife perspective will allow a species to achieve its population density potential over time. Also, given the same area and similar habitat conditions, a circular forest area with maximum core area available should have a higher population density potential than a non-circular forest. It can be expected that the negative effect on population potential due to non-circularity or non-compactness of the forest will be alleviated if the forest area is very large in comparison to the home range size. In the following section an analytical relationship will be developed to show the reduction in wildlife population density potential of a forest due to the decreased compactness relative to a circular forest. This factor can be termed 'compactness factor for population density'. Home range size of wildlife will be a critical component for such a relationship.

Compactness factor for population density

The normally accepted "home range" of a wildlife species can be considered to be a perfectly compact forest area, that is, a forest with a value of $\gamma=1$. Another similar forest of the same area with $\gamma<1$ may be expected to permit reproduction but cannot be expected to support the maximum population density potential. The actual population density potential in such cases will be lower than the maximum. To provide an analytical framework, denote population density potential for a non-compact forest as M_{nc}, and a hypothetical circular forest of same area and similar attributes as M_c. Now define the "compactness factor for population density" as:

$$w = M_{nc} / M_c. \qquad [3.1]$$

By definition the range of values of w will be [0, 1]. Consider total area of the forest as A and a critical minimum area required to sustain a wildlife population as $k{\cdot}H$, where k is a real number (≥ 1) dependent on wildlife and H is the home range size. Now define a "home range factor", m, as the ratio of $k{\cdot}H$ to A. The compactness factor for population density, w, will depend on γ as well as on the size of the forest area in relation to the recognized area of home range.

If area, A, of the forest is less than the critical minimum area ($k \cdot H$) then, by definition, a wildlife population cannot be sustained on this land and so w must acquire a value of zero. This means that the population would become extinct for $m>1$ and consideration of such values is irrelevant for us. Gurd (1997) discusses changes in population due to change in landscape composition and considers, however, home range as the smallest area for management. In this case $k=1$. Gurd (1997) considers, among others, forest fragmentation, but not the shape of the forest patch as a factor affecting wildlife population. For a highly fragmented forest, or a forest in the shape of a narrow strip, $\gamma \rightarrow 0$ and $M_{nc} \rightarrow 0$ and thus $w \rightarrow 0$. As γ increases from zero, meaning that a more compact forest is considered, w will also increase. The actual population density potential, M_{nc}, that is less than M_c, would be achievable for $\gamma<1$. The population density potential will be at its maximum at M_c when $\gamma=1$. Thus, w will increase with increasing γ. It may be further argued that for small values of m (situations where the forest area is very large in comparison with the critical minimum area) w will be much more sensitive to changes in γ at low values of γ but much less so at high values. Also for sufficiently small m, a reduction in γ from 1 should have marginal effect on w and thus, M_{nc} will be sufficiently close to M_c. In the same manner it may be argued that for large values of m (situations where the forest area is not very much more than the critical minimum area) w will be more sensitive to changes in values of γ at high values of γ and much less sensitive at low values. That is, at low values of γ the compactness factor for population density, w, is small enough to become relatively insensitive to small changes in γ. Similar relationships may be postulated between m and w except that w will decrease as m increases for a given γ. The exact combined effect of m and γ on w is difficult to visualize in the absence of empirical information, but broadly it may be said that there will be some degree of substitutability between m and γ for achieving a given w.

The above observations may be expressed mathematically in the following conditions:

$$w = f(m, \gamma) \tag{3.2}$$

$$0 < m \leq 1 \tag{3.3}$$

$$0 < \gamma \leq 1 \tag{3.4}$$

$$\partial w / \partial \gamma > 0 \tag{3.5}$$

$$\partial w / \partial m < 0 \tag{3.6}$$

If the marginal contribution of γ in increasing w is of the same order as the marginal contribution of m in decreasing w, then these effects would balance each other for $m = \gamma$. Also, considering the above, the rate of increase in w due to changes in γ and m should tend to be positive for $\gamma > m$ and *vice versa*. These can be mathematically expressed as:

$$\begin{aligned} \partial^2 w / \partial m \partial \gamma &> 0 \quad \text{for} \quad \gamma > m \\ \partial^2 w / \partial m \partial \gamma &< 0 \quad \text{for} \quad \gamma < m \\ \partial^2 w / \partial m \partial \gamma &= 0 \quad \text{for} \quad \gamma = m \end{aligned} \tag{3.7}$$

In reality, the marginal contribution of γ in increasing w may not be of the same order as the marginal contribution of m in decreasing w. One possible general relationship, obtained by trial and error, between w, m and γ that satisfies conditions [3.2] to [3.6] is:

$$w = e^{-\left(\frac{m^2}{1-m^2}\right)^x \left(\frac{1-\gamma^2}{\gamma^2}\right)^y} \tag{3.8}$$

where parameters x>0 and y>0. From equation [3.8] an expression for $\partial^2 w / \partial m \partial \gamma$ can be obtained which is >, <, or = 0 depending on whether 1 is greater than, less than or equal to the following, respectively:

$$\left(\frac{m^2}{1-m^2}\right)^x \left(\frac{1-\gamma^2}{\gamma^2}\right)^y \qquad [3.9]$$

For x = y equation [3.8] satisfies condition [3.7].

In the absence of any contrary information from ecological studies and to give a perspective to this analysis equation [3.8] can be accepted at this stage. The form of equation [3.8] indicates that a very small or a very high value of x or y would make w relatively insensitive to changes in m or γ. For x = y, this function is more or less symmetric in sense of the effect each of the variables m and γ has on the relationship between the other variable and w. For the sake of simplicity and illustration, and considering the 'good behavior' of the results, x = y = 1 can be assumed. Thus, the following relationship can be postulated:

$$w = e^{-\left(\frac{m^2}{1-m^2}\right)\left(\frac{1-\gamma^2}{\gamma^2}\right)} \qquad [3.10]$$

When plotted against m and γ the compactness factor for population density exhibits very plausible relations as depicted in Figure 3.1 and Figure 3.2. The γ-w plot in Figure 3.1, giving different values of m in equation [3.10], shows that for $\gamma=\varepsilon$ ($\varepsilon \rightarrow 0$)—an extremely fragmented forest or a forest in the shape of a very thin strip—may not support wildlife population even if its area is large. In this case w will be equal to zero. It is assumed here that the wildlife species considered for this analysis is affected by forest fragmentation. For a forest with $\gamma=1$ the compactness factor, w, is 1 irrespective of the size of the home range factor of the forest.

The m-w plot in Figure 3.2, considering different values of γ, shows that for m=1-ε (ε →0) the compactness factor for population density, w, becomes 1 for γ=1. For all other values of γ less than 1, w becomes zero. This means that any loss in compactness when the forest area equals the critical minimum area to sustain wildlife population is not acceptable from a wildlife perspective.

From Figure 3.1 it can be seen further that for m>0.5 a slight drop in γ at higher values of γ effects a sharp drop in w. This indicates that, in this modeling approach, a forest that is twice, or smaller than the critical minimum area is extremely susceptible to a reduction in wildlife population density if γ drops below 1. Therefore, it can be stated as a rule of thumb that a wildlife management unit must be at least twice the critical minimum area. Figure 3.3 shows the three-dimensional line plot of home range factor (m), compactness index (γ) and compactness factor for population density (w).

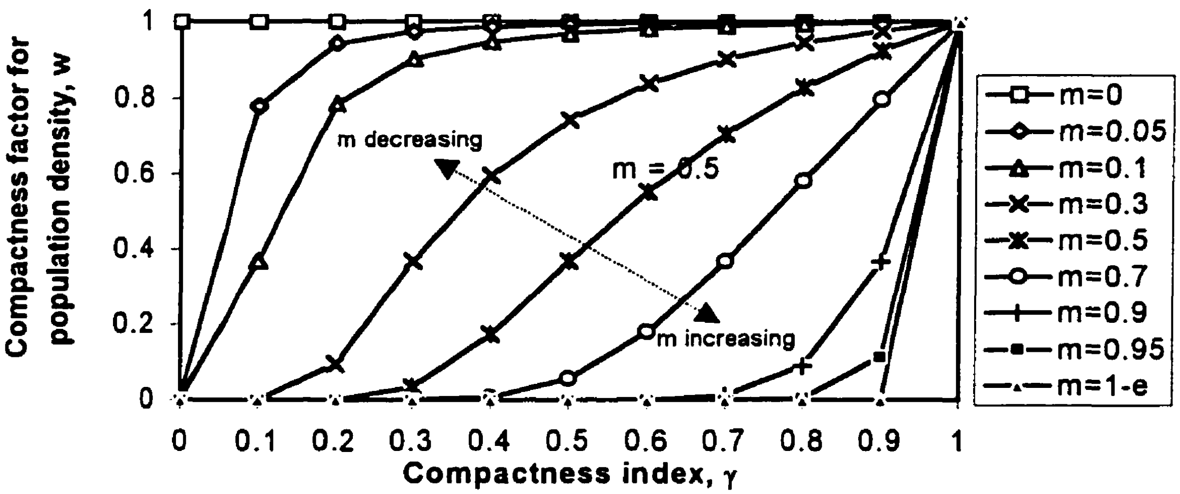


Figure 3.1. Effect of compactness index, γ, on population density with home range factor, m, as a parameter

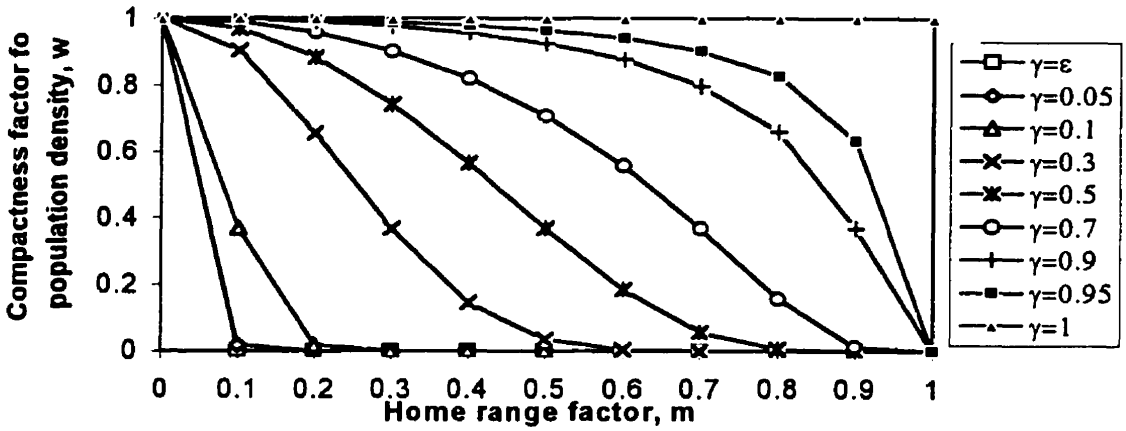


Figure 3.2. Effect of home range factor, m, on population density with compactness index, γ, as a parameter

Having postulated a relationship among home range factor (m), compactness index (γ) and compactness factor for population density (w), substitutability of one factor with the other will provide further insight. In the next section elasticity of substitution analyses in the three possible combinations, w with γ, w with m and γ with m are given.

Elasticity

a. Elasticity of w with γ:

Gamma elasticity, e_1, can be defined as (dw/w)/(dγ/γ). Considering m a constant, equation [3.9] yields:

$$\text{Elasticity} = e_1 = \left(\frac{dw}{d\gamma}\right)\left(\frac{\gamma}{w}\right) = \left(\frac{m^2}{1-m^2}\right)^x \left(\frac{2y}{\gamma^{2y}(1-\gamma^2)^{1-y}}\right) \qquad [3.11]$$

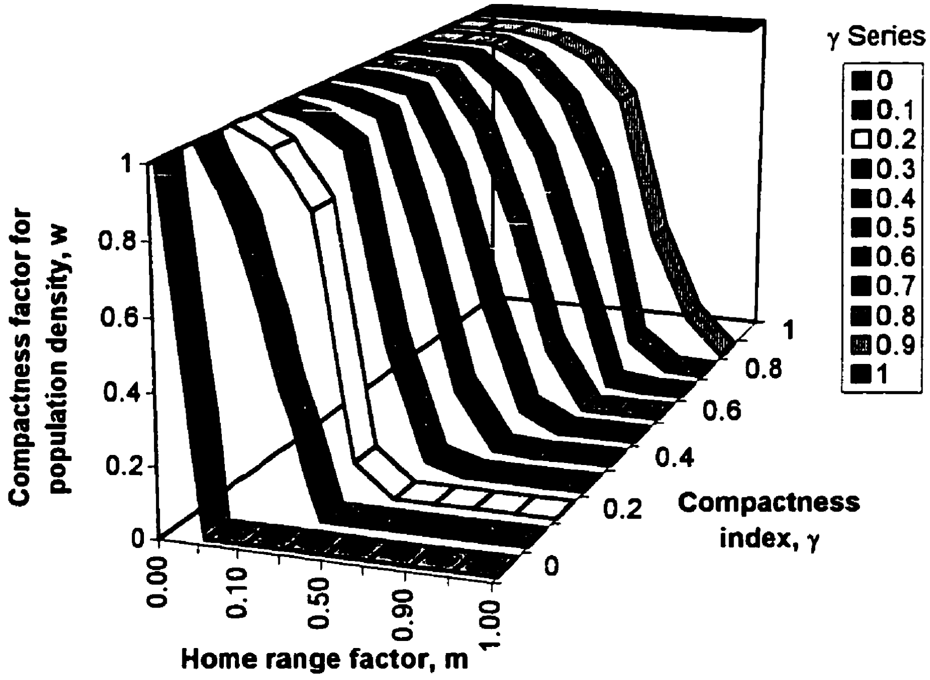


Figure 3.3. Three dimensional line plot of home range factor, compactness index and compactness factor for population density

Equation [3.11] shows that $e_1 \geq 0$. Considering $x = y = 1$, equation [3.11] can be rewritten as:

$$\gamma = \sqrt{\frac{2m^2}{e_1(1-m^2)}} \qquad [3.12]$$

Locus of γ-m points having the same gamma-elasticity, e_1, is shown in Figure 3.4.

b. <u>Elasticity of w with m</u>:

Scale elasticity, e_2, can be defined as (dw/w)/(dm/m). Considering γ a constant, equation [3.9] yields:

$$\text{Elasticity} = e_2 = \left(\frac{dw}{dm}\right)\left(\frac{m}{w}\right) = -2x\left(\frac{m^{2x}}{(1-m^2)^{x+1}}\right)\left(\frac{(1-\gamma^2)^y}{\gamma^{2y}}\right) \qquad [3.13]$$

The above equation shows that $e_2 < 0$. Considering $x = y = 1$, equation [3.13] reduces to:

$$e_2 = \frac{(-2)(1-\gamma^2)m^2}{\gamma^2(1-m^2)^2} \qquad [3.14]$$

and also, by rearranging, the following is obtained:

$$\gamma = \sqrt{\frac{2m^2/(1-m^2)^2}{(-e_2)-2m^2/(1-m^2)^2}} \qquad [3.15]$$

Locus of γ-m points having the same scale-elasticity, e_2, is shown in Figure 3.5.

c. Elasticity of substitution of γ for m:

Elasticity of substitution, e_s, can be defined as (dγ/γ)/(dm/m). This also indicates the change required in γ for a known change in m if w were to remain unchanged. From equation [3.9] we obtain an expression for dγ/dm and e_s can be written as:

$$e_s = -\frac{x(1-\gamma^2)}{y(1-m^2)} \qquad [3.16]$$

For x=y equation [3.16] can be re-written as:

$$\gamma = \sqrt{1+e_s(1-m^2)} \qquad [3.17]$$

Locus of γ-m points having the same elasticity of substitution, e_s, is shown in Figure 3.6.

Discussion

Consider that for a given forest and wildlife species the home range factor (m) and compactness index (γ) are known. Thus, the compactness factor for population density, w, can be determined. The calculated w can be used to adjust the potential wildlife population due to shape and fragmentation of the forest region. Further, various elasticities can be determined to analyze m-γ substitution options for a management decision, particularly for the creation of parks.

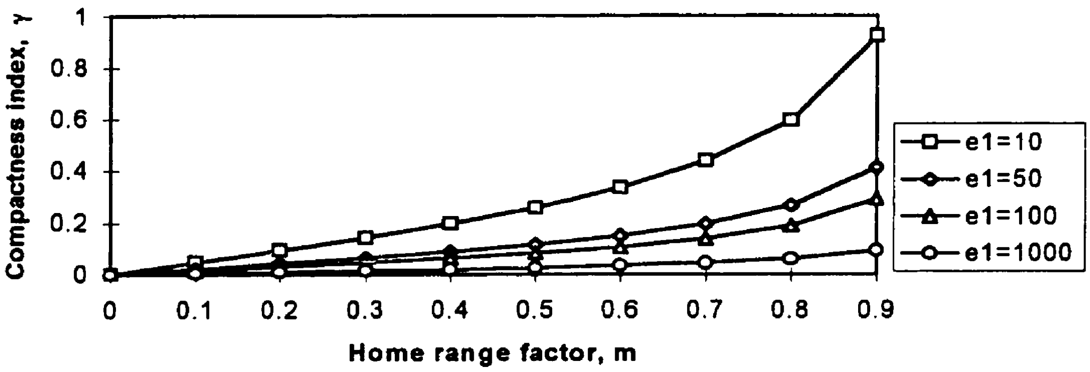


Figure 3.4. Gamma elasticity, e_1

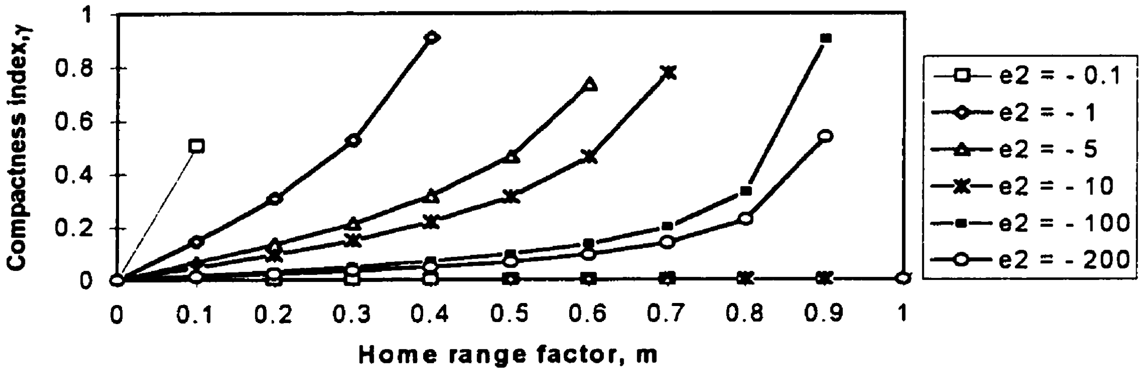


Figure 3.5. Scale elasticity, e_2

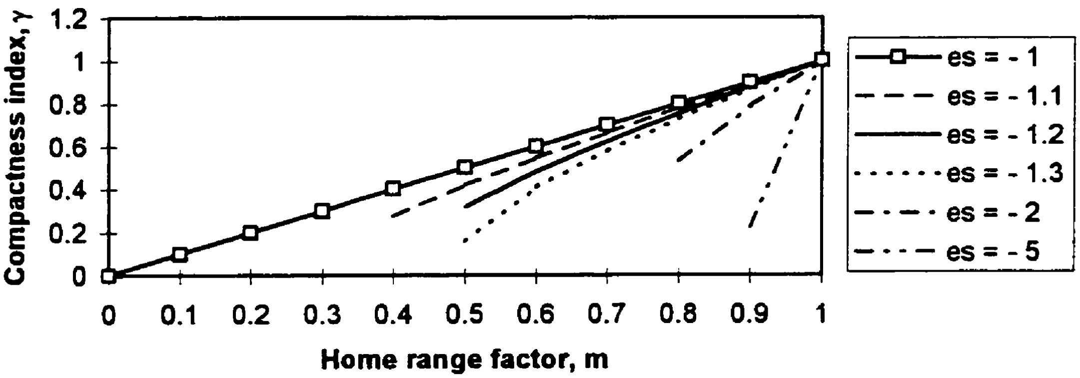


Figure 3.6. Elasticity of substitution, e_s

CHAPTER 4

Quantifying forest structure: An operational forest planning tool incorporating forest maturity and forest stand diversity

Introduction

'Forest management' connotes many aspects of forestry, such as the quantity of timber to harvest, silvicultural practices to adopt, or nontimber products to maintain. Forest management decisions traditionally attempt to optimize the long-term timber productivity of the forest, but the various goals of forest management, such as maximizing economic indicators, optimizing wildlife habitat and maintaining ecological diversity, are often in conflict with each other (Thompson et al. 1994). To achieve a forest management goal, a forest management plan that is implemented must be able to produce the desired results, and that is difficult due to uncertain events such as forest fire or pest attacks, that alter the forest. It is, therefore, critical to understand the impact of the implementation of a current forest operation plan on the future state of the forest.

Typically, timber harvest optimization techniques use the current age class structure and an optimization criterion as inputs to prescribe the best timber harvesting schedule (Davis and Johnson 1987). There are two shortcomings in these approaches. The first relates to the difficulty in assigning monetary values to the nontimber forest products such as wildlife habitat, forest diversity, or environmental benefits. Thus, most optimization criteria either do not consider nontimber values at all or assume some arbitrary values. In either case, the optimal harvesting schedule, in reality, may not be the foremost—meaning that an improvement in nontimber value estimates would change the timber harvesting schedule. However, considering nontimber values, Fogel et al. (1988) and Gunn (1991) used multicriteria and hierarchical techniques to provide timber harvesting alternatives for a forest manager.

The second shortcoming concerns the unforeseen changes in the forest due to natural disturbances such as fire, pest attack or wind-throw. The optimal timber harvest schedule may no longer be found desirable if an unforeseen event during the plan period alters the forest from what was considered initially. Attempts at dealing with this problem can be seen in Reed (1984) and Reed and Errico (1986) where the optimal harvest scheduling considering 'hazard function', meaning probability of forest damage, has been determined. Understandably, if the unforeseen event did not happen or happened with much more severity than accounted for in the model, then the forest inventory in the next period would be different than expected. The optimal timber harvest schedule for the next period can now be obtained again by running the optimization model with the new inventory. This method is in practice and commonly referred to as the "rolling horizon decision process". The difficulty with this methodology in forestry, in relation to optimization techniques where the target is to make extreme some economic criterion, is when there is excessive timber harvest—but optimal according to its objective function—and forest damage is more than anticipated in the beginning of the planning period. Thus, an undesirable forest inventory—the current forest inventory affects all future planning—in the next period puts pressure on forest planning for the future. Therefore, it becomes a formidable task to determine the best combination of timber and nontimber values through any of the standard optimization techniques; and implementation of harvesting schedules continues to be largely dependent on the judgment of the forest manager. A well computed timber harvesting schedule may, therefore, not be considered acceptable from the view point of whole forest management.

Development of price-quantity relationships for various nontimber products of the forest would eliminate the arbitrariness associated with nontimber values in an optimization model. However, this is not an easy task as most of the nontimber products are intangibles, and they do not have any well developed markets. Therefore, development of interdependence relationship of a forest product, tangible or intangible, with some common aspect of the forest such as forest structure, would be useful. This would require that the definition of forest structure include timber yielding capacity, age class structure, species and tree distribution in a forest. Such a definition would bring clarity to the understanding and purpose of maintaining a forest structure from timber and nontimber perspectives. Also, the forest management objective, instead of being based on economic optimization, may be directed at achieving a certain forest structure that provides for a known quantity of timber and nontimber products. This approach may not completely eliminate the difficulties associated with the optimization techniques as discussed above, but will improve control over the state of the forest. A forest rich in tree species and age class diversity is well suited to provide timber and nontimber values (Peters et al. 1989). For example Hunter (1990) states that a forest landscape with stands of many ages can support more wildlife species than a single-age landscape. A forest with many age classes is also compatible with the goal of obtaining a continuous supply of timber. Also, Peters et al. (1989) shows that a forest area rich in tree species can have a significant nontimber value. Hunter (1990) further points out that an uneven age class distribution of trees in a forest can cause problems for wildlife species that require forest of a particular age for habitat. Therefore, maintaining some desirable age class structure and distribution of trees as one forest management goal would be a useful strategy to realize the many products of a forest simultaneously. This also coincides with the forest management goal of obtaining a continuous supply of timber.

Thus for a known quantity of timber harvest, a certain distribution of trees can be maintained through appropriate timber harvesting and regeneration schemes. Such an idea provides a significant challenge to forest managers and requires explicit consideration of timber and nontimber values that would permit a trade-off in the production of timber and nontimber values. This idea is the focus of this chapter, that is, to develop a method to quantify forest structure, a key element in developing any timber-nontimber relationship.

In the following section significance of forest structure for nontimber values of the forest, in particular that of wildlife, is discussed. Utility of forest structure as a design tool for operational planning is also shown. Then, a forest maturity index, ϕ, that can also be used to measure states of forest depletion or deforestation has been developed. Strategies to achieve a desired forest maturity level are also discussed. After this, methodologies to determine ϕ for a multi-species forest are given. Next, through an example, a strategy for achieving the desired forest structure through a timber harvesting scheme is shown.

Forest structure as a design tool

Forests are host to many species of flora and fauna. Some wildlife species depend on the vertical structure of the forest for food, cover, and reproduction while some others depend exclusively on the horizontal structure. The distinct levels of tree height and understorey, crown cover, and canopy closure define the vertical structure of the forest. The spatial spread of the different age classes and species of trees in a forest define the horizontal structure of the forest (Porter 1986). Most of the large animals, particularly large ungulates, derive their habitat requirements from the age class distribution or the horizontal structure of the forest (Hunter 1990). On a similar note Salwasser (1985) states that timber and wildlife interactions are affected by cover types; geography of individual stands; and floristic and structural characteristics of individual stands. Horizontal structure will also integrate into vertical structure through different species and age classes of trees. Thus, horizontal structure of the forest can be said to represent an important aspect of the forest. In this thesis only the horizontal structure represented by the age classes and distribution of trees in a forest has been considered.

Forest stands of different ages in a forest are important for many wildlife species. For example, Thomas et al. (1976) reported for elk (*Cervus elaphus*) that younger stands provide the forage whereas the protective cover is available through the older stands. Thus, a forest with a low rotation age, despite the abundance of food it would provide, could not support elk because adequate cover from older stands would not be available. Similarly moose (*Alces alces*) require mature conifer stands for cover and wide open areas for foraging (Peek et al. 1976, Leptich and Gilbert 1989). Nautiyal (1988) shows analytically that consideration of nontimber values, including wildlife, of the forest affect optimal rotation age of a stand. Calish et al. (1978) concluded that a compromise on the rotation age of a forest would be necessary as all nontimber outputs cannot be maximized simultaneously. The mix of age classes in a forest, therefore, would determine the timber and nontimber productivity of the forest.

Growing stock, distribution of age classes, and existence of many tree species in a forest, define the state of the forest. Growing stock will be determined by the yield function of tree species and areas occupied by age classes in the forest. To capture the growing stock and, therefore, the long-term timber yielding capacity of the forest, a forest maturity index, ϕ, will be developed. For a regulated forest, the rotation age will determine the value of ϕ. Therefore, for such forests ϕ also becomes a measure of the age class structure. However, for a forest that is not (yet) regulated ϕ will only be a measure of the long term timber yielding capacity. It will not indicate much about the age class distribution that could be used to predict populations of some wildlife species.

A concept of forest structure that includes both forest maturity (and therefore timber yielding capacity) and its diversity could be used to develop interrelationships between timber and nontimber products. That means ϕ and F[1] together could be used as measures to relate a given timber yield in the long run with an expected wildlife population density, given the forest cutting scheme. For a geographically specific forest, the component γ of the forest variability vector F will be constant. Therefore, for the purposes of further discussion of a measure of forest structure it can be considered that its components are only ϕ and ν, the forest maturity index and the forest stand diversity index, respectively.

Therefore, let us denote the forest structure vector as $S\{\phi, \nu\}$. The vector **S** will give a quantitative indication of the state of the forest and can be used as a forest operation planning tool. Thus, its quantification is a useful starting point towards developing an operational forest management plan from timber as well as nontimber perspectives. If ϕ_d and ν_d are the desirable maturity and stand diversity indices for a forest, then an operational timber harvesting plan to achieve these can be made. The appropriate silvicultural systems, such as clear-cut, or selection, will help achieve the desired forest stand diversity over time. In the next section the forest maturity index, ϕ, will be developed and a method to achieve ϕ_d through appropriate timber harvests will be shown.

Quantifying forest maturity

From the timber management perspective a regulated forest is an ideal forest condition. A regulated forest is one that regains its earlier structure after a known quantity of timber is

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[1] F is the vector of forest variability index as discussed in Chapter 2, defined by forest stand diversity index, ν, and compactness index γ.

harvested. This is possible when the quantity of timber harvested equals the forest growth in a period. Most forests are not in a regulated state and therefore area control and volume control are the two major forest regulation strategies in actual practice (Davis and Johnson 1987). In the area control method there is no control over the volume harvested. In the volume control method, the volume harvested can be quickly estimated. In both approaches, the rotation length decision controls the area or volume to be harvested.

Allison (1985) simulated a series of annual harvests from a sample forest that resulted in a regulated forest after 23 years. It was theorized that for a given forest consisting of a single species with known yield function, a constant annual harvest can be determined that will convert the existing forest into a regulated forest in the long run. This regulated forest will be the classical "normal forest" with a number of one year age classes equal to the rotation age and each age class having the same area. The annual harvest will be the yield at the rotation age and from the area equal to the age class area. Thus, the periodic (annual) timber harvest so determined will leave the age classes of the forest unchanged in the long run because, in the next period, the forest growth will replenish the timber harvests. Allison (1985) called the regulated forest, described by its rotation age and a timber harvest, the equivalent normal forest (ENF) of the existing forest. The timber harvest that regulates the forest was termed 'ENF yield'. He also showed that the ENF yield is directly proportional to the 'mean annual increment' at the rotation age. Also, for a given forest, its ENF yield can be uniquely determined. The ENF yield equals the mean annual increment at the rotation age multiplied by the total area of the forest (Allison 1985). However, the reverse is not true: a given ENF yield may result from more than one age class distribution.

For any timber species that grows from seedling-stage, matures and ultimately dies, the 'mean annual increment (MAI)' will have a maximum at some point in its life span. Thus, technically it is possible to have a forest whose ENF will have the rotation age equal to the age at the maximum mean annual increment. Also, this forest will have an ENF yield that is the maximum possible for the species. Let us now define the following:

EY_{max} = ENF yield with rotation age equal to the age at the maximum MAI

EY_t = ENF yield for the forest with a rotation of t years

R_{mm} = Rotation age equal to the age at the maximum MAI

R_t = Rotation age of the forest at time t corresponding to its ENF.

It is implicit from the definition that EY_{max} and R_{mm} are constant for a given tree species on given site conditions. EY_t and R_t will change as the age class distribution in the forest changes due to timber harvest or forest damage. It is assumed that the forest is in "good" health and is growing as expected. If some disease is affecting forest growth then the normal yield (Plonski 1974) will have to be suitably adjusted to account for the loss in growth due to disease. If $R_t < R_{mm}$, then the forest can be termed immature as its rotation age is lower than R_{mm}. Also, if $R_t > R_{mm}$, then the forest can be termed overmature for a similar reason. This classification is strictly with respect to comparison of the forest with a forest that has an ENF with rotation age equal to R_{mm}. In both cases of $R_t < R_{mm}$, and $R_t > R_{mm}$, the ENF yield, EY_t, will be less than EY_{max}. EY_t and R_t succinctly capture the maturity and age class structure of a forest. Using EY_t and R_t, forest maturity index, $\phi(t)$, can be defined. Further, $\phi(t)$ can be defined to have a positive or negative value depending on whether the forest is immature or overmature. Thus, define forest maturity as:

$$\phi(t) = \frac{(R_t - R_{mm})}{|R_t - R_{mm}|} \cdot \frac{(EY_{max} - EY_t)}{EY_{max}} . \qquad [4.1]$$

Thus to determine $\phi(t)$, EY_t that corresponds to a specific R_t must be known; EY_t can be determined by simulating the effect of different timber harvest on the forest and selecting the one that regulates the forest in the long term (see Allison 1985). Since ENF yield is directly proportional to the mean annual increment at the rotation age, $\phi(t)$ can also be expressed as:

$$\phi(t) = \frac{(R_t - R_{mm})}{|R_t - R_{mm}|} \cdot \frac{(MAI_{max} - MAI_t)}{MAI_{max}} \qquad [4.2]$$

where MAI_{max} and MAI_t are the maximum mean annual increment at the rotation age R_{mm} and the mean annual increment at the rotation age R_t, respectively. Clearly, from equation [4.2], if $MAI_t = MAI_{max}$ then $\phi(t)$ will equal zero. Also, by definition, when $MAI_t = MAI_{max}$, R_t will equal R_{mm} and $EY_t = EY_{max}$. Thus, a forest with $\phi(t)$ equal to zero has the highest long term sustainable yield (LTSY) of timber equal to total forest area multiplied by MAI_{max}. Let us call the forest with $\phi(t) = 0$ the absolute normal forest (ANF).

Without loss of generality, $\phi(t)$ can be expressed as ϕ for a fixed t, which is uniquely determined if MAI_t is known. Thus, ϕ will always correspond to a point on the MAI curve at the rotation age. Therefore, theoretically, for an immature forest, ϕ will range from -1.0 for a forest that has just started to grow ($EY_t = 0$ or $MAI_t = 0$), to zero for a forest whose ENF yield corresponds to the ENF yield ($EY_t = EY_{max}$) at the rotation age R_{mm}. Likewise, for an overmature forest, ϕ will range from zero for a forest whose ENF yield equals EY_{max} and the rotation age corresponds to the age at maximum MAI; to +1.0 for a forest that consisted of old growth only, and has just died of overmaturity ($EY_t = 0$ or $MAI_t = 0$). Therefore, the range of ϕ is [-1.0, +1.0]. Only the age class distribution of the tree species and its yield function are required to uniquely determine ϕ. Further, since only timber yield has been considered in the determination of ϕ, the latter can be considered a design tool for timber management. It will be now shown how ϕ can be used as a measure of deforestation. Thereafter, timber harvesting strategies to achieve a desired forest maturity will be discussed.

A measure of depletion

Allison (1985) proposed that an equivalent area of a current forest can be determined so that EY_t of the now modified forest equals EY_{max}. This modified forest is the ANF with $\phi = 0$. For both immature and overmature cases $EY_t < EY_{max}$. Determination of this equivalent area *per se* does not indicate whether the current forest is depleted or not. Definition of ϕ more clearly identifies the immaturity or maturity of a forest through a negative or a positive sign, respectively. Also, the extent of immaturity or maturity, as defined, is clearly identified.

As stated earlier, an immature forest has a negative ϕ as $R_t<R_{mm}$. Therefore, a forest that has a negative ϕ can be said to be in a state of depletion. The degree of depletion is indicated by the value of ϕ. Alternatively, keeping the growing stock constant, the area of an equivalent forest with $\phi = 0$ can be determined. Theoretically, an immature forest can be 'shrunk' in size keeping the growing stock constant until $\phi = 0$. Area to be reduced from the actual forest area to achieve $\phi = 0$ is proportional to ϕ. This hypothetical forest area can be termed the equivalent forest area with $\phi = 0$. If A^{I}_{hyp} denotes the equivalent area of this hypothetical forest and the actual immature forest area is A, then the growing stock can be expressed as:

$$A^{I}_{hyp} \cdot EY_{max} = A \cdot EY_t . \qquad [4.3]$$

Thus, $$A^{I}_{hyp} = A \cdot \frac{EY_t}{EY_{max}} \qquad [4.4]$$

Applying equation [4.1] and considering $\phi<0$ for an immature forest, equation [4.4] can be written as:

$$A^{I}_{hyp} = A \cdot (1+\phi) \qquad [4.5]$$

Reduction in area to achieve $\phi = 0$ as in equation [4.5] is proportional to ϕ.

For an overmature forest, a timber harvest greater than EY_t will increase the value of EY_t in the next period. This will happen until the increased ENF yield equals EY_{max} or until $R_t<R_{mm}$. Thus, an overmature forest can be theoretically 'expanded' by adding land area keeping the growing stock constant until $\phi = 0$. Again as for the immature forest, this hypothetical forest area can be termed the equivalent forest area with $\phi = 0$. Also, as EY_t is constant for a given forest, the growing stock is proportional to the area of the forest. Thus, the land area to be added to an overmature forest to achieve $\phi = 0$ will be proportional to ϕ. Thus, the hypothetical equivalent area, A^{O}_{hyp} for an overmature forest can be defined as:

$$A^{O}_{hyp} = A \cdot (1+\phi) \qquad [4.6]$$

Equations [4.5] and [4.6] are similar in nature and therefore, can be combined by denoting A_{hyp} as the area of the hypothetical forest for either immature or overmature forest. Thus, the following can be written:

$$A_{hyp} = A \cdot (1+\phi) \qquad [4.7]$$

Thus, $A_{hyp}<A$ for an immature forest and $A_{hyp}>A$ for overmature forest and therefore, A_{hyp} can be used to estimate equivalent forest cover in a forest that may have varying degrees of depletion. If the depletion is more or less permanent then ϕ becomes a measure of deforestation.

Strategy to achieve a desired maturity level

As the growing forest is harvested (or not harvested) in a period, the age class structure and the growing stock will change in the next period, and hence, by definition ϕ will attain a new value. Therefore, technically speaking, by controlling the periodic harvests, a desired forest maturity level, ϕ_d, can be attained over time from a known current forest maturity level ϕ. The desired forest maturity index, ϕ_d, so chosen, may encompass the ecological or societal expectations from the forest in terms of the forest's utility to provide timber and other benefits such as wildlife habitat through its age class structure. For example $\phi_d = 0$ represents a forest that has the highest LTSY, and the oldest age class in the regulated forest will correspond to the maximum MAI age. This forest may provide the habitat conditions for wildlife species such as white tailed deer (*Odocoileus virginianus*) and moose that are dependent on the horizontal structure of the forest (Puttock et al. 1996). If $\phi_d = +0.50$ (say) is chosen, then this would mean that the objective is to have older stands but at the cost of a lower LTSY as compared to $\phi_d = 0$ case. This forest may better meet the ecological and biodiversity requirements, but the cost is the reduced LTSY. The criteria for selecting ϕ_d may be scientific or societal, but will not be discussed here.

For both immature and overmature forests three possibilities of ϕ_d, with respect to ϕ, will exist, which can be visualized on an Age-MAI plot, because ϕ will uniquely correspond to a point on the MAI curve. For the immature forest ϕ will correspond to a point on the left from R_{mm} on the MAI curve (Figure 4.1). The difference between the desirable forest maturity level ϕ_d (a chosen constant) and the current forest maturity level ϕ (which may change with time), can be used as a guide to determine the current harvest level. This will ensure that in the next period forest maturity is closer, if not

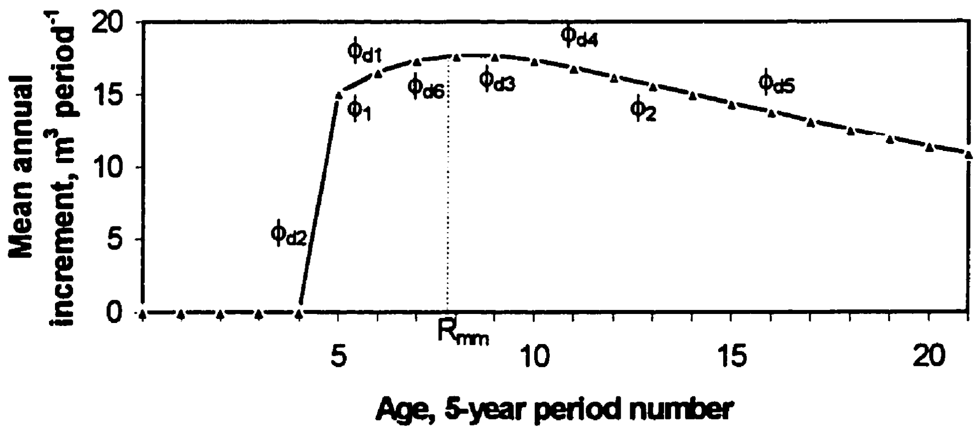

Figure 4.1. Forest maturity index points on MAI curve

equal, to ϕ_d. There are two possibilities for (ϕ_d - ϕ): it can have a negative or a positive value. For each of these, different harvesting strategies can be adopted.

Harvesting strategy-1: A negative value of (ϕ_d - ϕ) signifies that the forest needs to be depleted and, therefore, for ϕ to attain the value of ϕ_d, 'over harvesting' is desirable. Over harvesting refers to a harvest level that is clearly in excess of the current ENF yield. If the harvest is too high, the forest will be depleted more than desired. The highest level of harvest H_1 can be determined by simulating the forest for different ENF rotation ages and ENF yields. H_1 will be the harvest level that depletes the forest just enough for the now modified forest to have ENF yield equal to the ENF yield. This yield corresponds to a forest that has a forest maturity of ϕ_d. Thus, after harvesting H_1, ENF yield from the next period can be harvested in perpetuity maintaining $\phi = \phi_d$. If H_1 is greater than some specified maximum harvest level, H_{max}, a harvest level $H_{11} \leq H_{max}$ can be selected instead. This will, though, delay forest maturity in reaching the desired level. Selection of H_{11} may depend on some other requirement and at this stage this is not a concern. Denoting H(t) as timber harvesting in period t, the harvesting strategy-1 can be written as:

$$H(t)=\begin{cases} H_1 & \text{for} \quad \text{period}-1 \\ EY_t & \qquad\;\; \text{otherwise} \end{cases} \qquad [4.8]$$

Harvesting strategy-2: A positive value of (ϕ_d - ϕ) means that the forest needs to be enriched over time. Therefore, for ϕ to move progressively towards ϕ_d, there should be no harvest or a harvest lower than the current EY_t. This will ensure a net increase in the growing stock in the next period, and ϕ will be closer to ϕ_d. It is possible that a no harvest or some minimum specified harvest, H_{min}, in a period (say T) makes the value of ϕ go over the desired ϕ_d, making (ϕ_d - ϕ) negative. In such a case, a timber harvest H_2, instead of no harvest or H_{min}, is taken, which will deplete the forest just enough for the modified forest to have ENF yield equal to that of a forest with maturity ϕ_d. Thus, after harvesting H_2, ENF yield from the next period can be harvested in perpetuity maintaining $\phi = \phi_d$. When some minimum harvest must be taken, there will be a delay in forest maturity reaching the desired level. Selection of H_{min} may depend on some other strategy to fulfill a need. This harvesting strategy can be summarized as:

$$H(t)=\begin{cases} 0 \quad \text{or} \quad H_{min} & \text{for} \quad (\phi_d-\phi)\geq\varepsilon \\ H_2 & \text{for} \quad 0<(\phi_d-\phi)<\varepsilon \\ EY_t & \qquad\;\; \text{otherwise} \end{cases} \qquad [4.9]$$

where ε is a small positive number.

Harvesting strategies for the six possibilities of ϕ vis-à-vis ϕ_d, three for each of the immature and over-mature forests (Figure 4.1), can be determined as follows:

A. Immature forest:

Forest maturity index, ϕ_1, of this forest is represented on the left of R_{mm} on the MAI curve.

a. Case 1: This is for the desired forest maturity ϕ_{d1} corresponding to a point on the MAI curve on the left of R_{mm} and closer to it than the corresponding point for ϕ_1. In this case (ϕ_{d1} - ϕ_1) is positive and therefore, harvesting strategy-2 applies.

b. Case 2: This is for the desired forest maturity ϕ_{d2} corresponding to a point on the MAI curve on the left of R_{mm} and further away from it than the corresponding point for ϕ_1. In this case (ϕ_{d2} - ϕ_1) is negative and therefore, harvesting strategy-1 applies.

c. Case 3: This is for the desired forest maturity ϕ_{d3} corresponding to a point on the MAI curve on the right of R_{mm}. This means that the desired forest should attain overmaturity in future from the current immature state. In this case (ϕ_{d3} - ϕ_1) is positive and therefore harvesting strategy-2 applies.

B. Overmature forest:

Forest maturity index, ϕ_2, for this forest is represented on the right of R_{mm} on the MAI curve.

d. Case 4: This is for the desired forest maturity ϕ_{d4} corresponding to a point on the MAI curve on the right of R_{mm} and closer to it than the corresponding point for ϕ_2. In this case (ϕ_{d4} - ϕ_2) is negative and therefore, harvesting strategy-1 applies.

e. Case 5: This case is for the desired forest maturity ϕ_{d5} corresponding to a point on the MAI curve on the right of R_{mm} and further away from it than the corresponding point for ϕ_2. In this case (ϕ_{d5} - ϕ_2) is positive and therefore, harvesting strategy-2 applies.

f. Case 6: This is for the desired forest maturity ϕ_{d6} corresponding to a point on the MAI curve on the left of R_{mm}. In this case (ϕ_{d6} - ϕ_2) is negative and therefore, harvesting strategy-1 applies.

Therefore, it can be observed that timber harvest for each period for a forest can be determined by simulating the forest growth over time so as to attain the desired maturity level.

Maturity index for a multispecies forest

A forest usually has more than one tree species. The forest maturity index, discussed so far, refers only to a single species as only one yield function is considered to determine the ENF yield, EY_t. Determination of ϕ for a multispecies forest is of interest. A forest may have species mixed with others or they may be separate, i.e., patches of pure species. However, a forest is typically 'managed' on a stand level, thus stocking is measured at the stand level. The latter will, therefore, be considered. The key input to determine ϕ is the age class distribution and the yield function of the tree species. For the multispecies case there can be two approaches to determine ϕ. It is assumed that the age class distribution of all species and the stocking levels are known from an earlier forest survey. The first method (Method-1) would be to consider all species separately. The yield function of the species must be adjusted to reflect its stocking level. ENF yield, EY_t, for each species can be determined by simulating the forest condition considering various timber harvests. EY_{max} at the stocking level for the species is also known. Thus ϕ for a species can be determined using equation [4.1]. Let us consider η species, and the forest maturity index for each species has been determined to be ϕ_1, ϕ_2, ..., ϕ_η. The stocking level of these η species would correspond to the proportion of the species in the forest. Assuming uniform proportion across age classes for all species as $p_1, p_2, \ldots, p_\eta$, the overall combined forest maturity index, ϕ_0, can be estimated as the weighted ϕ for all species. Thus,

$$\phi_0 = p_1.\phi_1 + p_2.\phi_2 \ldots p_\eta.\phi_\eta \qquad [4.10]$$

Also, $p_1 + p_2 + \ldots + p_\eta = 1.0$.

The second approach (Method-2) would be to consider the weighted yield function of all species. The weights would equal the stocking level of all species in the forest. With the modified yield function, and assuming the same age class distribution for all species, EY_t and EY_{max} can be estimated, Thus, the forest maturity index for the whole forest, ϕ_0, can also be estimated. In this case, all future timber harvest will be determined by ignoring the tree species distinction. That is, the forest is considered to have a single notional species and its yield function is the weighted yield function. This method is an easier way of handling the multispecies situation than method-1. However, a shortcoming of this method, due to the distinct yield functions of different species, is that the maturity level of individual species will not be discernible. For example, one species may have overmaturity while the other species may be immature at the whole forest level. Also, Nautiyal and Innes (1984) showed that in a mixed even-aged forest management, faster growing tree species should be given more importance if the discount rate is high. The rotation age of a mixed forest, therefore, should change according to the value of the discount rate. The forest management practice may need to be tuned to accommodate these aspects and to achieve a long term objective of species management, such as in a shelterwood management.

As an illustration, consider a forest with age class distribution as in Table 4.1. Assume that this forest consists of jack pine (*Pinus banksiana*) site class II at 60%

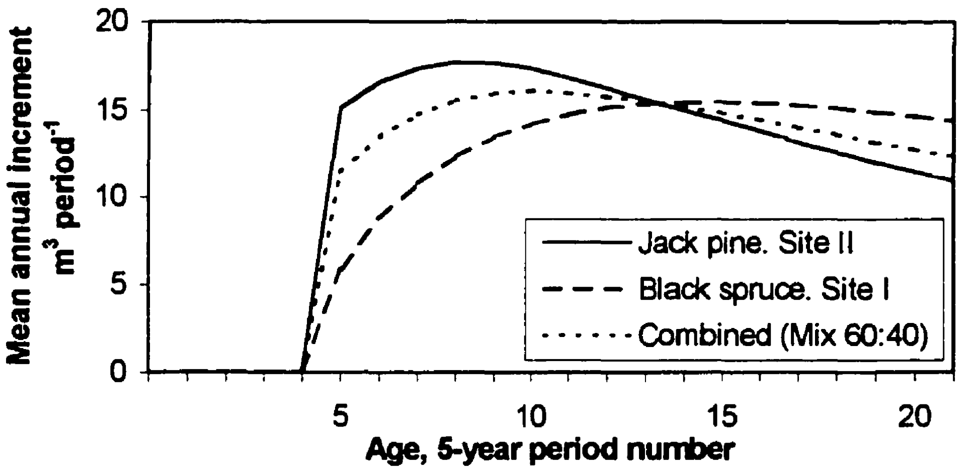

Figure 4.2. Mean annual increments for mixed species

stocking and black spruce (*Picea mariana*) site class I at 40% stocking. The overall forest maturity index considering the two methods described above, yields ϕ_0 equal to -0.079 by method-1 and -0.119 by method-2 (Table 4.2). The two methods give different values of ϕ_0 because the yield curve, and therefore, the MAI curve, for the two species are not symmetric to each other. This results in the weighted MAI curve having a different shape than either of the two (Figure 4.2). Furthermore, if the age class distribution of all tree species in the forest is not the same then method-2 cannot be applied.

As an illustration, an example in the following section describes how a desired forest structure defined by $\{\phi_d, v_d\}$ can be achieved through an appropriate timber harvesting scheme.

An example

For the sample forest consisting of jack pine site class II and age class distribution as shown in Table 4.1, the forest maturity index is ϕ_t = -0.021. This is an immature forest as its maturity index is negative. If this were a normal forest or close to one, with ten patches, its forest stand diversity index, ν, would be 0.00896. For this purpose, assume that the forest survey has indicated that this 1000 ha forest has 289 patches and therefore, its forest stand diversity index, ν, is 0.25. This indicates the unevenness of the forest on a 0-1 scale; the forest stand diversity index of a hypothetical normal forest can be used for comparative purpose. Also, assume that it is desired that this forest should have up to 14 age classes and the resulting long term sustainable yield (LTSY) of timber at 15000 m^3 $period^{-1}$ at this rotation age is acceptable. This will correspond to a forest maturity, ϕ_d, equal to +0.1519. The decision of having a rotation age equal to 14 (66-70 years) may not entirely be based on economic optimization. For example, a decision to have some minimum wildlife population density that is dependent on the age class distribution of the forest may force this or some other acceptable rotation age. If a relationship between age class structure and wildlife population density were available, then a trade-off analysis of timber harvest versus wildlife population density can be done.

Also, consider that it is desirable to increase the forest stand diversity index to 0.60 (say) (= ν_d) through appropriate timber harvesting practice and regeneration of the harvested areas. Consideration of some nontimber values may decide the value for this forest stand diversity index. A forest stand diversity index of 0.60 would correspond to a weighted number of patches equal to 917 and the average patch size will equal 1.09 ha. The focus here is not how to decide the value of this rotation age or the forest stand diversity, but to show strategies to achieve the desired forest structure. However, any of the spatial methods such as GISFORMAN (Baskent and Jordan 1991) or LANDMAN (Baskent 1997) may be used to determine patches to be harvested.

The current ϕ is equal to -0.021 and the target ϕ_d of +0.1519 means that the current immature forest is to attain overmaturity in time. The objective now is to adopt a

Table 4.1. Age class distribution—sample forest

Age class, years	Period	Area, ha	Age class, years	Period	Area, ha
Barren	0	141			
0 - 5	1	98	55 – 60	12	0
5 – 10	2	75	60 –65	13	0
10 – 15	3	121	65- 70	14	0
15 – 20	4	165	70 – 75	15	0
20 – 25	5	115	75 – 80	16	0
25 – 30	6	112	80 – 85	17	0
30 – 35	7	45	85 – 90	18	0
35 – 40	8	55	90 – 95	19	0
40 – 45	9	73	95 – 100	20	0
45 – 50	10	0	100 +	21	0
50 – 55	11	0		TOTAL (ha)	1000

Table 4.2. Overall forest maturity index for multispecies

	Method 1 (Yield functions of species considered separately)		Method 2 (Combined yield function)
	Jack pine (60% stocking)	Black spruce (40% stocking)	Jack pine (60%) and black spruce (40%)
R_{mm}, periods	8	15	10
R_t, periods	6.9292	7.3396	7.0891431
EY_{max}, m^3	10612.5	6186.667	16090
EY_t, m^3	10385.857	4540.4	14809.947
$\phi_{species}$	-0.0214	-0.266	-
ϕ_0	-0.119		-0.079

timber harvesting scheme that leads to attaining the desired forest maturity. In this case the objective involves crossing the 'hill', that is, the age at maximum MAI; and, harvesting strategy-2 as described earlier for case 3 must be used. This strategy entails that there be no harvesting until $0 < (\phi_d - \phi) < \varepsilon$, where ε is a small positive number. Thereafter, by simulating the forest, a harvest H_2 can be determined that results in the modified forest attaining the desired ENF yield and thus, the desired forest maturity. The simulation results are shown in Table 4.3. The successive changes in ENF yield and the forest maturity index as a result of lower harvests is graphically shown in Figure 4.3.

Let us now consider the forest stand diversity index. The current stand diversity index is 0.25 and this is to be increased to 0.60. The current average patch size is 3.46 ha. Through appropriate timber harvesting and regeneration over time, the average patch size is to be reduced to 1.09 ha. This means that the timber harvesting should, preferably, be in patch sizes not exceeding 1.09 ha on an average. The best strategy to achieve the desired forest maturity index as indicated in Table 4.3, suggests no harvesting in the first three periods. From a forest stand diversity perspective this is not desirable and there should be some timber patch harvesting to increase the number of patches in the forest. This can be achieved in many ways. Assuming that the timber harvesting is approximately in 1 ha patches, one of the many harvesting strategies that achieves the desired forest maturity and stand diversity indices, is presented in Table 4.4. The desired forest structure is achieved in period 12 after harvesting. Obviously, attaining ϕ_d is relatively easier and faster than attaining v_d.

Discussion and conclusion

A desired forest structure can be achieved over time through a properly designed harvesting scheme, considering quantity of timber and size of harvested areas. The timber harvesting scheme does not consider any explicit value of a nontimber product. Nor does it consider parameters such as, price, cost, discount rate, or planning period, as is done in most of the timber optimization techniques. However, current harvesting cost can be considered when evaluating harvesting options to achieve a desired state of the forest. If the forest remained as expected in the next period, then the timber harvesting would be the same as planned for the period. Most of the mathematical optimization methods would give a different solution for an optimization run in the next period considering no unexpected changes in the forest. In this approach such an anomaly is avoided because of the attempt to reach a desired state of the forest that will be good for obtaining many products instead of optimizing timber flow over a time period. Another advantage of making an operational plan using this concept of forest structure is that the effects of clear-cuts, large or small, can be quantified through the forest stand diversity index, ν. Development of refined wildlife habitat models, with forest structure as input, will greatly help in understanding timber and nontimber trade-offs. This will be discussed in the next chapter.

Table 4.3. Best strategy to achieve the desired ϕ_d for the sample forest of jack pine, site class II (R_{mm} = 8 periods; EY_{max} = 17687.5 m^3 $period^{-1}$; and ϕ_d = +0.1519)

Time elapsed, period	Actual harvest, H(t), m^3 $period^{-1}$	ENF rotation after the harvest, R_t, Periods	ENF yield after the harvest, EY_t, m^3 $period^{-1}$	Forest maturity index, ϕ	$(\phi_d - \phi)$
0	-	6.9292854	17309.76	-0.021	0.1729
1	0	8.8033	17670.3906	0.0009	0.1510
2	0	11.03	16798.2774	0.0502	0.1017
3	0	13.58	15247.4227	0.1379	0.0140
4	12600	14	15000	0.1519	0
5	15000	14	15000	0.1519	0
6	15000	14	15000	0.1519	0

Table 4.4. Revised strategy to achieve the desired ϕ_d and ν for the sample forest jack pine, Site class II (R_{mm} = 8 periods; EY_{max} = 17687.5 m^3 $period^{-1}$; and ϕ_d = +0.1519)

Time elapsed, period	Actual timber harvest H(t),		ENF rotation after the harvest, R_t, periods	ENF yield after the harvest, EY_t, m^3 $period^{-1}$	Forest maturity index, ϕ	Weighted number of patches, N_w	Forest stand diversity index, ν
	Volume, m^3	Area, Ha					
0	-	-	6.9292854	17309.76	-0.021	289	0.25
1	3500	22.0126	8.4155	17678.24	0.0005	311	0.266
2	3500	20.1729	10.11	17286.35	0.022	331	0.281
3	3500	18.9189	12.06	16169.9834	0.0857	350	0.294
4	3600	18.8486	14.00	17687.5	0.1519	369	0.307
5	15000	78.6138	14.00	17687.5	0.1519	447	0.36
6	15000	80.399	14.00	17687.5	0.1519	527	0.409
7	15000	78.71	14.00	17687.5	0.1519	605	0.453
8	15000	77.12	14.00	17687.5	0.1519	682	0.493
9	15000	76.89	14.00	17687.5	0.1519	758	0.531
10	15000	73.89	14.00	17687.5	0.1519	831	0.564
11	15000	73.22	14.00	17687.5	0.1519	904	0.59
12	15000	71.57	14.00	17687.5	0.1519	917	0.60

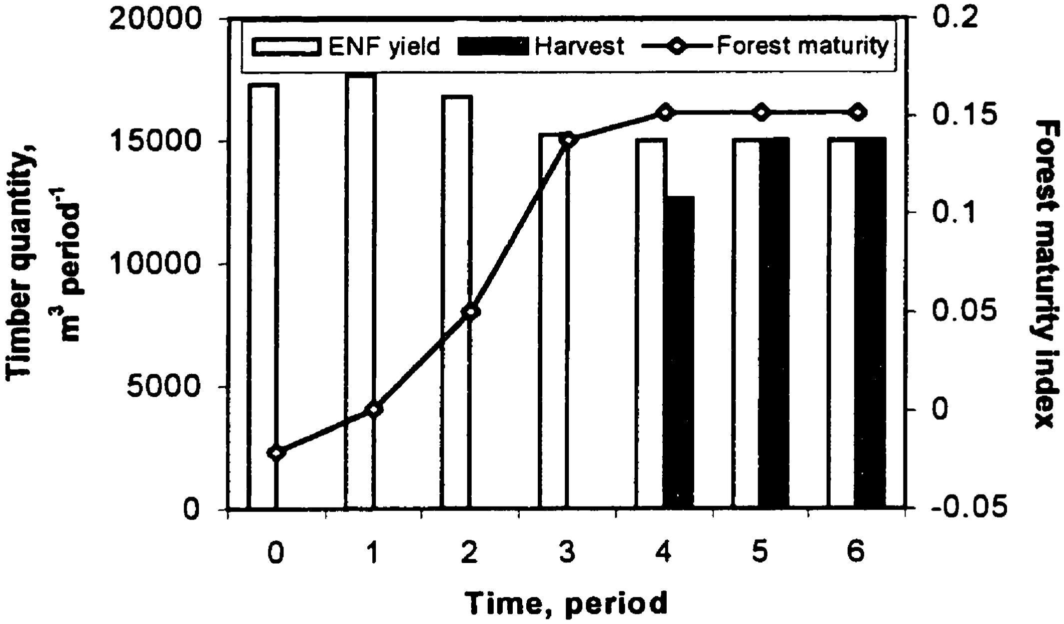

Figure 4.3. Best strategy to achieve the desired forest maturity index

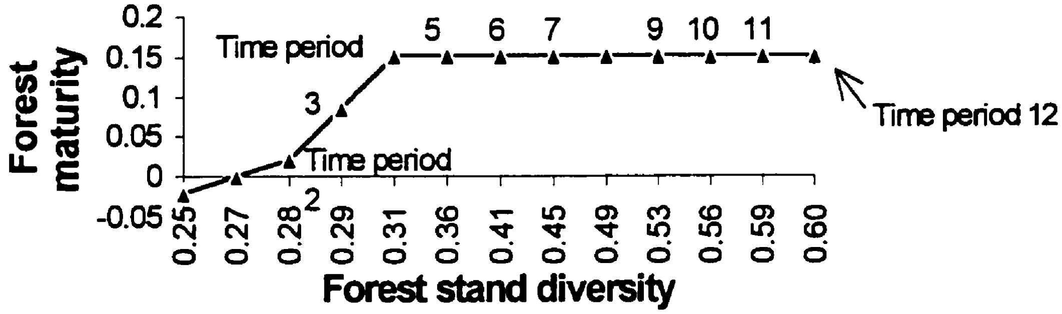

Figure 4.4. Forest stand diversity and maturity indices over time

CHAPTER 5

Modeling dynamic wildlife population density in a forest: A case of moose (*Alces aices*)

Introduction

Our understanding of the quantifiable relationships among the many products of a forest is quite limited (Gregory 1972, Nautiyal 1988). Lack of such relationships forces us to make *ad hoc* assumptions about the contribution of a forest product, mostly nontimber, in an optimization model (Davis and Johnson 1987). Availability of quantifiable relationships among the many outputs of the forest are important for the development of any integrated forest planning, as proposed by Heilman (1990) and Kimmins (1992). These relationships can be static or dynamic. But the latter are more useful because forests are essentially dynamic systems; even with no human intervention they change due to growth and loss.

Attempts have been made to develop static models, referred to as habitat models, that relate a wildlife population to its habitat (Naylor 1991). Habitat models, without accounting for all factors that determine population density, provide a qualitative measure of the potential of an area to support a wildlife species or species group. Habitat Suitability Indices (H.S.I.) (Naylor 1991), which are also habitat models, attempt to rate the perceived ability of habitat to meet wildlife requisites. Naylor (1991) estimated that over 300 H.S.I. models are in some stage of development. These models consider the characteristics of habitats to estimate the population potential but do not take into account the current population density and are useful in developing conducive habitat components in a managed forest. Static habitat models can be turned into dynamic habitat models if a method is developed to first quantify the habitat components, and then to mathematically track these habitat components over time. This, however, is difficult due to the qualitative nature of habitat models and the problems of relating management actions to habitat components.

Though a challenging task, development of dynamic models of wildlife populations that relate them to a forest management action, such as timber harvesting, would be particularly useful. With such relationships, timber harvests can be compared with nontimber benefits such as wildlife density. Because of the complications involved in such models they often tend to become an exercise in manipulating mathematical equations if a purely theoretical perspective is taken (Hastings 1997). On the other hand, many scholars who have attempted to develop empirical models to explain a complex biological phenomenon have remained confined to deterministic models (Belovsky 1986, Puttock et al. 1996). Such deterministic models may well serve the purpose of predicting populations that remain reasonably high at all times. However, in situations where populations can reach low levels, stochastic models can provide useful insights especially in the estimation of extinction probability (Nisbet and Gurney 1982). Further, to keep a population model mathematically tractable, assumptions about the components determining the population must be made. The validity of the model, therefore, would depend on the relevance of these assumptions to reality. Also, the efficacy of a model depends on how well it is able to look into the future (Pielou 1977).

In this chapter a model of dynamic relationship between timber output and a wildlife population density has been developed. A wildlife population density depends on the character of a forest, and changes as the forest undergoes a transformation with time. This fact is modeled, by taking into account that timber harvesting alters the environment for a wildlife, which in turn affects the population potential of a forest.

As will be discussed in later sections, the well-known logistic equation has been considered as the basis of population change. The carrying capacity concept (Crête 1989) in this logistic model has been modified to reflect the dynamic nature of the environment that affects the potential of a forest to support wildlife. With the introduction of dynamic population potential—similar in concept to carrying capacity in the logistic equation—the mathematics involved becomes quite complex. Therefore, the population potential is so defined that its upper bound is the carrying capacity; any unfavorable environmental factor will reduce the population potential to below the carrying capacity. To be able to still draw meaningful inferences from the model this chapter develops difference equations for prey and predator, and simulates the changes in population at discrete times. The simulation procedure is facilitated if the population potential is constant in the intervening period and changes only at discrete times[1]. Since the focus of this study is a given forest, it has been assumed that there is no immigration and emigration of species. Birth rate has been considered density dependent and the death rate is severely density dependent in line with the logistic equation (Clark 1976). The simulation, considering the modified logistic equation, presents deterministic as well as stochastic behavior of the wildlife population and thus provides an insight into the underlying mechanisms.

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[1] To show when a continuous equation can be written as a difference equation consider a continuous equation such as $dY/dt = f_1(Y, X_i)$, where Y is a time dependent decision variable, i is number of the independent variable and X_i are independent variables. If X_i are constant at time t and are replaced by K_i^t then this equation can be written as $dY/dt = f_2(Y, K_i^t)$ and its solution can be obtained relatively easily. Now assume that the last equation has a continuous solution of the form:

$$Y(t) = f_3(K_i^t, (t-t_0), Y(t_0)),$$

where $Y(t_0)$ is some initial value of Y(t) at time t_0. As K_i^t remain constant in the time interval [t, t+1], the above continuous solution to Y(t) can be written as a difference equation $Y(t+1) = f_4(K_i^t, Y(t))$. Functions f_1, f_2, f_3, f_4 may have any mathematical form. Thus, as long as a solution of the f_3 form is obtained, decision variable Y(t) can be truly determined for X_i at discreet times without obtaining a continuous expression for Y(t).

A home range of a wildlife species consists of various habitat components needed for food, cover, reproduction, etc. that are not evenly distributed. An important aspect of a wildlife population is the spatial dimension of its habitat which is affected by the geographical location of various habitat components. Proximity of different habitat components to each other may determine the movement patterns across these components and may affect the birth and predation rates. Therefore, the population potential of wildlife in a forest will depend, amongst other factors, on the geographical shape of the forest. One way of doing this is to factor the population potential based on a shape parameter (Forman 1995). The location aspects of birth and mortality are captured in the concept of population potential of the forest that has been used in the model.

Scientific knowledge, besides having observational data, is also about having a theory. The theory can be expressed as a hypothesis, a conceptual scheme or a model. The interaction between theory (how it is expected to work) and observational data (how it actually works) leads to progress from qualitative to quantitative (Thornley and Johnson 1990). This chapter takes a small step forward in that direction.

The proposed model has been developed in the context of central Ontario where timber and nontimber conflict in forest management is most prominent. Its stage by stage construction is described in the following sections.

Study area and species considered

The eastern, central and southern regions of Ontario and Quebec have the highest human population density in Canada. As a result, the mixed conifer and hardwood forests in this region are under public pressure to provide multiple outputs sustainably (Anon. 1993b, Anon. 1994). Timber revenues from these regions are significant (Anon.

1993a), and therefore intensive management can be practiced. In view of these observations the Great Lakes-St. Lawrence Forest Region of Ontario (Figure 5.1), specifically Algonquin Park, was selected for developing the model. Algonquin Park is managed for multiple use and its management plan reflects the public feelings about the forest (Anon. 1994).

Algonquin Provincial Park is situated in central Ontario (45^0 39'N, 78^0 39'W) and occupies approximately 7685 km^2 with irregular topography over granitic bedrock, with mixed forests and numerous lakes. The area has forest types found in the Algonquin-Pontiac Section of the southern Great Lakes-St. Lawrence Forest Region (Farrar 1995). The forests of the Park are primarily mid-to-late successional. The mixedwood forest in the Park has approximately 22%, 38% and 35%, respectively, in early, middle and late successional stages by Working Group[2] for the complete management unit (Anon. 1994). Hunting of moose was not permitted in the Park before 1991; after that, Golden Lake First Nations Band has been permitted to hunt moose. Moose is one of the most studied ungulates in Ontario and extensive moose population data and Forest Resource Inventories (F.R.I.) are available. The Park is managed for multiple uses including camping, wilderness, canoeing and hiking, wildlife and timber production. Commercial timber production in the Park in 1993/94 amounted to approximately 416,500 m^3 at shipment value of $240 million (Algonquin Forestry Authority 1994a). The Algonquin Forestry Authority (1994b) report states that the regional target for the Algonquin Park Management Unit is to maintain present diversity of forest cover. In addition, the target is to produce a continuous supply of up to 630,000 m^3 of raw material for the forest industry by the year 2020.

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[2] Working Group is an aggregate of stands having the same predominant species and managed under the same rotation and broad silvicultural system (Anon. 1986).

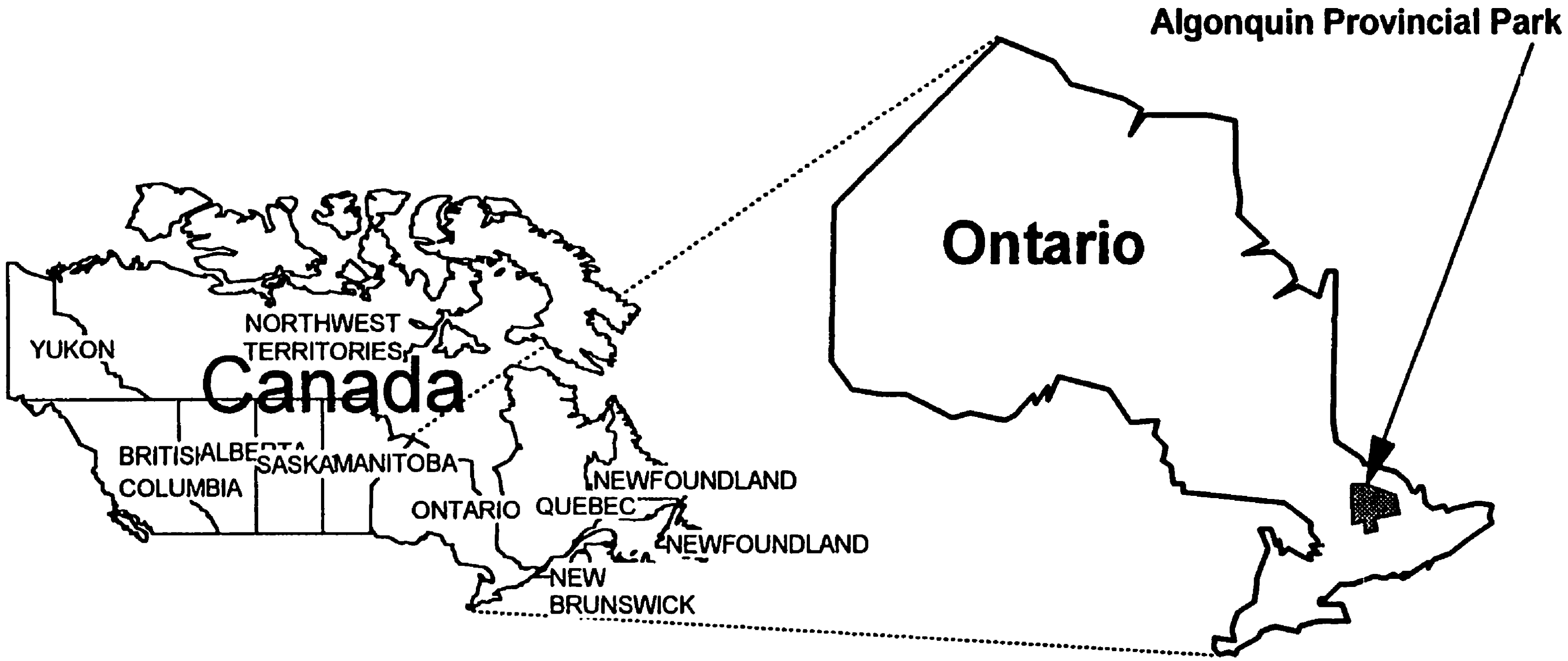

Figure 5.1. Location of Algonquin Park (Anon. 1986)

Moose as the representative species of Ontario has been selected because Baker and Euler (1989) contend that provision of moose habitat might simultaneously provide habitat for approximately 70% of all vertebrates in Ontario. For example, moose habitat management may also affect the population of gray wolf (*Canis lupus*), black bear (*Ursus americanus*), beaver (*Castor canadensis*), and many bird species. Moose is potentially useful as an umbrella species and can be harvested. Moose is a large ungulate with a home range of 5-10 km^2. The physical size and abundance of moose permit easy aerial identification and it can be more conveniently identified in winter than any other wildlife species in the area. Bisset (1987) reported that moose hunting in Ontario contributed approximately $34 million in Provincial revenues. In addition, the fact that moose largely depends on horizontal structure of the forest helps development of the proposed model in this chapter.

Habitat and population densities of moose are affected by variations in climate, landform, and vegetation (Telfer 1984). Food availability, predation, escape cover, and environmental conditions determine the pattern of habitat use by moose (Peek et al. 1976, Mastenbrook and Cumming 1989). Areas that offer a wide variety of plant types and ages with mature conifer stands for cover, and open areas for food, are preferred (Peek et al. 1976, Leptich and Gilbert 1989). In the summer nutritional demand is greatest as the animals accumulate energy for winter (Belovsky and Jordan 1978). Successional species such as aspen, poplar and white birch found in disturbed and recently harvested areas are the preferred forage in spring and in summer (Peek et al. 1976, Addison et al. 1980). In mid- to late winter moose appear to be forced by weather conditions to use mature, dense, conifer-dominated stands.

Modeling moose population

Timber harvesting guidelines for the study area reflect the current management strategies for the provision of moose habitat in the Great Lakes-St. Lawrence Forest Region of Ontario. These guidelines identify specific aspects of habitat such as mineral licks, calving sites, and feeding areas, and outline timber management strategies (Anon. 1988). Habitat models to predict responses of moose population to habitat abundance have been proposed (Allen et al. 1988). The approach considered is that the nature of habitat supporting wildlife is dynamic and therefore population density will change with time, not only because populations build up and fall over time but also because the potential density varies with the variation in habitat.

From an initial level, a wildlife population will grow or decline according to the rates of birth and death. The simplest expression for this in a time dependent fashion, ignoring the effects of immigration and emigration, is:

$$\frac{dN_1}{dt} = B(N_1) - D(N_1) \qquad [5.1]$$

where N_1 is the population of the wildlife at time t, and B and D are the birth and death functions dependent on the current population N_1. Birth function, B, can be considered density dependent and can be expressed as $B(N_1) = a.N_1$. Death function can be considered severely density dependent and can be expressed as $D(N_1) = b.N_1^2$. Thus, equation [5.1] can be written as

$$\frac{dN_1}{dt} = aN_1 - bN_1^2 \qquad [5.2]$$

Alternatively, [5.2] can be written as:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) \qquad [5.3]$$

such that $r_1 = a$, and $K_1 = a/b$. Equation [5.3] is the well-known logistic equation, and is also referred to as the Verhulst-Pearl equation (Nisbet and Gurney 1982). This form of equation indicates that the population will reach the value of K_1 as $t \to \infty$, when dN/dt equals zero. The parameter K_1 is known as the carrying capacity, indicating the maximum population that the environment can support, and r_1 is termed the intrinsic birth rate.

Situations more complex than the simple birth-death process, such as the one depicted by equation [5.3], become increasingly difficult to handle. Further, environmental factors that affect wildlife population are complex in nature and lead to intractable mathematics when incorporated in the logistic equation which is differential in nature as presented in equation [5.3]. Therefore, it would be appropriate to use a difference form of this equation. This is particularly suitable in forestry where tree age class is considered discrete. A model based on a discrete equation can be easily simulated.

Considering time increments in steps of Δt instead of dt, equation [5.3] can be approximated as:

$$\frac{\Delta N_1}{\Delta t} = r_1 N_1 \left(1 - \frac{N_1}{K_1}\right) \qquad [5.4]$$

For most purposes, time can be considered to increase in steps of 1. Thus, Δt will equal 1 and equation [5.4] can be re-written as a difference equation:

$$N_1(t+1) = N_1(t) + \Delta N = N_1(t) \cdot \left[1 + r_1\left(1 - \frac{N_1(t)}{K_1}\right)\right] \qquad [5.5]$$

For small values of r_1, $N_1(t+1)$ will approach K_1 as $t \to \infty$. However, for higher values of r_1, $N_1(t+1)$ for some $N_1(t)$ lower than K_1, may exceed K_1 making the term $[1 - (N_1(t)/K_1)]$ negative. Thus, in the next period wildlife population, $N_1(t+2)$, will become less than K_1.

Hence, for higher values of r_1, $N_1(t)$ will oscillate around K_1 and the amplitude of oscillation will depend on the value of r_1. The primary reason for this oscillation, for larger values of r_1, is the assumption of constant rate of change in N_1 over time [t, t+1]. The oscillation in N_1 purely because of a high intrinsic birth rate, r_1, does not seem to reflect the logistic process, described by equation [5.3], well. This anomaly in the behavior of N_1 can possibly be eliminated if the differential equation [5.3] is solved for N_1.

Considering r_1 and K_1 as constants, equation [5.3] for the initial condition $N_1 = n_0$ for $t = t_0$ yields:

$$N_1(t) = \frac{K_1}{1 + \frac{K_1 - n_0}{n_0} . e^{-r_1(t-t_0)}} \qquad [5.6]$$

This can be re-written as the following exact difference equation:

$$N_1(t+1) = \frac{K_1}{1 + \frac{K_1 - N_1(t)}{N_1(t)} . e^{-r_1}} \qquad [5.7]$$

Equation [5.7] can be used as a difference equation to simulate the values of N_1 for subsequent time periods.

Variable environment

Fluctuations in wildlife populations, due to demographic stochasticity[3], are very small for the majority of natural populations (Chamov and Schaffer 1973, Gurney and Nisbet 1978, Nisbet and Gurney 1982). Population fluctuations driven by environmental

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[3] Demographic stochasticity refers to fluctuations arising because population changes in the discrete number of members are caused by a succession of individually unpredictable births and deaths.

stochasticity[4], except for the most stable environments, will overshadow the effects of demographic stochasticity (Nisbet and Gurney 1982); the effects of a variable environment on wildlife population fluctuations over time are, therefore, included in this model.

Most studies dealing with the effects of environmental variability on wildlife population have focused on heuristic approaches by allowing a parameter in the deterministic equation to 'wobble'. The resulting population fluctuations are then studied. This approach is useful to gain insights into the consequences of environmental variability. However, assumption of a 'wobbly' nature of variation brings in severe limitations. For example, a sinusoidal variation in a parameter is sure to result in a more or less similar variation in the population. Thus, any analysis of population dynamics based on this behavior becomes suspect. Because of these difficulties a different approach to address the question of environmental variability has been taken in the proposed model. Population at discrete times assuming environmental variations that depend on forest age class structure, predation levels, and hunting has been simulated. In this simulation the logistic equation for the population has been retained, except that the carrying capacity, K_1, has been made a function of various environmental components. The approach followed is quite general and can be applied to any other herbivore that is sensitive to the age class structure of the forest, as will be discussed in the next section.

Population potential

The variability in the environment that affects growth or decline of a wildlife population can be natural or human made. In managed forests timber harvesting is a

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[4] Environmental stochasticity refers to aperiodic environmental variation and also to the resulting population fluctuations.

major activity and a cause of environmental variability (Kimmins 1992). McLeod (1997) argues that the concept of carrying capacity has meaning in deterministic and slightly variable environments. In a highly variable system the deviation from equilibrium is expected to be high and, therefore, the concept of carrying capacity will have little meaning. McLeod (1997) contends further that carrying capacity can be considered as a short-term potential density rather than a long-term equilibrium density. However, if for any reason the variable environment attains a steady state, or some periodicity then equilibrium population density, re-defined to accommodate periodicity, will be reached over time. For any logistic process, fluctuating environment can be modeled by appropriately defining the birth and the death rates, B and D, respectively, in equation [5.1]. This is what has been done in this model by allowing K_1 in equation [5.3] to fluctuate with time (Nisbet and Gurney 1982, Renshaw 1991). In the rest of this section, a time dependent expression of K_1 has been developed.

Caughley (1976) presented an interactive model of growth, such as equation [5.1], depicting dependence relationship of a large herbivore and its forage resource. He proposed that when a herbivore population is introduced into a hitherto unused habitat, its population grows until forage biomass diminishes and changes in composition with time. Over a sufficiently long period a dynamic equilibrium is reached between herbivore density and forage resources. The population K_1 at this equilibrium is called the carrying capacity (Macnab 1985). In most of Canada and particularly in Quebec, however, moose does not seem to follow the interactive model of growth (Crête 1989), apparently because of the presence of two major predators of moose in North America: the black bear (*Ursus americanus*) and the gray wolf (*Canis lupus*). Messier and Crête (1985), and Crête (1987) concluded that even without human hunting, because of predation, moose density tends to stabilize much below carrying capacity. Empirical evidence from available case histories (van Ballenberghe 1987) suggests that when alternative prey is scarce, the naturally regulated bear/wolf/moose systems produce population equilibria far below the carrying capacities set by moose-forage interactions. In one interesting finding (Cushman 1985), it has been reported that at Isle Royale, in the absence of any predator and with luxuriant browse, the moose population increased sharply from an initial immigration. Soon, due to over browsing, its population dropped significantly, thus indicating an intricate relationship between browse and population growth. With the arrival of wolves on Isle Royale, the moose-wolves interaction resulted in stable populations over time; moose population remaining much below carrying capacity level. Likewise, Ballard et al. (1990) stated that most of the studies of moose suggest that predation can, and often does regulate moose population growth at levels below food carrying capacity. Stephens and Peterson (1984) and Wilton and Garner (1991) emphasize that complex relationships between predators of moose, including anthropogenic influences, are important in determining population levels. Thus, it can be said that a wildlife population potential is dependent on predation rate; a higher predation would mean a lower wildlife population density in a forest. Mathematically it can be stated that the population potential will equal the carrying capacity less the unfavorable environmental factors, of which predation is a component.

Salwasser (1985) emphasized that timber and wildlife interactions are affected by four major characteristics of the forest. First is the distribution of cover types and successional stages. Second, the proportions of forest types and stages play an important role for cover from predators. Third, the geography of individual stands provides for the habitat needs within the home range. Fourth, the floristic and structural characteristics of individual stands are important for the browse and reproduction needs of a wildlife species. In a short run, physical parameters such as soils, climate, elevation, or slope, are not under the control of a natural resource manager except for some long term impacts, e.g., prolonged fertilization or drainage; or degradation of a site leading to loss of nutrients, soils, etc. The manager also has virtually no control over the potential richness of cover types. A forest manager through silvicultural practices, however, can control successional stages of cover types present. Old growth, for example, can be eliminated, and the number of successional stages can be increased through regeneration, stand tending and harvesting. Thus, any timber harvest will affect the environment for wildlife and therefore, the population potential of a forest.

The size of a stand, and its location relative to other stands, can determine whether moose habitat needs are met within its home range area. Composition and structure of vegetation is a major determinant of habitat suitability (Holt et al. 1995) and thus, as expected, the empirical habitat model developed by Puttock et al. (1996) has a significant contribution from stand composition and structure. They proposed a linear relationship of moose density as a function of various habitat characteristics. In their study Puttock et al. (1996) identified moose habitat characteristics, including stand characteristics such as age class, stocking level, canopy closure and stand type. Other characteristics generally not under the control of a natural resource manager, such as muskeg area, treed wet-lands, water area and snow depth, were also considered to develop a linear relationship for moose density and these factors. Thus, if noncontrollable habitat characteristics are assumed to remain constant, then moose population potential can be considered to depend on stand characteristics represented by the stand area in different age classes.

In view of the above, the term K_t in the logistic equation [5.3] has been re-defined, without loss of generality, to mean population potential dependent on environmental factors. Thus, the wildlife population density will always tend to reach this potential, which may keep changing with time. This also means that the population density equilibrium as a steady state, stable cycle, or limit cycle, but actually almost periodic or recurrent, over time can be reached depending on the dynamic behavior of the environmental factors affecting K_1. Thus, we can now define a dynamic K_{1t} as the population potential that is expected to be lower than the 'carrying capacity'. Hunting by humans, at times, is a major cause of moose loss (Boutin 1992). Therefore, introduction of a hunting component, H_t, in the definition of K_{1t} is desirable. Thus, factors that will affect K_{1t} can be summarized as:

a. theoretical carrying capacity of the forest, K_{1m};

b. (i) forest age class structure providing food and reproduction opportunities, $f_5(T_i)$

   (ii) predation effect, consisting of cover available and predation, $f_6(T_i, p_1, N_2)$

where f_5 and f_6 are mathematical functions, i represents habitat, T_i is the proportion of forest area in habitat i, $(1/p_1)$ is prey 'efficiency' in evading predators, and N_2 is the predator population density in the forest; and

c. hunting by people, H_t.

Therefore, an expression for K_{1t} can be written as follows:

$$K_{1t} = f_7(K_{1m}, f_5, f_6, p_1, N_2, H_t)$$

Or, $$K_{1t} = f_8(K_{1m}, T_i, p_1, N_2, H_t)$$

where f_7 and f_8 are mathematical functions. Considering that predation, represented by $p_1 \cdot N_2$, and hunting by humans do not affect the forest age class structure and are independent of each other, but directly affect the 'carrying capacity' by effectively lowering it to $(K_{1m} - p_1 \cdot N_2 - H_t)$, the above equation can be modified to:

$$K_{1t} = f_9[(K_{1m} - p_1 \cdot N_2 - H_t), T_i] \qquad [5.8]$$

where f_9 is some mathematical function.

If the variables, K_{1m}, T_i, N_2, and H_t, in equation [5.8] are assumed to be statistically independent, then the functional form of f_9 and values of coefficients of the variables in equation [5.8] will always remain valid. This assumption may be difficult to maintain in general, but it can be assumed that the variables remain statistically independent in the range they occur in the simulation. Thus, for the simulation, the coefficients will remain constant. Expression for K_{1t} from equation [5.8] can be substituted in the logistic equation [5.3]. If K_{1t} is considered a continuous function, then a mathematical solution for N_1 from equation [5.3] becomes intractable. Though, not an easy task, the relationship of population potential of a forest, K_{1t}, with habitat components can be empirically estimated from the population and habitat data and thus, functional form f_9 could be known. For the estimation of K_{1t}, population at the time of data collection can be considered at its potential. Further, by considering K_{1t} as discrete and as remaining a constant in the time interval [t, t+1], difference equation [5.7] can be used to simulate the population dynamics of moose functional form f_9 provided that population dynamics parameters r_1, K_{1m}, p_1, and N_2 can be estimated.

Predator population dynamics

The logistic equation for predator, similar to equation [5.3], can be written as:

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{K_2}\right). \qquad [5.9]$$

An expression for K_2 considering it dynamic can be written as:

$$K_{2t} = K_{2m} + p_2 N_1 \qquad [5.10]$$

where K_{2m} is the predator population potential in the absence of its prey; and p_2 is the predator "efficiency" in killing its prey.

Assuming K_{2t} as a constant in the time interval [t, t+1], equation [5.9] will result in:

$$N_2(t+1) = \frac{K_{2t}}{1 + \frac{K_{2t} - N_2(t)}{N_2(t)} . e^{-r_2}} \qquad [5.11]$$

Equation [5.11] will be applied to simulate changes in predator population.

Equilibrium populations and stability

Before making an attempt to simulate the population of prey, N_1, and predator, N_2, it will be useful to study the stability of the two-species model, equations [5.3] and [5.9]. To analyze the equilibrium state, consider equations [5.3] and [5.9] as:

$$\frac{dN_1}{dt} = r_1 N_1 \left(1 - \frac{N_1}{a_1 - b_1 N_2}\right) \qquad [5.12]$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(1 - \frac{N_2}{a_2 + b_2 N_1}\right) \qquad [5.13]$$

where a_1, a_2, b_1 and b_2 are constants. In the population simulation, discussed later, a_1, a_2, b_1 and b_2 remain constants in the time interval [t, t+1]. Thus, conclusions in this section regarding equilibrium states would still be valid, but rather than being absolute the equilibrium states would be dynamic depending on the values of a_1, a_2, b_1 and b_2.

The equilibrium populations for the system of equations [5.12] and [5.13] will correspond to the condition:

$dN_1/dt = dN_2/dt = 0.$

Equations [5.12] and [5.13] can then be solved to obtain:

$$N_1^* = \frac{a_1 - a_2 b_1}{1 + b_1 b_2} \qquad [5.14]$$

$$N_2^* = \frac{a_2 + a_1 b_2}{1 + b_1 b_2} \qquad [5.15]$$

where N_1^* and N_2^* are the equilibrium prey and predator populations, respectively. To study the dynamics and stability of N_1 and N_2, the following observation can be made:

i) $dN_1/dt > 0$ for $N_1 + b_1 N_2 < a_1$;

ii) $dN_1/dt < 0$ for $N_1 + b_1 N_2 > a_1$;

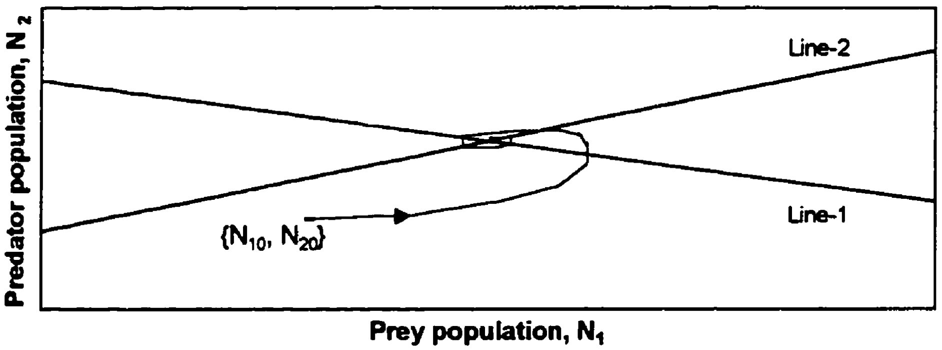

Figure 5.2. Population trajectory for the two-species model

iii) $dN_2/dt > 0$ for $-b_2N_1 + N_2 < a_2$; and

iv) $dN2/dt < 0$ for $-b_2N_1 + N_2 < a_2$.

Thus, on a N_1 - N_2 phase plane (Figure 5.2) for the two-species model, the intersection of line-1: ($N_1 + b_1N_2 = a_1$), and line-2: ($-b_2N_1 + N_2 = a_2$), will be the equilibrium point $\{N_1^*, N_2^*\}$. Further, for a point below line-1 N_1 is increasing ($dN_1/dt > 0$) and vice-versa. Also, for a point below line-2 N_2 is increasing ($dN_2/dt > 0$) and vice-versa. Therefore, the populations starting from an initial point (N_{10}, N_{20}) on a phase plane will spiral-in anti-clockwise until they reach the equilibrium point as shown in Figure 5.2. For the two-species model depicted by equations [5.3] and [5.9] a_2, b_1 and b_2 are constants, and a_1 varies with the forest age class structure as will be shown in the next section. Also, a_1 will be constant for a regulated forest. Thus, the two-species model will have stable equilibrium if forest age class structure remains constant, i.e., regulated forest conditions have been achieved. Otherwise, N_1 and N_2 will fluctuate according to the variations in the values of a_1. However, the tendency of N_1 and N_2 will be to move towards the current equilibrium point as depicted by Figure 5.2.

Estimating population potential function and parameters

Developing relationships to explain a biological process, especially wildlife population variations due to change in its habitat, is a formidable task. The difficulty comes from our limitations in identifying the components of nature such as habitat, predation, disease and other specific environments, and their role in affecting the population of wildlife. It may not be possible to include all components because of our limited knowledge or intractability of the mathematics involved, but certain components can be identified that may elucidate, to a large extent, the variations in wildlife population. Further, to allow quantitative analysis these components must take quantitative forms rather than being qualitative.

An empirical moose habitat model for moose in Algonquin Park, using forest inventory data from 1978 and moose population density assessment from 1976-1980, was estimated by Puttock et al. (1996) in terms of habitat components identified by them. The moose population and forest resource inventory data were aggregated at the township level in the Park. On an average, 52.3% of the township area surveyed was classified as providing moose habitat. Puttock et al. (1996) provide details of the forest resource inventory data organization and moose habitat classification. They considered linear, logarithmic and Box-Cox models.

The habitat components affecting moose population were identified as:

(a) Browse (BR): percent area of stands 1-20 years old and stands with ≤ 30% stocking[5];

(b) Barren and scattered (BS): percent area of barren and scattered forest type;

(c) Late winter (LW): percent area of conifer stands greater than 60 years old with greater than 50% canopy cover[6];

(d) Early winter conifer (EC): percent area of conifer stands greater than 20 years and less than 60 years old;

(e) Early winter deciduous (ED): percent area of stands with 30-70% hardwoods by basal area;

(f) Open muskeg (OM): percent area of open muskeg;

(g) Water (WA): percent area of water;

(h) Snow depth (SN): average snow depth in cm; and

(i) Treed wetlands (TW): percent area of treed wetlands.

Data on these components collected by Puttock et al. (1996) have been used in the proposed model. The objective now is to develop a more robust empirical relationship of these habitat classes with the moose populations as recorded.

In these estimates analytical caution is needed. Moose census is taken by aircraft and accurate sighting of moose is affected by forest cover, snow, light conditions, experience of flight crew, and speed and type of aircraft (Gasaway et al. 1983, Bisset 1991). As moose usually prefer to remain in cover during the day, there is a possibility that the population in late winter areas will be under-reported.

It is difficult to theorize beforehand the mathematical specification that would describe the relationship between moose population and its habitat components. Such

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[5] Stocking is defined as the basal area relative to the basal area of a normal stand.

[6] Canopy cover determination described by Naylor et al. (1992)

Table 5.1. Translog estimate of moose population density, dependent variable = LN(moose population density), R^2 = 0.751

Regression term	Coefficient value†	Standard error	Confidence level, $P \leq$
Constant	-13.680	4.442	0.01
LN(LW)	12.923	3.637	0.01
LN(EC)	-3.867	1.150	0.01
LN(WA)	-0.593	0.287	0.07
{LN(LW)]^2	-2.549	0.710	0.01
LN(BR)*LN(EC)	0.478	0.143	0.01
LN(BS)*LN(LW)	0.062	0.017	0.01
LN(BS)*LN(EC)	-0.548	0.136	0.01
LN(LW)*LN(EC)	1.365	0.426	0.01
LN(LW)*LN(ED)	-0.286	0.103	0.05

† Three significant figures after decimal are being reported in sense of accuracy

problems are often encountered in the estimation of production functions and other relationships in economics. A general specification suitable for capturing the accurate relationship from empirical data is the translog functional form (Christensen et al. 1973, Berndt 1991). This translog functional form was used in an attempt to empirically estimate the moose habitat relationship. The regression results are presented in Table 5.1. The results when used for simulation produced relatively large fluctuations in population around its mean value. This probably happened because of the weakness in the data which was that there were not enough observations and observations for LW areas were in all probability under-estimates, as mentioned above. The estimated translog specification was therefore rejected. Nevertheless, late winter was represented in four of the six interaction terms, signifying that LW is an important interaction variable in the relationship. This is in accordance with observations regarding sensitivity of moose population to late winter areas (Coady 1982, Ballard et al. 1990).

Next, an empirical model of the linear form including the square and cross-multiplied terms (the translog specification had all these terms in logarithmic form) of the habitat was considered. The regression result after dropping the non-significant terms yielded $R^2 = 0.734$. However, this relationship was not able to capture the population behavior at low LW values. This was evident from simulation of the population dynamics after incorporating the empirical expression for population potential. Simulation results, essentially, produced unilaterally increasing population even at very low or zero LW values. This was against logical expectations.

The above results also indicate that the census data used were either inadequate in low LW areas, or under-reported for high LW areas, thereby reducing the difference in population in low and high LW areas. Alternatively, it can be said that the data for low LW areas had poor impact on the regression results. Thus, a new form of equation that possibly could capture the population behavior at low LW situations was considered. This form is a combination of linear and non-linear terms based on earlier linear and translog estimations. If this form does not adequately explain the population variation, then the non-linear regression components should turn out to be insignificant making the equation linear – an already tested form. The considered equation for regression was:

$$M_{ts} = [\alpha_0 + \alpha_1{*}(BR_{ts}) + \alpha_2{*}(BS_{ts}) + \alpha_3{*}(LW_{ts}) + \alpha_4{*}(EC_{ts}) + \alpha_5{*}(WA_{ts}) + \alpha_6{*}(SN_{ts}) \\ + \alpha_7{*}(BR_{ts}){*}(BS_{ts})]{*}(1-\exp(-\alpha_8{*}LW_{ts})) \qquad [5.16]$$

where M_{ts} is moose population density, animals km^{-2} for township ts, α_0 to α_8 are regression coefficients. The final regression result is shown in Table 5.2. The significance level of α_5 is at $P < 0.22$, α_8 is at $P < 0.29$, and all other coefficients have P

< 0.07. The significance level of α_5 corresponding to water is on the margin ($P < 0.20$ is considered not good). This variable is expected to be constant for a forest and therefore significance level of α_5 can be accepted. The significance level of α_8 is low. However, considering that the census data for LW areas may be in error (Gasaway et al. 1986, Bisset 1991), α_8 can be also accepted. If the census data for the high LW areas were correct, population density difference in low and high LW areas would be more significant and this would have improved the confidence level in the estimation of α_8. The result in Table 5.2 is, therefore, acceptable.

In this model, habitat variables WA and SN when assumed not to be under management control can be considered fixed at their 1978 mean values of 12.17% and 51.8 cm, respectively. After substituting the mean values of WA and SN the model [5.16] is expressed as:

$$M_{ts} = \{0.791 + 0.127\,(BR_{ts}) - 0.067\,(BS_{ts}) - 0.031\,(LW_{ts}) + 0.058\,(EC_{ts}) - 0.003\,(BR_{ts})(ED_{ts})\}[1 - \exp(-0.062 * LW_{ts})]. \qquad [5.17]$$

Further, since the population data includes the effect of predation, the empirical relationship – which does not have predation component – needs to be converted to conform to equation [5.8]. This will make analysis of predation possible. Assume further that the habitat components of a forest under consideration are represented by their mean values from the data used in the empirical estimation of the coefficients of equation [5.17]. Let us denote the proportion of conifer areas in age class i as A_i and suppose each age class is of five years interval. Then BR will consist of areas in age classes A0 to A4, LW will consist of areas in age classes A13 to A21, EC will consist of areas in age classes A5 to A12 and ED will be the deciduous areas of all age classes. BS is barren and scattered area and remains unchanged unless the harvested area does not regenerate properly.

Table 5.2. Non-linear estimate of moose population density

Regression term	Coefficient	Estimated value*	Standard error
Constant	α_0	1.596†	0.783
Browse (BR)	α_1	0.127‡	0.060
Barren and scattered (BS)	α_2	-0.067‡	0.027
Late winter (LW)	α_3	-0.031‡	0.018
Early winter–conifers (EC)	α_4	0.058‡	0.027
Water (WA)	α_5	-0.013§	0.010
Snow depth (SN)	α_6	-0.013‡	0.006
(BR)*{Early winter–deciduous (ED)}	α_7	-0.003†	0.002
Exponential term coefficient	α_8	0.062††	0.055

* Three significant figures after decimal are being reported in sense of accuracy

‡ $P < 0.05$, † $P < 0.07$,

§ $P < 0.22$, †† $P < 0.29$.

Moose are not new to Algonquin Park. Thus, it is fair to say that the moose population is close to its potential and any variation in population density would be due to variations in the environmental factors affecting moose population. Equation [5.17], therefore, reflects the moose population potential rather than population itself. Thus, equation [5.8] can be considered a general form of and similar to equation [5.17]. Predation effect is not explicitly shown in equation [5.17], but is assumed to be built-in. The variables in equation [5.17] are considered statistically independent at least in the range of values of the variables in the simulation. Therefore, it can be surmised that the constant term in equation [5.17] when expanded that equals 0.791 is a special case of $(K_{1m} - p_1 \cdot N_2 - H_t)$. Also, at the time there was no hunting in the area so the term H_t equals zero.

Crête (1989) concluded that, according to forage production and moose needs in eastern Quebec where his study was conducted, the carrying capacity exceeded 2 animals km^{-2}. His study area with tree species, presence of predators, and earlier logging, closely resembles the study area of equation [5.16]. Therefore, for modeling purpose K_{1m} in equation [5.8] can be considered to equal 2.

To estimate the intrinsic birth rate, r_1, a review of birth rates for moose must be made. The pregnancy rate for moose is 0 to 0.47 for yearlings and 1 to 1.2 for adults (Coady 1982). Also, approximately 11 to 29 % pregnant moose bear twins. This works out to approximately 1.0 births per cow per year, or approximately 0.5 births per moose assuming 50% cows in the population. Therefore, the intrinsic birth rate can be approximated as $\log_e(1+0.5)$. This equals 0.4 (= r_1). There may be error in the estimation of r_1, but for purposes of simulation this estimation can be considered reasonable. Various other studies (Gasaway et al. 1983, Stewart et al. 1985) have indicated varying degrees of increase in moose population when predators were removed from a forest. Though black bear is a predator, proportion of animal matter in its diet is small, and that too mostly in the form of colonial insects (Pelton 1982). Therefore, gray wolf should be considered as the predator for modeling purpose. Gray wolf population in Algonquin Park has been reported at around 1 wolf every 26 km^2, which translates into 0.038 animal km^{-2} (Paradiso and Nowak 1982, Boutin 1992). Using the estimated values of K_{1t} and K_{1m}, the value of $p_1 \cdot N_2$ is calculated to be 1.20885. Thus, p_1 will equal 31.8118. The value of K_{1t} for period 1, that is, the current period, is calculated to 0.2993; the initial moose density is 0.35. The difference in the initial K_{1t} and the initial population density can be attributed to fluctuations in moose population density.

Similar to the estimation of r_1, the intrinsic birth rate of predators, r_2, is estimated to be 1.38. It is assumed that without moose, its major food source, the predator population would drop to a low level of 0.006 animal km^{-2} (or 1 animal every 167 km^2). Thus, K_{2m} in equation [5.10] can be taken to equal 0.006. Therefore, $p_2 \cdot N_1$ is calculated to 0.032 and hence, predator 'efficiency' p_2 will equal 0.0914.

Simulation

Several models that formulate wildlife population dynamics have been developed (Nisbet and Gurney 1982, Renshaw 1991). These models, however, do not consider forest structure. RAMAS (Akçakaya 1997), a GIS modeling tool, can be used to simulate population dynamics considering wildlife habitat dynamics. However, to predict populations RAMAS requires habitat maps as time series input. These habitat maps must be generated from any other landscape model simulating forest change. Forest Resource Inventory data (Anon. 1986) provide moose population data at the Ontario Base Map (OBM) level. This can be collated with the stand structure for that OBM. Thus, for the forest, moose habitat map can be generated in greater detail. However, to generate moose habitat maps as a time series for different timber harvest scenarios needs a different focus. The objective of this research is to generate moose population dynamics as affected by timber harvest. This is made possible considering that moose habitat components affected by forest management can be represented by the age class structure of the forest. Thus, the available Microsoft Excel® and VisualBasic® software tools have been used to simulate the effect of conifer and hardwood timber harvest on age class structure of the forest and moose population density over time. An initial forest on a 1000 ha basis with age class distribution as found in Algonquin Park and shown in Table 5.3 has been considered. A 60:40 mix of jack pine (*Pinus* *banksiana*) (site class II) and black spruce (*Picea mariana*) (site class I) as conifers (54.5% area), aspen (*Populus tremuloides*) (site class II) as hardwood species (41% area) and barren (4.5% area) has been considered for the simulation. It is, however, possible to consider other conifers and hardwood species; the conifers species mix or hardwood species mix would affect the normal yield of the conifers and the hardwoods in the simulation. To depict a case closer to reality, the regeneration of harvested area has been considered at 90%, barren area regeneration at 10%, and probability of annual loss due to forest hazard such as fire, pest infestation, or windthrow (Martell 1980; Reed and Errico 1986) is 0.001. However, any other value of these parameters within the range can be selected. Timber harvest from the oldest age class first has been considered. Further, harvested as well as hazard damage areas from all age classes move into the regenerating age class zero in the next period. Considering that there is artificial and natural regeneration of harvested area, it has been assumed that 30% of the harvested area regenerate to hardwood species. However, this percentage can be made to vary each period. During the simulation run, if at any time the population becomes negative then it is forced to become zero. The initial moose population density is 0.35 moose km^{-2} and there is no hunting in the forest.

For comparative purposes, the moose population for different timber harvest levels keeping the predator population constant over time and at its initial value can be simulated which is akin to single species dynamics according to the logistic process. However, simulation results considering variable predator population are being presented. This approach is similar to the classical two-species population dynamics. The results are reported in Figure 5.3 for four timber harvest scenarios and no predator scenario. The initial predator population potential, K_{2t}, is defined to equal:

$$K_{2t} = K_{2m} + p_2 \cdot N_1(t-1).$$

Table 5.3. Area wise age distribution: 54.5% conifers -- 60% jack pine (site II), 40% black spruce (site I); 41% hardwood – aspen (site II); and 4.5% barren

Age class	Interval, years	Gross volume m^{3}ha^{-1}		Forest area, Ha		Age class	Interval, years	Gross volume m^{3}ha^{-1}		Forest area, ha	
		Conifers	Hard-wood	Conifers	Hard-wood			Conifers	Hard-wood	Conifers	Hard-wood
0	Barren			45		11	50-55	175.8	276.5	13	12
1	00-05	5.6	8.5	18	0	12	55-60	189.3	301.0	15	17
2	05-10	16.9	25.5	22	0	13	60-65	201.6	321.5	55	11
3	10-15	28.1	42.5	15	0	14	65-70	212.4	338.5	55	9
4	15-20	39.4	59.2	10	0	15	70-75	222.4	352.5	78	15
5	20-25	57.1	82.0	10	0	16	75-80	230.9	363.5	22	11
6	25-30	80.7	112.5	12	13	17	80-85	237.9	371.5	11	18
7	30-35	103.1	146.5	10	0	18	85-90	244.2	377.0	19	11
8	35-40	124.3	181.5	0	0	19	90-95	249.5	380.5	35	18
9	40-45	143.8	215.5	15	13	20	95-100	254.3	383.0	22	6
10	45-50	160.9	247.5	0	14	21	100+	258.5	384.0	108	242
Total area including barren = 1000 ha										545	410

The approach so far in simulating the population dynamics has been deterministic in nature. Stochasticity will now be introduced into the population dynamics.

Stochasticity

Population size $N_1(t)$, considering the deterministic model equation [5.1], may be calculated at any future time t given population n_0 at any previous time t_0. However, if there is a state of stochasticity in the system, then we cannot predict the state at any future time. The best that can be done is to calculate the probability distribution of population size by observing different states of the system that is achieved starting from the same initial state and time (Nisbet and Gurney 1982).

Consider a large number M of such states. Then probability that the population is exactly N individuals at time t can be defined as:

$$p_N(t) = \lim_{M\to\infty}\left\{\begin{matrix} (1/M) & \text{multiplied} & \text{by} & \text{number} & \text{of} & \text{states} & \text{containing} \\ & \text{exactly} & N & \text{individuals} & \text{at} & \text{time} & t \end{matrix}\right\}$$

In the small time increment h, probability that there is:

i) an increase in population by 1 = $\mathrm{Prob}\{N(t+h) = N(t)+1\} = B[N(t)].h$

ii) a decrease in population by 1 = $\mathrm{Prob}\{N(t+h) = N(t) - 1\} = D[N(t)].h$

iii) no change in population = $\mathrm{Prob}\{N(t+h) = N(t)\} = 1 - \{B[N(t)] + D[N(t)]\}.h$

where B[N(t)] and D[N(t)] are the birth and death rates at time t as expressed in equation [5.1].

Thus, for $h = \Delta t$, and $\Delta t \to 0$, we can write a general form to express stochasticity in population (Nisbet and Gurney 1982):

$$\frac{dp_N(t)}{dt} = D(N+1)\cdot p_{N+1}(t) - [B(N) + D(N)]\cdot p_N(t) + B(N-1)p_{N-1}(t) \qquad [5.18]$$

Equation [5.18] can be solved to obtain an expression for $p_N(t)$ that will be a distribution in t and, therefore, it will have a mean and variance. For simple birth-death processes equation [5.18] is relatively easy to solve for $p_N(t)$. However, as the expressions for B(N) and D(N) become complex, equation [5.18] becomes almost impossible to solve. Also, by definition:

$p_0(t)$ = probability of extinction at time t, and

$p_0(\infty)$ = probability of ultimate extinction.

A general expression of probability of ultimate extinction, $p_0(\infty)$, for an initial population n_0 for a closed system with no immigration has been determined to be (Renshaw 1991):

$$p_0(\infty) \quad \text{for} \quad n_0 = E_{n_0} = \left(\frac{\sum_{n_0}^{\infty} S_i}{1 + \sum_{i=1}^{\infty} S_i} \right) \qquad [5.19]$$

$$\text{if} \quad \sum_{i=1}^{\infty} S_i \quad \neq \quad \infty \quad \text{and} \quad \text{it} \quad \text{converges},$$

where $S_i = \dfrac{D(1).D(2)....D(i)}{B(1).B(2)....B(i)}$.

It would be useful to determine probability of ultimate extinction, $p_0(\infty)$, at different times for the simulated example. To determine this we must obtain the birth and death rates at the time for all populations lower than the current population. To determine these birth and death rates, the absolute moose population rather than the population density must be considered, and therefore, the extinction probability becomes sensitive to the size of the forest as well. A quick calculation indicates that even for a population of 10 moose 100 km^{-2} the probability of ultimate extinction is infinitesimally small. Therefore, for the sake of brevity this probability for all times will not be calculated. It is sufficient to say that there is no danger of ultimate extinction as long as the population density remains above 10 moose 100 km^{-2}. For death rates greater than birth rates, typically when population is more than the potential or the carrying capacity, $\sum_{i=1}^{\infty} S_i = \infty$ and therefore, ultimate extinction is certain. Also, equation [5.18] can be numerically solved considering a small increment, h, in time. Smaller values of h will give more accuracy, but h = 0.1 can be considered good enough for this analysis. At time t = 1 (initial time) $p_{N=35}(1) = 1.0$ and all other probabilities are equal to zero. For each of the successive time increments of 0.1 up to t= 21, a value of $p_N(t)$ with N in the range [0, 150] using equation [5.18] is estimated. Selection of 150 as an upper limit to N is arbitrary as $p_{N=150}(t \rightarrow \text{large})$ is expected to be zero and as a verification this is found to be true in the simulation. Then for each successive time mean population m(t) and variance $\sigma^2(t)$ is estimated. Thus, the range within which the population will wander due to stochasticity at 95 % confidence level will be $m(t) \pm 2\sigma(t)$. Also, from this solution $p_0(t)$, the probability of extinction at time t will be known. For the stochastic prey population simulation the two species model equation [5.3] and [5.9] was considered. The timber harvest considered was as for the case depicted in Figure 5.3b. The resulting plot is shown in Figure 5.4. For this case $p_0(t)$ is essentially zero up to t = 21. That is, there is negligible danger of extinction.

Validation

Validation criteria

To validate a model, the outcome of simulations must be compared with experimental results (Haefner 1996). In forest management the response time to stimuli can be decades or centuries, especially when considering tree growth, timber harvest and their impact on large ungulates. Therefore, it becomes a difficult task—almost impossible—

to obtain experimental data within a pragmatic time frame. Available data, collected in the past, have already been used to estimate the parameters of the model and cannot be used for validation. Therefore, a verification of the expected behavior of the model can be considered sufficient at this time. The following describes the dynamic characteristics of the moose population that will be verified.

a. Any timber harvest or a natural forest disturbance generates opportunities for moose browse to increase (Peek et al. 1976; Payne et al. 1988; Mastenbrook and Cumming 1989). Therefore, if there is no timber harvest but forest disturbances are large enough, moose population should remain relatively unchanged. For little or no forest disturbance moose population should decrease due to reduced availability of forage.

b. If there is excessive timber harvest in the forest, then the moose population should increase in the beginning due to increased availability of forage. Then, as the predator population also increases, moose population should start decreasing because of increased loss due to predation. Moose population may attain a low equilibrium or even become extinct (Peek et al. 1976; Payne et al. 1988; Mastenbrook and Cumming 1989).

c. Moose population, due to the presence of predators, is somewhat cyclic in nature as reported by Peterson (1984).

d. A Lotka-Volterra model indicates stable cycle for prey-predator populations over time. The prey-predator population should 'spiral-in' if stable limit cycle or an equilibrium is attained over time (Clark 1976; McLeod 1997). Moose population in the presence of predators may achieve equilibrium around its present level or 'escape' and reach another equilibrium as stated by Bergerud et al. (1983).

e. If predators are removed then moose population should increase until it reaches its capacity (Ballard and Miller 1990).

f. It can be conjectured that if additional predators are introduced, then moose population should decrease and, with this, the predator population should also decrease as less food becomes available to them (van Ballenberghe 1987).

In addition, to give credence to this model the basic assumptions and values of the model parameters used must be reviewed.

The model will be evaluated on each of these characteristics. Furthermore, if the characteristics of the model are as expected then the true validity would depend on the validity of the logistic equation [5.3] and equation [5.17] that are the basis of this dynamic model.

Conclusions

Figure 5.3a shows that without timber harvest and at the considered forest hazard level (= 0.001) moose population drops marginally to 0.245 animal km^{-2}. However, if the forest hazard level is made zero, with no timber harvest moose population stabilizes at 0.21 animal km^{-2} as a low equilibrium. This is made possible because adequate late winter habitat—considered essential for survival—remains available. Figure 5.3b shows the population dynamics with timber harvest that attempts to maintain a mature forest. The population remains relatively unchanged. This verifies point (a) of the validity section.

When timber harvest is increased, moose population increases in the beginning due to the increased availability of browse and then the population decreases due to an increase in predator population and loss of habitat. Prey and predators then achieve a low equilibrium, almost to the point of extinction. This is shown in Figure 5.3c. For very high timber harvest in the initial periods, moose population increases in the beginning but soon drops sharply due to loss of cover and hence excessive predation, but soon recovers due to lower timber harvest in later periods. This is shown in Figure 5.3d. Thus, point (b) of the validity section is substantiated.

Higher timber harvest creates large cut-overs that favor moose population. These cut-over areas would regenerate and provide different habitats as the trees grow over time. Any major forest disturbance may also create such a situation. Thus, over time moose population should fluctuate depending on the contribution of these cut-overs to moose habitat. Figure 5.3d depicts one such scenario with high timber harvest in the first three periods. This shows that moose population increases in the beginning and then drops as less cover is available. It starts increasing again from period 16 due to favorable conditions created by low timber harvest. Thus, if the forest age class structure in period 1-16 is somehow maintained for other periods, then moose population will be cyclic. Therefore, point (c) of the validation section can be considered to have validity only for specific timber harvest or forest disturbance.

Phase diagram (Figure 5.5) indicates that the trend of prey-predator populations fluctuation is as expected. However, for timber harvest that does not substantially alter the predominance of older age trees in this forest, the prey-predator population may not show cyclic behavior, but the tendency will always be to move in the anti clock wise direction to reach an equilibrium point. This suitably corroborates the population characteristic as expressed in point (d) of the validation section.

When the predator population is made zero, moose population increases to a higher level as shown in Figure 5.3e. This is in line with Boutin (1992) who stated that moose densities around a low-density equilibrium are regulated by predation; thus, without predation moose population should ‘escape’. On the other hand, when the

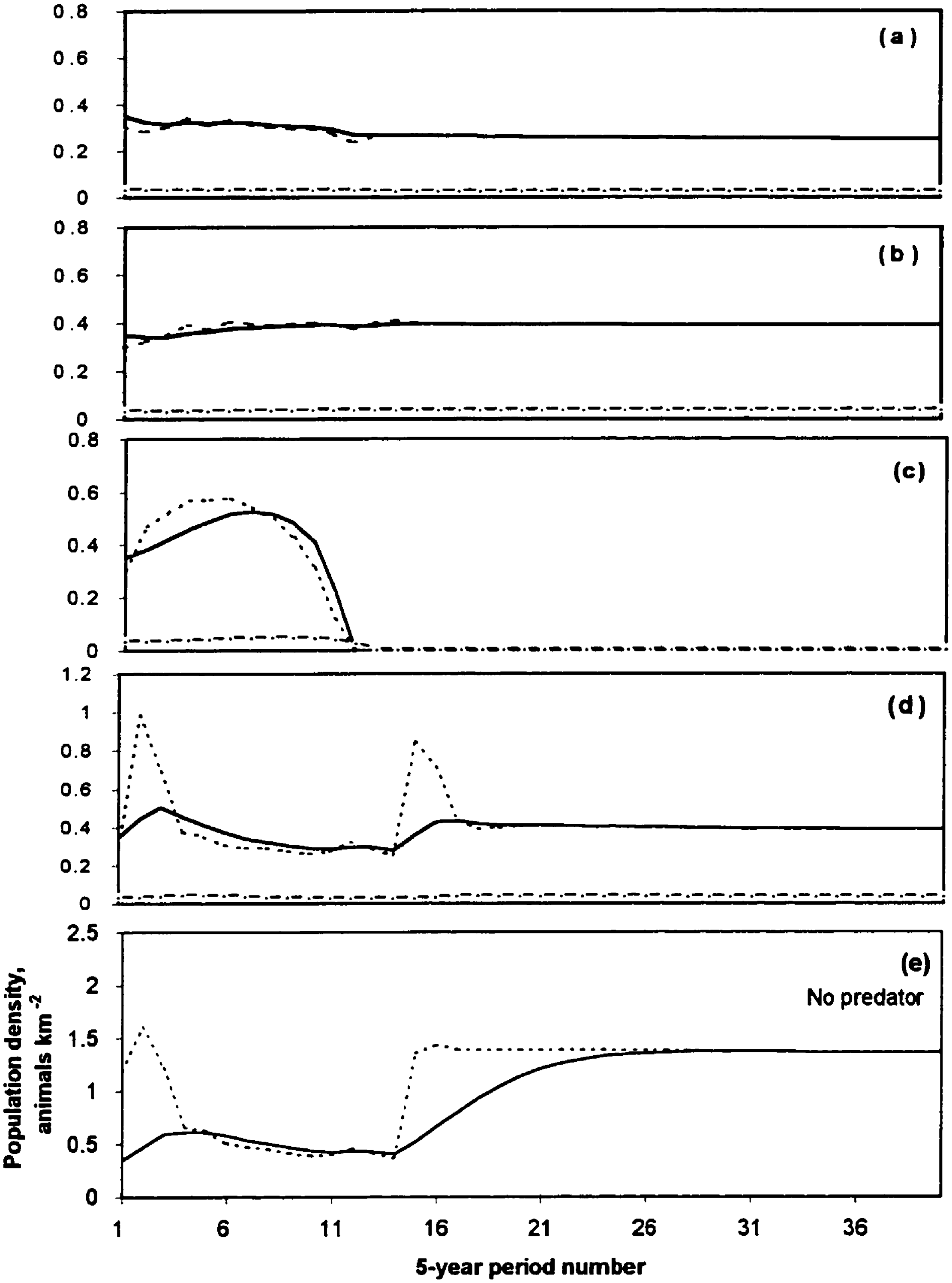

Figure 5.3. Moose population dynamics with timber harvest in m^3 $period^{-1}$ 1,000 ha^{-1} set at (a) 0; (b) conifers 3,000 and hardwood 1,500; (c) conifers 12,000 and hardwood 10,000; (d) conifers and hardwood each at 50,000 in period 1, 20,000 in period 2 and 3, and thereafter as in (b); and (e) no predator but timber harvest as in (d); Prey potential ------ , predator -.-.-.- , prey ——— .

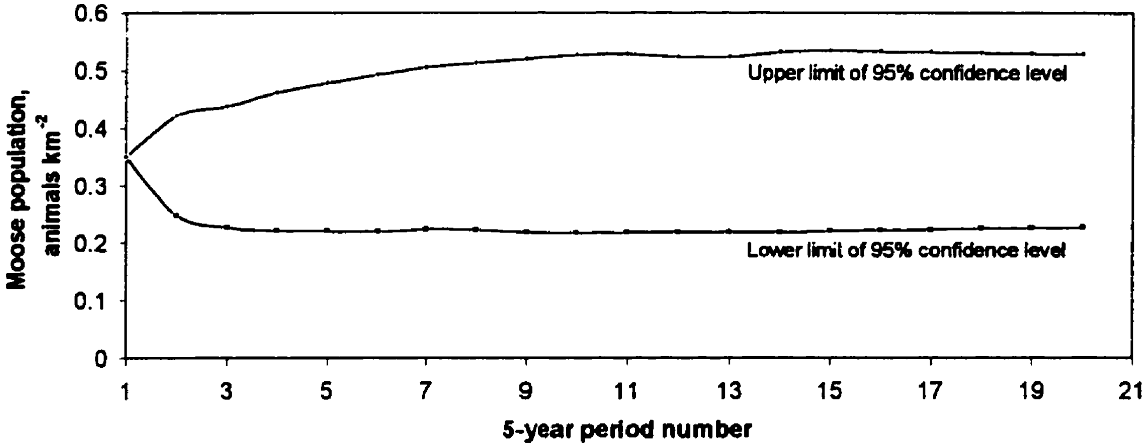

Figure 5.4. Moose population at 95% confidence band for timber harvest as in Figure 5.3b

predator population is increased, there is a drop in moose population, but soon predator population also drops due to less food available. Thus, a dynamic eqilibrium of prey-predator populations is reached. Therefore, points (e) and (f) of the validity section are accepted as satisfied.

Various timber harvests were simulated to achieve a regulated forest in the long run (Table 5.4) and the moose population density in the long run (80 periods) was obtained. From the MAI data it is known that timber harvest is maximized at rotation age period 10 and 11—the age at maximum MAI—for the conifers and hardwood species considered, respectively. This clearly shows that if wildlife is considered with timber, the optimal rotation age of a forest will be affected as indicated by Calish et al. (1978) and Nautiyal (1988). Figure 5.6 is a plot of long-term timber harvest and the moose population density achieved. The shape of the curve indicates that wildlife density increases with timber harvest to a point, then starts decreasing with higher timber harvest due to unfavorable habitat conditions. This validates the theoretical perspective given by Gregory (1972) and Nautiyal (1988). The top right hand portion of

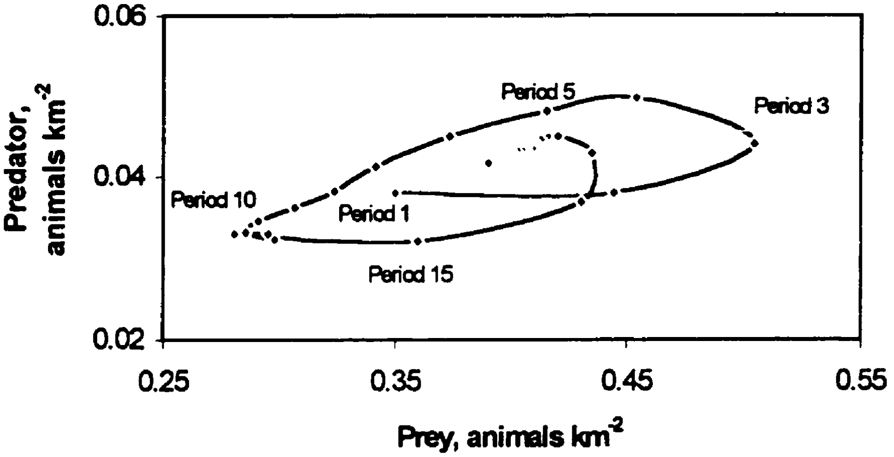

Figure 5.5. Phase diagram of prey-predator over period 1-40 with timber harvest as simulated for the case in Figure 5.3d

the curve in Figure 5.6 is particularly similar to the one proposed by Nautiyal (1988) and of interest for management decision. In the absence of more robust data, this will be accepted at this time. Also, the product transformation curve similar to Figure 5.6 can be drawn for the time period of interest.

Discussion and conclusion

From the analysis in the previous section the simulation model is able to analytically explain the dynamic moose population observations made in the past. As the values of the parameters and the coefficients become more robust due to better estimation procedures, the model can be used for a wide range of situations. One of the difficulties faced in enumerating moose in late winter areas (LW habitat type) is that they escape aerial observation (Gasaway et al. 1986). Thus, due to error-prone population data from LW areas, the sensitivity of population to changes in LW is lowered in the model. If this enumeration error is eliminated, then moose density should become more sensitive to LW habitat in the model.

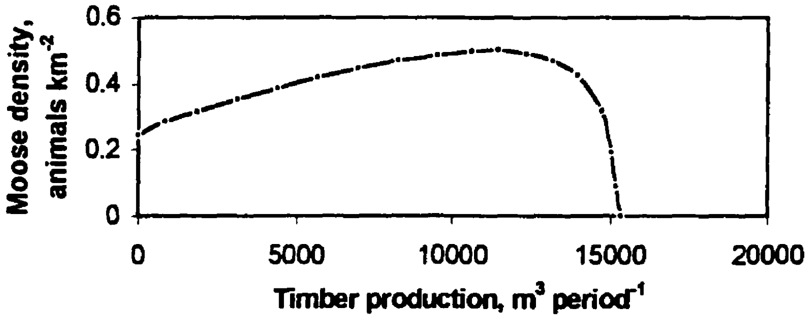

Figure 5.6. Long-term moose density with timber harvest

Further, if the rotation age of conifers in the forest is lower than period 13, the LW habitat is reduced to zero. Due to habitat requirements, this results in the population dropping to a low value. Thus, for every long-term timber harvest that regulates the conifer trees in the forest above its MAI maximum age, a unique population level will be achieved. If this were not the case, that is, the population can be sustained at lower rotation ages also, then for a timber harvest corresponding to two rotation ages—one lower and the other higher than the MAI maximum age—different population levels may be achieved. Therefore, the curve in Figure 5.6 for this case may double-back to indicate two population levels for the same timber harvest. Also, the product transformation curve in Figure 5.6 changes with time indicating that moose-timber harvest interaction is not universal. Under changed conditions their interaction is different, but is governed by the combined effect of complex biological processes, such as, forest-prey-predator interactions. The product transformation curve for wildlife and timber harvest discussed by Gregory (1972) and Nautiyal (1988) implies the existence

Table 5.4. Long-term moose density with timber harvest

Timber harvest, m^3 period^{-1} ‡			Average age of the forest, period	Moose population, animals km^{-2}
Conifers	Hardwood	Total		
0	0	0	19.386	0.2457
1357	500	1857	17.900	0.3171
2904	1500	4404	15.910	0.3875
5247	3000	8247	12.818	0.4716
7345	5000	12345	9.040	0.4917
8224	6500	14724	6.708	0.3187
8388	6800	15188	6.144	0.0890
8447	6900	15346	5.920	0

‡ A period contains 5 years (see Table 5.3)

of a mechanistic system, such as in manufacturing industry, also governing biological production. This, however, is not the case and this simulation shows that a biological system, such as, moose and timber harvest behaves differently under changed environmental conditions and therefore, a product transformation curve of biological systems is conditional on its environment.

The approach can be used to evaluate timber management strategies that also provide for a desirable moose population. The methodology used for the simulation of the moose population is quite general and can be used for any other species that is sensitive to the age class structure of the forest. The driving element of the model is the concept of population potential that is akin to the carrying capacity but different in meaning. However, the insights derived from the results of simulation for a selected timber harvest are useful in making inferences about the future state. Also, for a given timber harvest scenario, a hunting level that does not bring the moose population dangerously low can be estimated. The stochastic population variations are helpful in visualizing the extremes of population fluctuations. They would help in devising strategies if the moose population were to become too low. Mortality of the moose population due to epidemics such as the brain fever that afflicts the population from time to time has not been considered. This modeling approach has limitations – for to model a natural process compromises must be made. Nonetheless, it provides useful insights about the moose and timber harvest in a forest. Application of better values of various parameters used in the model will greatly enhance the predictability of future moose population given timber harvest schemes.

CHAPTER 6
Whole-forest management

Introduction

In earlier chapters concepts of forest stand diversity, ν, compactness index, γ, and forest maturity index, ϕ, have been developed and discussed. To achieve a certain forest stand diversity and forest maturity, a timber harvest strategy can be fashioned. The area of Algonquin Park, considered for this study, is very large compared to the home range of moose. Thus, the home range factor, m, is very small and therefore the compactness factor for population, w, has been considered to equal 1. Using a simulation model to obtain moose population densities over time by varying the timber harvest, many forest management scenarios can be developed. A flow chart providing an overview of the whole forest management considering timber and wildlife harvests is shown in Figure 6.1. This scheme can be used to develop forest management scenarios, any of which can be chosen to meet the objectives.

Forest management scheme

From the available forest resource inventory, values of forest maturity, forest stand diversity and compactness indices including wildlife population density can be determined; the compactness index is expected to remain unchanged unless land use changes. A particular forest management practice will affect the forest maturity index, forest stand diversity index and wildlife population density over time and desired values of these measures must be determined in consultation with experts and various other interest groups. This will provide a direction for forest management practice to adopt, as the objective would be to change the current state of the forest to a desirable state over time as schematically shown in Figure 6.1. This is essential especially in a forest where timber and wildlife production is allowed. A comparison of the current values of these measures with the desirable values will provide direction to develop a timber or a wildlife harvest scheme. Thus, over time, an appropriate timber harvest scheme will help achieve the desired state or at least be close to the desired state of the forest.

To determine the appropriate production level—including no production—a harvest level can be chosen and its effect on forest age class structure and wildlife population over time can be "observed" using simulation programs. The forest maturity index, forest stand diversity index and wildlife population density achieved over time will be known. If this compares favorably with the acceptable values of these indices and wildlife population density then this will become a forest management scenario. For unfavorable results the forest can be repetitively simulated for different production levels until acceptable values are obtained. If even after repetitively selecting different production levels the forest does not achieve the chosen state, then the desired state of the forest with the wanted wildlife population density may not be feasible. The pre-decided desirable values of these measures, in such cases, need to be re-evaluated and a new combination chosen. The production level that satisfies the forest management objective can be saved as a forest management scenario. Starting all over again can generate another scenario. Thus, various scenarios that meet the forest management objectives can be developed. The best scenario, based on social or economic criterion, can be chosen for implementation. In the next time period the current forest resource inventory can be taken and the entire simulation exercise repeated to select the best forest management scenario.

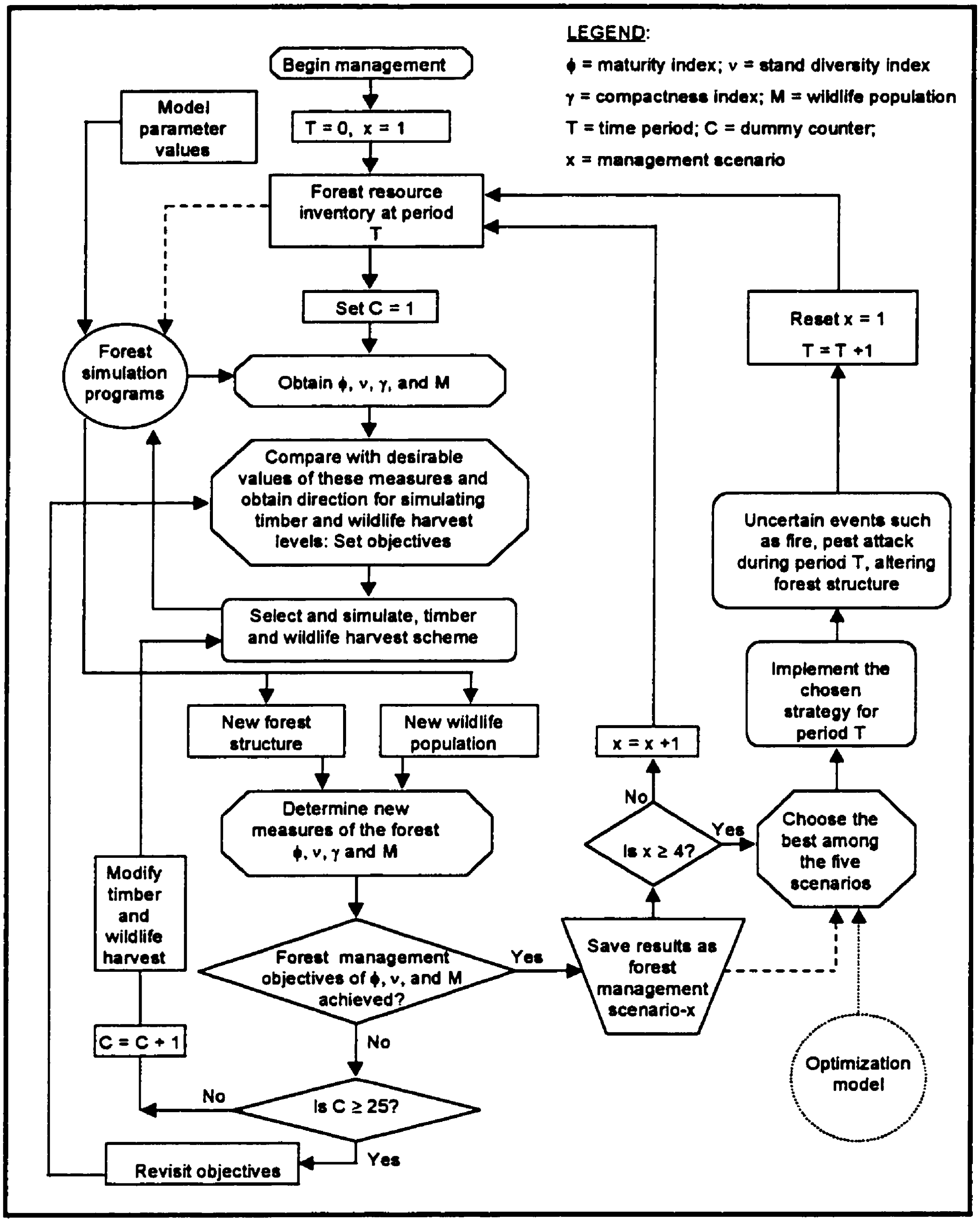

Figure 6.1. Forest management flow chart

In this scheme, the forest resource inventory in the next survey may provide a different than expected state of the forest. This may happen because uncertain events such as forest fire, pest infestation or windthrow were of different proportions than accounted for in the simulation model. Thus, from the revised forest resource inventory, a new set of forest management scenarios can be developed.

Forest management scenarios

For the given forest, i.e., Algonquin Park, different timber harvests of conifers and hardwood have been simulated to obtain the long run moose population and forest maturity index. The results are presented in Table 6.1. As the long run timber harvest increases, moose population density also increases reaching a high of 0.5024 animal km^{-2} in scenario-10. It starts declining as timber harvest is increased further. For a very high timber harvest that depletes the forest of moose habitat, moose population density reduces and ultimately drops to zero in the long run as shown in scenario-17 in Table 6.1. From a timber management perspective, scenario-17 is the best as it produces maximum timber in the long run, but the forest is depleted to the extent that it can no longer support moose population. Thus, scenario-17 from a whole-forest management perspective is not a desirable option. Therefore, the optimum option will be somewhere between scenario-10 and scenario-17. It also will be noted that as the long run timber harvest increases from zero, forest maturity index decreases from 1. The acceptable forest maturity indices from a production perspective will be those between scenarios-10 and 17. If forest maturity index higher than these is desired in the long run, then the same may be achieved for a different timber harvest in the initial periods, but at a lower wildlife population density than achievable. As the forest maturity index also reflects the value society wants to put to the growing stock, a combination of this index and wildlife population density can be chosen

Table 6.1. Forest management scenarios

Scenario	Long run timber harvest, m^3 period^{-1}			Long run moose population, animals km^{-2}	Forest maturity index†	
					Conifers	Hardwood
	Conifers	Hardwood	Total		ϕ_s	ϕ_h
1	0	0	0	0.2457	1.0	1.0
2	1357	500	1857	0.3171	0.86	0.95
3	2123	1000	3123	0.3528	0.77	0.90
4	2904	1500	4404	0.3875	0.69	0.85
5	3682	2000	5682	0.4198	0.61	0.80
6	4464	2500	6964	0.4479	0.53	0.76
7	5247	3000	8247	0.4716	0.45	0.71
8	6031	3500	9531	0.4874	0.36	0.66
9	6535	4000	10635	0.4982	0.31	0.61
10	6969	4500	11469	**0.5024‡**	0.27	0.56
11	7345	5000	12345	0.4917	0.23	0.51
12	7665	5500	13165	0.4699	0.19	0.47
13	7946	6000	13946	0.4256	0.16	0.42
14	8224	6500	14724	0.3187	0.13	0.37
15	8331	6700	15031	0.1933	0.12	0.35
16	8388	6800	15188	0.089	0.12	0.34
17	8447	6900	15347	0	0.11	0.33

† Yield at the rotation age of MAI_{max} for the conifers = 9493.1 m^3 period^{-1} and for hardwood = 10305.9 m^3 period^{-1}

‡ Maximum value reached

that best meet the social objectives. Thus, the best scenario can be analytically selected using an optimization technique or be based on social values.

Limitations

Some of the limitations in this procedure are:

1. Forest stand diversity, ν, *per* se does not affect the wildlife population in the model. It has been used only to quantify forest structure.
2. Forest stand diversity, ν, is not sensitive to the tree species, but it does account for the number of tree species in the forest.
3. Effect of ν on suitability of wildlife was not studied. It can be surmised that distinct ν values in association with stand age would be typical of different wildlife species.
4. The forest maturity index, ϕ, is a true measure of the timber yielding capacity and age maturity of the forest. However, it is possible to have more than one age structure to have the same timber yielding capacity. Since the focus of ϕ is on timber yield, this aspect is not really a limitation.
5. The wildlife population model uses parameters and estimated coefficients that may be in the error. Unless better estimates are obtained these can be considered reasonable.
6. No distinction in sex or age structure has been made in the wildlife population dynamics model. Also, age specific mortality has not been considered. The entire population has been considered as a unit for birth and death rates. Thus, no age specific analysis can be made.

Applications

The method will find application in the following form:

1. Different timber harvests can be simulated to study their impact on wildlife population density.
2. Desired forest maturity can be achieved over time through appropriate level of timber harvests.

3. The forest maturity index, ϕ, can be used to measure the state of depletion of a forest in comparison to a standard. The standard considered is a forest with Long Term Sustained Yield equal to timber yield corresponding to the age at maximum mean annual increment.
4. Effect of the intensity of wildlife hunting on future wildlife population can be simulated. This means that the effect of issuing more or fewer hunting licences than the current practice in a region can be studied.
5. If forest land use changes due to, say, construction of a dam or reversion of farmland to forestry, then the effect of the lost (or increased) forest land on wildlife population potential can be studied. If the land inundated by a dam is compensated, the model allows analysis of effect of location of compensation area -- whether contiguous to existing area, in large or small fragments, etc.

Suggested future research

The method can be made more robust by continuing research in the following areas:

1. Effect of tree species mix on forest stand diversity.
2. Range of values of forest stand diversity suitable to different wildlife species.
3. Timber harvest strategies at a micro level to achieve desired forest stand diversity, ν.
4. Effect on stand diversity of different timber harvesting regimes including a clearcut. Through this, impact of different timber harvesting regimes on wildlife populations may be quantified.
5. Effect of compactness index on a wildlife population.
6. Effect of forest succession on a wildlife population dependent on horizontal structure of the forest and integration with the population model.
7. Wildlife population dynamics considering age structure

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