Effects of Clear-cutting and Alternative Silvicultural Systems on Wildlife in Ontario's Boreal Mixedwoods

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ABSTRACT

Increased emphasis on alternatives to large-scale clear-cutting operations requires a better understanding of the effects of such alternatives on wildlife and wildlife habitat. This report summarizes the ecology of boreal mixedwoods, briefly describes various silvicultural systems, and examines both the stand-level and larger-scale effects of these systems on songbirds, small mammals, ungulates, and furbearers.

RÉSUMÉ

Vu la tendance à remplacer la coupe à blanc à grande échelle par d'autres méthodes, il importe de mieux comprendre les effets de ces dernières sur les espèces sauvages et leur habitat. Les auteurs présentent un résumé des caractéristiques écologiques des forêts mixtes boréales, décrivent brièvement diverses méthodes sylvicoles et examinent les effets de celles-ci, tant au niveau du peuplement qu'à plus grande échelle, sur les oiseaux chanteurs, les petits mammifères, les ongulés et les animaux à fourrure.

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EFFECTS OF CLEAR-CUTTING AND ALTERNATIVE SILVICULTURAL SYSTEMS ON WILDLIFE IN ONTARIO'S BOREAL MIXEDWOODS

1.0 INTRODUCTION

Current levels of clear-cutting may well decrease over the coming years as forest managers employ a wider variety of silvicultural options. Several factors are influencing this movement: namely, a shift in emphasis toward natural regeneration (Ontario Ministry of Natural Resources 1993); a growing demand for the production of hardwood and softwood products from the forest (Brennan 1991, Ontario Ministry of Natural Resources 1992); increased public interest in forest management and widespread sentiment favouring alternative harvesting systems; and a growing body of evidence indicating that a variety of harvesting and silvicultural methods must be practiced if ecosystem values such as biodiversity and integrity are to be protected (Hunter 1990, Booth et al. 1993, Thompson and Welsh 1993).

This report reviews the potential impacts of alternative silvicultural systems in Ontario's boreal mixedwoods on individual species and groups of wildlife. In a companion report (Wedeles et al. 1995), the authors examined the implications of alternative silvicultural systems from a timber management perspective. The intent of that report was to provide forest managers with information that will enable them to assess and evaluate the practicality of several alternatives for managing timber in boreal mixedwoods. In recent years it has become clear that the responsibilities of forest managers extend far beyond producing timber - other forest values and products must be managed in concert. Wildlife concerns are often the principal nontimber values that must be considered. Although many forest values (e.g., soil fauna, nutrient cycling, and aesthetics) are not covered in detail in these two reports, the information presented should provide forest managers with an understanding of the opportunities offered by alternative silvicultural systems.

Although there is a growing interest in managing forests and other natural ecosystems for biodiversity (Noss and Harris 1986, Salwasser 1990, Boyle 1991, Probst and Crow 1991, Franklin 1993), most wildlife management in Ontario is species based. Furthermore, managing for broader objectives (e.g., conservation of biodiversity, ecosystem integrity) does not free forest managers from the need to understand the ecology of individual species and the effects of silvicultural activity on these species. As ecosystem management becomes more common in Ontario, such information will be required to ensure that individual species can be accommodated in broad forest management approaches.

In an effort to keep the scope of this review tractable, the authors have explicitly limited the definitions of both wildlife and silvicultural systems. Recent definitions of wildlife (or wild life), which have been suggested and adopted by various management agencies (Wildlife Ministers' Council of Canada 1990, Ontario Wild Life Working Group 1991), include all wild mammals, birds, reptiles, amphibians, fishes, invertebrates, plants, fungi, algae, bacteria, and other organisms. This review has a narrower focus, in that it examines only birds and terrestrial mammals. From a silvicultural perspective, this review examines the impacts of silvicultural systems, rather than the effects of specific techniques (e.g., mechanical site preparation, chemical tending, etc.). Only inasmuch as specific techniques are associated with a silvicultural system are they incorporated into these discussions.

Silvicultural systems are typically named according to the harvesting method used (Forestry Canada 1992). As harvesting methods are usually employed to facilitate a specific manner of regeneration, names that refer to silvicultural systems often (but not always) imply an approach to both regeneration and harvesting. When referring to the shelterwood silvicultural system, for example, a forester would understand that not only is the forest to be harvested in a series of successive cuts of a specific type, but that natural regeneration will be fostered.

The effects of most silvicultural systems on wildlife species are not well understood. Due to this lack of information, the authors were often forced to extrapolate the likely effects of alternative systems on a particular species based upon that species' habitat needs, or suspected habitat affinities. For many species, it is difficult to assess the precise role that mixedwoods play in providing their habitat needs, as they occupy forests that contain many cover types. Thus, is also difficult to determine the effect of mixedwood harvesting on a wildlife population. In many instances the authors have made the implicit assumption that effects on wildlife in mixedwoods would be comparable to effects in other boreal forest types. Little differentiation of effects based on forest cover types has been discussed in the literature.

Although the original intent of this report was not to examine the effects of clear-cutting on wildlife, it has been appropriate in many instances to use the effects of clear-cutting as a basis for comparison with "alternative" systems, since clear-cutting of some form is the traditional approach to mixedwood harvesting.

Harvesting and other forest management operations may affect wildlife at a variety of spatial scales. In this report attempts have been made to distinguish between standlevel and largescale effects. The loss of marten (Martes americana) habitat in one stand because of harvesting is a stand-level effect. Effects at larger scales (i.e., the forest level or landscape level) often occur from the cumulative nature of stand-level effects. The loss of one stand for marten may not be severe but, when viewed in a larger context, the loss of many stands throughout a forest may have significant effects.

2.0 THE ECOLOGY OF BOREAL MIXEDWOODS

This section presents an overview of boreal mixedwood ecology and discusses some of the concepts relevant to later sections of the report. (*See* Wedeles et al. [1995] for a more extensive treatment of mixedwood ecology.)

2.1 Definition of Boreal Mixedwoods

Before the development of Ontario's current inventory system, productive forest land in the province was classed into one of four broad cover types: coniferous, deciduous, mixedwood, and reproducing forest (Dixon 1963). Under this system, if less than 75 percent of the stems in a stand were either coniferous or deciduous, the stand was classified as mixedwood. While useful at the time, this approach is too limited to suit the needs of today's forest managers.

A seemingly obvious way to define a boreal mixedwood forest is according to its tree species composition. Any tree species can occur in mixed associations, although the five species that most often occur in admixtures in Ontario's boreal forest are white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P), balsam fir (*Abies balsamifera* [L.] Mill.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Descriptions based on species currently occupying a site are inadequate, however, because they fail to account for the site's potential to support mixtures of species.

When planning silvicultural operations, it is as important to know the nature of the site as it is to know the types of trees that are found there (although the two are clearly related). To facilitate this, a site-based definition of mixedwoods has evolved. Thus, boreal mixedwoods are defined as "sites that support, or could support, good growth of the five main component species..." (Weingartner and Basham 1979 in McClain 1981).

Boreal mixedwood stands can occur on fertile landforms and soil types ranging from fresh to well drained (Pierpoint 1981, Baldwin et al. 1990, Sims et al. 1990). Since considerable variation exists within such a broad site generalization, boreal mixedwood sites might best be defined by describing the growing conditions under which they are not found. Excessively wet areas develop black spruce and eastern white cedar (*Thuja occidentalis* L.) stands; excessively dry areas develop jack pine (*Pinus banksiana* Lamb.) stands. Such extreme moisture conditions are associated with poor nutrient availability. The remaining sites, with intermediate moisture and medium to rich nutrient regimes, are capable of growing mixedwoods. The obvious variability within such an allencompassing boreal mixedwood site type represents the essence of both management problems and opportunities.

The most recent and comprehensive attempt to classify boreal mixedwoods in an ecological context was completed for much of northern Ontario's commercially important forest during the last decade. Northwestern Ontario's Forest Ecosystem Classification (FEC) (Sims et al. 1989, Sims and Uhlig 1992) identifies 38 vegetation cover types or classes based on an analysis of more than 2 000 plots, where the relative abundance of tree, shrub, herb, and moss cover was recorded in mature undisturbed forests. Of the 38 cover types, seven are considered to be conifer dominated boreal mixedwoods and six are hardwood dominated boreal mixedwoods. Ontario's Eastern Clay Belt is floristically and topographically less complex than northwestern Ontario, and thus only 22 vegetation types are identified in its FEC (Jones et al. 1983). Documentation of FECs in both regions describes in detail the common plant and soil/site associations of boreal mixedwood sites that are the focus of this review.

Despite the potential of the FEC as a planning tool, the provincial standard for planning and reporting forest management activities is the Forest Resource Inventory (FRI), which was developed in the 1960s (Ontario Ministry of Natural Resources 1993). This system describes forest cover and can be correlated to FEC types. The FRI description of forest cover is limited to the relative abundance of commercial tree species based on basal area estimated from aerial photographs, and does not account for other plant species. However, important stand structure attributes of wildlife habitat, lacking in FEC classes, are included in the FRI. These habitat attributes include stocking (an indication of canopy closure), age, and estimates of productivity from height/age relationships. While the FRI describes even-aged forest structure reasonably well, it has limited utility in uneven-aged forests. This is a significant institutional barrier to managing boreal mixedwoods under alternative silvicultural systems.

2.2 Extent of Boreal Mixedwoods in Ontario

Armson (1988) calculated that there were approximately 7 million ha of mixedwood forest in the province, assuming that approximately one-third of each of the poplar,

white birch, and spruce FRI working groups represented boreal mixedwoods. This estimate was based on an implicit species-mixture definition of mixedwood forests, and while knowing the amount of land covered by mixtures of tree species may be useful, it is not consistent with a site-based definition of mixedwoods. As such, the extent of mixedwood sites in the province may be significantly underestimated.

Adapting statistics provided by Dixon (1963) to a site-based definition, McClain (1981) estimated that approximately 45–50 percent of northern Ontario's productive forestland could be classified as boreal mixedwoods. This estimate is in close agreement with Brennan (1991), who reported that northern mixedwoods and northern hardwoods comprised 49 percent of Ontario's forest cover. Given that northern Ontario has about 21 million ha of productive forest land (Ontario Ministry of Natural Resources 1993), it can be estimated that 10–11 million ha are boreal mixedwoods.

2.3 The Physical Environment of Boreal Mixedwoods

Rowe (1972) described eight forest regions in Canada. The largest of these is the Boreal Forest Region, which forms a continuous belt from Newfoundland to the Yukon. Boreal forests occur in climates marked by long, dry, cold winters and short, moist, mild summers. Black spruce, the most abundant tree species in North America's boreal forest, forms vast pure stands, particularly in the northern latitudes. Commercial mixedwoods abound in the moister, southern portion of the boreal forest, where hardwoods are more common.

Hills' (1952) pioneering forest ecology work divided Ontario into site regions. These were defined by gradients of temperature and humidity, which increase from the north to south and west to east, respectively. Wickware and Rubec (1989) built upon Hill's work, and a variety of other surveys of surficial geology and soil types, to create a hierarchical, ecological land classification scheme for Ontario. According to their system of classification, boreal mixedwoods occur principally within five climatic ecoregions. Twenty-two ecodistricts, each characterized by a distinctive pattern of relief geology, geomorphology, vegetation, soils, water, and fauna are nested within these five ecoregions.

The large number of ecodistricts that support boreal mixedwoods attest to their diverse nature across Ontario (see Wedeles et al. 1995 for more detail). Besides these large-scale patterns of variation, there are considerable differences in both localized climate (Whitewood and MacIver 1991) and topography (Sims and Baldwin 1991). The variation in physical environments across Ontario's

boreal mixedwood range is an important evolutionary force shaping adaptive gene complexes of plants and animals. Thus, one can expect regional differences in plant responses to silvicultural treatments—differences that may alter the effects of such treatments on wildlife habitat suitability.

2.4 The Dynamics of Boreal Mixedwoods

Climatic and edaphic conditions can account for only some of the plant and animal adaptations to boreal mixedwoods. A history of disturbance, in the forms of weather, fire, insects, and man, also contributes to boreal mixedwood stand development. These processes interact with existing forest and stand structures, operating over both short-(succession) and long-term (evolution) horizons. An understanding of these processes is necessary for resource managers to make reasonable forecasts about the future development of stand, forest, and wildlife habitat conditions arising from the application of alternative silviculture systems.

2.4.1 Evolutionary Ecology

With the exception of white spruce, most boreal mixed-wood species in Ontario are also commonly found in pure even-aged stands. It is unlikely, therefore, that these species have coevolved or exist in a mutualistic state. Reconstructions of forest cover at the peak of the last ice age show that boreal tree species cohabited at sites with temperate species and migrated along the retreating ice edges fairly rapidly in response to climatic improvements for tree establishment and growth (Ritchie 1987). Thus, most boreal tree species do not depend on one another for their survival, and should do equally well in pure or mixed stands.

A larger plant and animal community perspective is considerably different from a tree community focus. (See Wedeles et al. 1995 for a review of tree communities in the boreal mixedwood forest.) Tree canopy layers alter the microenvironment in ways that directly influence floristic composition of the understory as well as of the fauna and microfauna on a given site. For example, moisture conditions created beneath the closed canopy of conifers allow feathermosses to thrive independently of the nature of the substrate (Kershaw et al. 1994). Thus, the floristic composition of the understory of a mixedwood stand may be influenced more by stocking or canopy closure than by overstory species composition or edaphic/substrate characteristics.

Unlike temperate and tropical forest trees, which rely to varying degrees upon animal vectors, all commercially important boreal tree species rely upon wind to transfer pollen and seed. This suggests an absence of coevolution between animals and trees. Ecosystems where coevolution is present, such as tropical rainforests or, to a limited degree, temperate forests, are more complicated in this respect.

Despite the absence of animal vectors of boreal forest tree pollen, important plant–animal interactions have evolved over the millennia. For instance, boreal tree species have developed defenses against insect and mammal herbivory (Rodgers et al. 1993). In a thought-provoking study, Smith (1970) described evidence for the coevolution of lodgepole pine (*Pinus contorta* Dougl.) cone characteristics and the jaws of pine squirrels (*Tamiasciurus douglasi*). Squirrels that relied upon east slope lodgepole pine (*P. contorta* var. *latifolia* Engelm.) had larger and more muscular jaws compared with coastal squirrels that relied upon nonserotinous lodgepole pine (*P. contorta* Dougl. var. *contorta*).

The authors know of no equivalent work investigating coevolution of boreal mixedwood species. However, Smith (1970) suggested that coevolution of small mammals and conifers might explain seed-crop periodicity and a variety of other tree seed characteristics, such as the resin within balsam fir seed. As white-footed mice (*Peromyscus leocopus*) prefer white spruce seed over balsam fir seed (Abbott 1962), this might explain the relative abundance of fir in the understorey of boreal mixedwoods. One wonders if the late flushing of black spruce evolved from the selection pressure of eastern spruce budworm (*Choristoneura fumiferana* [Clem.]) outbreaks.

Other forms of plant and animal interactions may also exist in the boreal forest, yet remain to be discovered. Mycorrhizae have been shown to improve tree establishment and growth by increasing root absorption surface area, translocation of nutrients, and disease resistance (Pritchett 1979). Recent work in the Pacific Northwest has demonstrated that mycorrhizae also allow for the transfer of nutrients between plants of different species. This form of mutualism is reshaping perceptions of forest ecosystem function and classical neo-Darwinian theories of evolution (Amaranthus and Perry 1994). In the same geographic region, Maser et al. (1978) demonstrated the importance of small mammals as vectors of mycorrhizae spores. McComb and Hansen (1992) also suggest that the burrowing of small mammals is important for soil aeration and that it mixes organic matter, thereby benefiting tree growth.

Plants and animals evolve morphological and chemically complex adaptations to their physical environment. Animals can also exhibit behavioral adaptations. Some of the more obvious animal adaptations to the harsh climate of boreal forests include migration and hibernation. But many animals use different habitats at different times of the year. The authors are unaware of any studies that demonstrate within-species animal behavioral adaptations to different environments in Ontario. Most animals found within Ontario's boreal forest are common throughout the range of this forest, but evidence does exist for geographic variation in animal behavior in other boreal forests. Crête (1988), for example, implied that migrating behavior is unique to the Alaskan subspecies of moose (Alces alces andersoni), and Hansson (1986) described geographic variation in the feeding behavior of voles (Clethrionomys spp.) in Sweden.

What are the implications of these evolutionary forces in the context of alternative silvicultural systems? The application of various systems may evoke different selection pressures and change tree mating patterns and plant–animal community interactions. Animal behavioral responses to different habitat types will also vary between regions and site types. Genecology studies are required to explore and understand the consequences of alternative silvicultural systems upon the genetics of in boreal mixed-wood tree species.

2.4.2 Succession and Stand Dynamics

Succession and stand dynamics are interrelated concepts, with the former being the traditional domain of ecologists and the latter that of foresters (Oliver and Larson 1991). The processes that make up succession and stand dynamics work on time scales much shorter than evolution. Stand dynamics refer to changes that alter ecosystems to a lesser degree than that normally associated with succession. Succession is generally viewed as the gradual change of a community (or stand) from one type to another, although theories of successional mechanisms are a source of great debate (see Wedeles et al. 1995).

Aside from forest management activities, fire and insects have the greatest impact on boreal forest structure and succession (Dix and Swan 1971, Cogbill 1985). Fire intervals range from 20 to 135 years in Ontario's boreal forest, with drier climates having more frequent and hotter fires (Ward and Tithecott 1993). However, no single successional pathway appears to follow fires. Postfire vegetation is a complex function of the preburn stand characteristics, time of burn, severity of burn, and other site-specific features (Zoladeski and Maycock 1990, Payette 1992).

Eastern spruce budworm epidemics tend to occur in 40–70 year cycles. In eastern Canada, higher rainfall reduces the role of fire and increases the importance of budworm as a means of cycling balsam fir stands (MacLean 1984). Zoladeski and Maycock (1990) noted a similar pattern in the balsam fir forests of northwestern Ontario.

Silviculture systems attempt to mimic, to one degree or another, successional processes. Most forest management endeavors seek to encourage specific patterns of succession so as to create desirable forests. The application of different silvicultural systems can maintain boreal mixedwoods or gradually shift them to favor the development of pure species stands.

Although stands of a single species are common features of the fire-driven boreal forest ecosystem, there may be advantages to growing trees in mixtures. For example, the conifer component of a stand can provide cover and the hardwood component can provide food for many boreal wildlife species, such as moose or ruffed grouse (*Bonasa umbellus*).

Many foresters in Ontario have observed that pure white spruce plantations are subject to intense budworm attack and frost damage. These problems may not be as prevalent for white spruce in mixedwood stands. Pfister and Hay (1988), (in Danell et al. 1991a), suggested an "Associational Plant Refuge Hypothesis". They predict that highly palatable plant species gain protection from herbivores when associated with plants of lesser palatability. This may be the case for white spruce in a mixedwood stand under budworm attack, but the hypothesis has yet to be tested.

Through nutrient cycling, herbivores play important roles in forest succession and stand dynamics. Pastor et al. (1993), studying the effect of moose browsing on nutrient cycles, developed two hypotheses. In the first, moose were predicted to enhance site productivity by allowing sunlight to reach the forest floor, and by depositing droppings. In the second hypothesis, moose decreased nutrient availability in the litter layer by encouraging the development of spruce through preferentially feeding on hardwoods. Their study of moose exclosures on Isle Royale found the latter hypothesis to be supported.

Some evidence suggests that tree mixtures are inherently more productive than are single species stands, both from a site-utilization and nutrient-cycling perspective. For example, the calcium content and deep root systems of poplar can improve site quality and the growth response of conifers by ameliorating nutrient and moisture regimes (Matthews 1989). Experimental mixed plantations of Scots pine (Pinus sylvestris L.) and Norway spruce (Picea abies L. Karst.) are significantly more productive than are single species plantations. Soil microbes and fauna may be more diverse in the mixed litter, thereby making nutrients more readily available and possibly stimulating the production of fine roots (McKay and Malcolm 1988, Cannell et al. 1992). As the following sections of the report illustrate, greater site productivity is generally associated with higher wildlife carrying capacities. In this manner, mixedwood forest may be highly desirable from a wildlife management perspective.

Strong and La Roi (1983) noted that the different rooting habits of mixedwood tree species allow such trees to exploit varying niches without competing with one another. Specifically, the roots of spruce trees tend to exploit the surface layers of the soil, while those of pine and poplar deeply penetrate the soil horizon. For these and other reasons, boreal mixedwoods should be able to produce more biomass when compared with pure stands of the same species. The question remains as to whether tree interrelationships in boreal mixedwoods are positive or negative (Odum 1993). Studies of the productivity interrelationships of boreal mixedwood trees in Ontario are underway (MacDonald 1993).

Most scientists agree that within-stand structural diversity and species composition leads to greater species diversity for both plants and animals. Songbirds, for example, are more diverse and reach much higher densities in mixedwoods than in other boreal forest types. Higher diversity may in turn buffer the forest against species extinction and may build resistance to environmental change. However, diversity is not like an economic commodity; more is not always better. At a global or perhaps even forest-level scale, maintaining maximum species richness is an important goal. At any smaller scale (the forest stand for example), quality is more important than quantity (Noss 1993). Increasing the number of species in a landscape, as could by done by fostering only mixedwood stands, does not necessarily contribute to forest health or proper forest management. The role of high diversity mixedwood stands relative to the lower level of diversity common to the boreal forests should be considered in assessments of the value of mixedwoods.

2.5 Landscape Ecology and Biodiversity

Until recently, the processes of climate, evolution, succession, and stand dynamics were thought to provide an adequate explanation of forest cover patterns. Forest pattern itself has now been perceived to influence forest ecosystem function. This understanding of pattern influencing process is the foundation of landscape ecology, which emerged as a science in the late 1970s.

Ecosystems and their related processes and patterns are scale dependent. At large scales, the shape and spatial arrangement of vegetation types have a significant impact on the movement of materials and energy within a system (Turner 1989). Because wildlife can move across many stands and may depend upon the forest, open or nonforested land, and aquatic ecosystems, landscape ecology embodies a powerful new way of thinking (McGarigal and Marks 1994).

Alternative systems to the conventional clear-cutting of boreal mixedwoods will generate different vegetation patterns in the forested landscapes of Ontario. Therefore, studies involving a variety of silvicultural systems should be conducted to determine the large-scale impacts of these new patterns.

Several examples of managing forests to mimic natural disturbance regimes are currently underway. The small openings created by spruce budworm damage have led researchers to test small patch cutting in an experimental forest area managed by Laval University (L. Belanger, pers. comm.). On the White River Forest in northern Ontario, clear-cut size, orientation, and distribution are planned to follow historical fire patterns (Domtar Forest Products 1993).

It would seem that seed-tree systems, and to a lesser extent shelterwood systems, mimic certain types of fire. In addition, shelterwood and selection systems mimic tree gaps created by differential mortality of trees reacting to a variety of biotic and abiotic forces. Although fire and budworm are the most obvious and important agents of change, smaller scale disturbances are also present in boreal mixedwoods. Thus, a greater latitude in the application of silvicultural systems makes sense within the forest mosaic of northern Ontario.

Hunter (1990) argued persuasively that different patch sizes and different silvicultural systems throughout the landscape should maintain or enhance diverse forest and stand structures.

In an attempt to rationalize the relative importance of different patch sizes in a forest, Hunter (citing Harris 1984, among others) examined size distribution in nature for lakes, soil types, and stands. An inverse "J" distribution with very high frequencies of small patches (10–100 ha) versus few large patches was revealed. This often matches patterns caused by spruce budworm attacks in northeastern North America. However, these observations were made in forests that are not dominated by the large and frequent fires of the boreal forest. When Hunter (1993) examined boreal forests in northern Quebec and Labrador, he found that patch sizes of 1 000–10 000 ha were the most common, and that physiographic features, namely drainage and lake patterns, influenced patch size. He concluded his analysis with an ethical perspective:

In terms of human spatial scales and human life spans, a 5 000 ha clear-cut would stretch to the horizon and last almost forever, and thus seem like a catastrophe best avoided. To view ecosystems from a larger spatial and temporal

perspective requires more than just a basic knowledge of ecology and evolution: it requires a profound understanding.

2.6 Conclusion

Boreal mixedwood tree species respond to silvicultural systems in a fairly predictable manner. However, the responses of the forest ecosystem and wildlife habitat are more difficult to predict.

An imperfect state of knowledge about forest and wildlife ecology, and the wide array of stand conditions associated with boreal mixedwoods, demands an adaptive management approach (Lee 1993) that recognizes the uncertainty of natural systems behavior (Ludwig et al. 1993) This is best accomplished by maintaining a diverse forest structure and experimenting with a broad array of silvicultural systems.

3.0 SILVICULTURAL SYSTEMS

3.1 Clear-cutting

"Commercial" clear-cutting or removing all of the merchantable timber from a site (Davidson et al. 1988), has long been the standard practice in Ontario's boreal mixedwoods. Thus, commercial clear-cuts may, or may not, have all standing timber removed, depending upon the merchantability of the trees on the site. Most authors who have written on the history of boreal mixedwood management in Ontario, or provided a dated description of "present" management practices (e.g., MacLean 1960, Heikurinen 1981, Armson 1988), report a harvesting and silvicultural scenario that is best described as commercial clear-cutting followed by planting or natural regeneration. Harvested areas not commercially clear-cut were usually subjected to "selective" or "partial" cutting that could often be characterized as high-grading.

Commercial clear-cutting is still the dominant silvicultural system used in boreal mixedwoods in Ontario (Scarratt 1992, MacDonald 1993), and it is the traditional method used in other North American mixedwood forests similar to those of Ontario (western Canada, Schneider 1988; eastern spruce—fir, Blum et al. 1983; Alaska white spruce—hardwood mixtures, Zasada and Argyle 1983). Commercial clear-cutting of Ontario's boreal mixedwoods has typically focused on the harvesting of mature jack pine, black spruce, and white spruce. Balsam fir, aspen, and white birch are disregarded. These practices arose from the utility of softwood species for both pulp and timber, combined with limited markets for hardwoods. However, as the commercial utility of the hardwood (mainly aspen) component of mixedwood forests increases, based on

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growing demand for products such as aspen-based Oriented Strand Board (Beck et al. 1989, Brennan 1991), the species mix taken from boreal mixedwoods is likely to change accordingly. While merchantability is the primary (or only) factor determining harvest in a commercial clear-cut, both merchantability and renewal considerations are key factors in a silvicultural clear-cut. Smith (1986) suggested the term "silvicultural clear-cut" be used to refer to areas where there has been a complete removal of vegetation and where all the growing space is available for new plants. Boreal forest management in Ontario and elsewhere has suffered from an imprecise use of terms related to clear-cutting, and the traditional lack of differentiation between commercial clearcutting and silvicultural clear-cutting is a prime example of this.

Clear-cutting (either commercial or silvicultural) is used in most applications because it is, in theory, the simplest way of creating an even-aged stand (Smith 1986, Matthews 1989). The regeneration objective of boreal silviculture in Ontario has usually been to create even-aged black spruce, white spruce, or jack pine stands. Although there is an equivocal record of success in achieving this objective on mixedwood sites in Ontario (Brand and Penner 1991), this rationale for use of the clear-cut silvicultural system still persists (Arnup et al. 1988).

3.2 Modified Clear-cut Systems

3.2.1 Seed-tree System

In the seed-tree system, the stand is cut clear, except for a few trees that are left standing either singly or in groups to provide seed to restock the cleared area (Smith 1986, Forestry Canada 1992). There is relatively little documentation on the use of the seed-tree system in boreal mixedwoods. Lyon and Robinson (1977) conducted an extensive investigation of the utility of this system for regenerating white spruce in Ontario. They found the system could be successful if windfirm individuals were selected for retention, and if mechanical site preparation was used to ensure a receptive seedbed. The periodicity of white spruce seed crops is a concern when applying the system and requires that the cuts and site preparation be timed to take advantage of good seed years.

The use of the seed-tree system for regenerating black spruce is severely hampered by the susceptibility of this species to windthrow (Blum et al. 1983, Arnup et al. 1988). While it may be practical to use the system if groups of trees rather than individuals are left standing, even then one is perhaps only forestalling, and not preventing, blowdown. However, given the more frequent and reliable production of seed from black spruce as compared with white spruce (Sims et al. 1990, Bell 1991), the system may be practical in some circumstances.

3.2.2 Strip Cutting

Strip cutting involves harvesting a crop of trees in strips, over one or more operations (Forestry Canada 1992). The most common implementation of strip cutting is a two-cut system in which alternate strips are cut; intervening strips are left uncut. In progressive strip clear-cutting, more than two cuts are used in a progression across a designated area so that a higher proportion of uncut area is left after the first cut. A leave period between each cut is provided in which natural regeneration can take place (Jeglum and Kennington 1993).

Strip cutting implies natural or assisted natural regeneration. The premise being that by leaving a seed source close to a cutover area, a natural supply of seed will facilitate reforestation, and that uncut strips will provide the cut area with some protection from harsh environmental conditions following harvest.

In Ontario's boreal forests, strip cutting has been used primarily in black spruce stands. The relatively low productivity of black spruce lowland sites has made them good candidates for this approach, because they often do not warrant the expense of planting, yet are unlikely to suffer from competition. However, strip cutting may also have some application on mixedwood sites. Jeglum and Kennington (1993) suggested that strip cutting has good potential for white spruce—black spruce—trembling aspen mixtures, and for white spruce—tamarack (*Larix laricina* [Du Roi] K. Koch) mixtures. The presence of black spruce and tamarack on these sites indicates that they would be less productive than rich mixedwood sites, and therefore less prone to competition problems.

Strip cutting has been recommended to reduce the susceptibility of spruce—fir forests to spruce budworm (Lancaster 1984, Blum 1985); by splitting the forest into a variety of age classes the suitability for widespread budworm infestation declines.

Operational concerns associated with strip cutting include strip width, strip orientation, and site preparation. For black spruce and white spruce, strip widths of about 40–60 m are most commonly recommended (Jarvis et al. 1966, Auld 1975, Jeglum 1987, Bell 1991). For birch, strips of approximately 50 m are common (Marquis 1969, Perala and Alm 1990).

With regard to strip orientation, the long axis of the cut is usually made at a right angle to the prevailing wind direction so as to facilitate seed dispersal. This also minimizes windthrow, which is more likely to occur if the prevailing wind direction is parallel to the cut (Alexander 1986, Smith 1986). Jeglum and Kennington (1993) suggested that for black spruce regeneration in Ontario, strip orientation may be more important for protecting the

germinant than for seed dispersal. The leave strips provide protection from the drying effects of sun and wind and preserve moisture longer in surface horizons. Resulting conditions facilitate seedling germination and establishment.

Site preparation is an important operational consideration for strip cutting applications, particularly if spruce reproduction is the objective. Studies in the prairie provinces have shown that strip cut mixedwood sites that have been site-prepared have two to ten times as many white spruce seedlings as sites that have not been prepared (Jarvis et al. 1966, Johnson and Gorman 1977).

From a silvicultural point of view, a drawback to the strip cut method is that it restricts the types of silvicultural tools that can be used. For example, the threat of the adjacent uncut forest catching fire restricts the use of prescribed burns, and aerial tending is often impractical due to the interspersion of cut and uncut areas.

3.2.3 Two-pass Harvesting

Two-pass harvesting² (Wedeles et al. 1995), was developed largely for implementation in the mixedwoods of Alberta and Saskatchewan (Brace and Bella 1988, Brace Forest Services 1992, Sauder 1992). Using careful harvesting techniques, commercially viable crops of both hardwoods and softwoods are harvested from the same land during separate operations. Mature hardwood is removed from a stand in such a way as to minimize damage to immature softwoods and advance regeneration. The remaining softwoods form the second cut some years later when they have reached a harvestable size.

Two-pass harvesting is the logical result of several related factors: namely, the recent increase in the value of aspen and poplar; the historical difficulty of reestablishing white spruce by planting; the growth response benefits of releasing white spruce from aspen competition; and the desire to minimize waste and maximize the potential fiber harvest from mixedwood sites.

The two-pass harvesting system, as employed in western Canada, is intended for application in mixedwoods having a white spruce understory and an aspen and poplar overstory. Ontario's mixedwoods contain other species, the most significant being balsam fir. The utility of the system in Ontario will be influenced by the amount of fir and shrub species present in the mixedwood stands, the ability to control fir and shrub regeneration, and the merchantability of the fir.

Studies of two-pass harvesting in western Canada (Brace Forest Services 1992, Sauder 1992) indicated that con-

ventional feller bunchers and skidders could be used effectively in the first cut of the two-pass system if necessary precautions were taken to protect residual trees. In Ontario, there is considerable interest in Scandinavian single-grip harvesters and cut-to-length (CTL) systems (Jewiss 1992). Although the western studies did not show that CTL harvesters were more effective in avoiding damage to standing trees, as experience with them increases they may perhaps provide "soft" alternatives to traditional harvesting technologies.

3.3 Shelterwood System

In the shelterwood system, the stand is removed in a series of cuts made at reasonably short intervals. A key aspect of the system is the establishment of essentially even-aged reproduction under the protection of the partial forest canopy or "shelterwood" (Smith 1986, Forestry Canada 1992). While a shelterwood system can involve three or more stand entries, for economic reasons it generally only involves two such entries. The trees left after the initial cut are usually the most vigorous. As such, they are the best trees for a seed source and for additional volume growth before the final cut (Blum et al. 1983).

There are four general variations to the spatial and temporal arrangement of cuts in a shelterwood system: namely, uniform, strip, group, and irregular (Smith 1986, Matthews 1989). In the uniform system, which is the most commonly used system in North America, the forest canopy is opened uniformly over the entire stand. In the strip system, several entries are made into the stand as cutting stages move progressively across the stand in strips. In the group system, the cut occurs in a pattern of expanding groups or patches. Groups are generally arranged to correspond to existing patches of advance regeneration, with all of the groups eventually converging to cover the entire stand. In the irregular system, the regeneration period is extended beyond that of a traditional shelterwood, thereby resulting in a new stand that is less even-aged. As different species seldom reach maturity at the same stages of stand development, the irregular shelterwood method provides the flexibility to manage for several species at once.

In Canada, the uniform shelterwood method has been used in boreal mixedwoods of the Prairie Provinces, and the spruce—fir forests of the Maritimes (Baldwin 1977, Hannah 1988). Very little operational application has occurred in Ontario. Based on experience from elsewhere in the country, Wedeles et al. (1995) concluded that the shelterwood system may be most appropriately used in Ontario's boreal mixedwoods to help regenerate white spruce and possibly white birch in areas where balsam fir

² Recently, the term "two-phase" harvesting has been used to describe this silvicultural system. The authors use the term two-pass harvesting here to be consistent with most of the relevant literature.

and aspen would otherwise dominate. Leaving a high proportion of white spruce or white birch in the shelterwood overstory after the initial cut, with a few scattered aspen (to suppress sucker growth), may encourage the regeneration of these species.

Operational considerations associated with shelterwood harvesting include cutting patterns (number and timing of cuts, number and type of trees removed), site preparation, and damage to residual trees.

The initial cut should be made before a stand has reached maturity, so that the residual trees can continue to grow rapidly without danger of windthrow and decay (Blum et al. 1983). The least desirable trees should be removed in the initial cut. If the objective is to encourage the regeneration of one or more particular species, such as white spruce or white birch, then trees of any undesirable species (e.g., balsam fir, aspen) should be removed.

The number of trees removed in the initial cut is generally determined by observation and experimentation, and will vary for different species and sites (Smith 1986). The residual canopy should provide a reasonable trade-off between controlling unwanted vegetation and providing enough light for seedling establishment (Godman and Tubbs 1973).

The final cut should occur as soon as the seedlings have established deep root systems, can be exposed to complete sunlight, and dominate the unwanted vegetation. If there is no delay in the development of the new regeneration, this usually occurs 3 to 10 years after the initial harvest. As the final cut will often cause injury to the new stand, it should take place while the seedlings are still flexible. Winter logging, where snow covers the seedlings, can help protect the new stand.

Some form of site preparation to control balsam fir and other vegetation, and at the same time provide a receptive seedbed, seems essential to encourage white spruce regeneration under the shelterwood system (Jarvis et al. 1966).

3.4 Selection System

The selection method consists of frequent and careful felling of trees in all size classes, either singly or in small groups or strips (Forestry Canada 1992). The resulting stand structure can be considered a mosaic of small evenaged stands. The care required to maintain both horizontal and vertical stand structure sets the selection system apart from selective cutting (i.e., economic selection, diameter limit cutting, partial cutting, high-grading). The selection system maintains a large inventory of potentially harvestable growing stock compared with selective cutting and evenaged management systems.

The idealized, irregular, uneven-aged stand in a selection forest has an inverse J-shaped curve depicting a frequency size class distribution with a high number of individuals in young age/size classes and a small number in large age/size classes. The selection method involves removing trees in several age/size classes so that the idealized distribution is maintained. By setting a maximum diameter goal for a stand, establishing a cutting cycle (interval between fellings), and determining a minimum basal area, a variety of wood production and multiple use goals may be realized in a selection forest.

Selection harvesting maintains a diverse stand structure on a site throughout the management cycle. For this reason, selection harvesting is useful when commercial forestry needs to be conducted in a manner that is sensitive to environmental issues and is concerned with protecting water quality in riparian areas by maintaining forest cover, retaining scenic values, protecting sensitive soils from erosion and loss of nutrients, or maintaining some forms of wildlife habitat.

The selection system has become fairly common practice in central Ontario's tolerant hardwoods (Anderson et al. 1990). Experience with the system in the province's boreal mixedwoods is rare, however, because of the predominant even-aged forest structure, poor road access prior to the 1980s, the dominant pulpwood end use, and the traditional nonuse of hardwoods.

Selection harvesting might be used in boreal mixedwoods to manage for high-value, largediameter veneer logs. It could also be useful for coping with problems associated with imbalanced age/size class structures. Ontario's boreal forest presently has an abundance of mature to overmature forest and young forest; however, a considerable shortfall of commercially available wood is anticipated in 20-40 years when the older forests are no longer commercially viable and the younger forests are not yet harvestable. Rather than accelerate diameter growth through juvenile spacing, it may be possible to manage overmature stands by removing large trees prone to decay. This would create openings and allow smaller trees to reach harvestable size. In this way, older stands could be made to last longer, rather than relying upon efforts to speed up the development of younger stands.

Operational concerns associated with selection harvesting include minimizing residual stand damage, ensuring appropriate regeneration, and regulating the cut. Residual tree damage from felling and skidding is a significant concern when implementing selection systems. Scrapes and broken tops of residual trees following cutting allow the entry of infectious agents. This can lead to significant losses in subsequent harvests. Careful planning and operating are needed to avoid such damage.

Despite careful management of tree size distribution and harvesting in selection systems, successional changes in species composition may occur unless additional measures are used to ensure regeneration of desirable species. Selection cutting in boreal mixedwoods tends to regenerate tolerant firs and gradually eliminates intolerant hardwoods. Although this would decrease the requirement for herbicides, increased fir composition may reduce the growing space for the more commercially valuable spruce trees and may attract budworm. Mechanical site preparation to expose seed beds and reduce fir and other competing vegetation may be necessary in selection forests. The use of group selection rather than individual tree selection may make for more effective site preparation activities and spruce reproduction.

4.0 EFFECTS ON BIRDS

Mixedwoods are by far the richest boreal habitat for birds; approximately 150 species breed here (Welsh 1981, 1987; James 1984c). Densities of 600–1 000 pairs/km² are common and, during severe insect outbreaks, densities of 2 000 pairs/km² often occur. In comparison, jack pine stands and lowland conifer forests generally support only 100–200 pairs/km², upland spruce may support 200–400 pairs/km², and mixed age deciduous stands rarely have more than 600 pairs/km² (Welsh 1981).

Approximately 85 species of terrestrial perching birds are totally dependent on some stage of the boreal forest for their livelihood. Of these, approximately 20–25 species are wood warblers (family Parulidae). Other significant groups are thrushes (family Turdidae), finches and sparrows (family Fringillidae), flycatchers (family Tyrannidae), swallows (family Hirundinidae), vireos (family Vireonidae), and woodpeckers (family Picidae).

4.1 Habitat Affiliations

Each bird species has its own habitat needs and affinities. While it is not practical to review the requirements of each species here, some particular aspects of bird habitat affiliations are worthy of note and relevant to subsequent discussions. The habitat requirements of many of Ontario's forest nesting birds have been summarized by James (1984a, 1984b, 1984c) and Baker and Euler (1989). Cadman et al. (1987) described the distribution and habitat affiliations of all birds that breed in Ontario.

4.1.1 Snags and Dead and Downed Timber

Snags provide habitat for birds by supplying nesting cavities, and perching and foraging sites. Approximately 25 species of birds native to northern Ontario are cavity nesters (James 1984a). In some locations, the lack of suitable nesting sites may limit the presence of such birds (Dickson et al. 1983). Birds such as woodpeckers feed on

the insects that invade trees when they die. Dead and downed woody materials (i.e., logs and slash) also provide important habitat for ground-nesting and foraging species, such as juncos (*Junco* sp.) and sparrows.

4.1.2 Stand Age

Many species of forest-dwelling birds have affinities for particular successional stages (Conner and Adkisson 1975; Crawford and Titterington 1979; Titterington et al. 1979; Welsh 1981, 1987; DeGraaf et al. 1993; Farr 1993), although not all share this characteristic (Webb et al. 1977, Welsh 1987, Degraaf et al. 1993, Farr 1993). Breeding bird communities are found in mixedwood forests of all ages.

Some of the most relevant work on this subject in Ontario has been completed by Welsh (1981, 1987, 1988), who conducted bird surveys near Manitouwadge in a number of mixedwood stands that ranged from 1-220 years since the last disturbance. He found significant differences in bird species composition in stands of various ages, based on a classification of study plots as early, mid-, or late successional. Species typical of early successional forest included the alder flycatcher (Empidonax alnorum), chestnut-sided warbler (Dendroica pensylvanica), mourning warbler (Oporornis philadelphia), and white-throated sparrow (Zonotrichia albicollis). Midsuccessional species included the veery (Catharus fuscenscens), red-eyed vireo (Vireo olivaceus), black and white warbler (Mniotilta varia), and American redstart (Setophaga ruticilla). Late successional species included the yellow-bellied flycatcher (Empidonax virescens), golden-crowned kinglet (Regulus satrapa), bay-breasted warbler (Dendroica castanea), and ovenbird (Seiurus aurocapillus). Crawford and Titterington (1979) found similar results based on the five seral stages they used to classify bird habitat in spruce-fir forests in Maine. So also did Temple et al. (1979), who used four seral stages to classify mixed forests in the state of New York.

Welsh (1987) noted that some bird species occur in stands of all ages. He grouped species into three categories based on their manner of habitat use: namely, 1) species that have almost identical habitat associations in very different seral stages (e.g., Swainson's thrush [(Catharus ustulatus]); 2) species that take advantage of opportunities that occur in a particular successional stage and are replaced by others at an older stage (e.g., white-throated sparrow [early] and ovenbird [late]); and 3) species that are extremely versatile, can occupy very different niches, and thus persist in many stages (e.g., magnolia warbler [Dendroica magnolia]).

There is some uncertainty about the relationship between stand age and bird species diversity. Welsh (1987) found no discernable trend in either bird density or species diversity in stands older than 1 year (although the postharvest stands he studied had been selectively cut and therefore contained some live trees). Similarly, Back (1979) found no relationship between bird species diversity and ecological age in aspen-birch forests, based on census data from the Lake States, New England, New Brunswick, Ontario, Manitoba, and Saskatchewan. This is contrary to the findings of Temple et al. (1979) (based on studies in mixed hardwood-coniferous forests in New England, Quebec, Ontario, Michigan, and Minnesota), and Capen (1979) (for white pine [Pinus strobus L.]-red pine [P. resinosa Ait.]-jack pine communities). DeGraaf et al. (1993) found that species richness was similar in regenerating/seedling, sapling, and mature stands, and that pole-timber stands had the fewest breeding bird species in New England hardwoods, spruce-fir, and white pine communities. Other similar studies found that bird density and species diversity were lowest in midsuccessional pole-sized stands (Conner and Adkisson 1975, Yahner 1986, Thompson et al. 1993).

In an insightful analysis, Telfer (1993) compared habitats used by 146 bird species in boreal forests of the prairie provinces with the amount of land in young (0–25 years), immature (26–50 years), mature (51–150 years), and old (>150 years) forests. He found that young and immature forests had fewer species than expected based upon their areal extent, and mature and old forests had more species than expected. Mature forests had the greatest species diversity. Although old forests had relatively low species diversity, they had the greatest discrepancy between this and areal extent.

The value of old forests as habitat for certain birds and other wildlife is stressed repeatedly in the literature (Hunter 1990, Thompson and Welsh 1993). Telfer (1993) suggested that songbird use of old forests is higher than expected because they contain more snags and woody debris than do other forest types. Many bird species that use mature forests will also use old forests, as will some species that are more common in the young and immature age categories. In old mixedwood forests, which may contain only an occasional large tree (probably white spruce) in the overstory and smaller trees emerging through small gaps in a mountain maple (*Acer spicatum L.*)—beaked hazel (*Corylus cornuta Marsh.*) thicket (Rowe 1961, Day and Harvey 1981), it would not be uncommon to find bird species that are also found in younger stands.

4.1.3 Structural Diversity and Tree Species Mixtures

The high diversity of bird species in mixedwoods can be explained both by the diversity of plant species and the structural diversity of the forests. Several studies have shown the positive relationship between structural diversity and bird species diversity (MacArthur and MacArthur 1961, Anderson 1979, Noon et al. 1979, James and Wamer 1982, DesGranges and Rondeau 1993a). The more plant species in a stand, the greater the structural diversity; consequently, mixed-species stands are often more structurally diverse than are single-species stands.

There is relatively little literature on songbird use of individual tree species in boreal mixedwood forests. Temple et al. (1979) used an ordination technique based on the vegetation surrounding the singing perches of territorial males (which they assumed was a reflection of the vegetation in the bird's territory) to identify tree species and habitat affinities of bird species in the mixed forests of northern Wisconsin (Table 1). Although these forests are less boreal than Ontario's boreal mixedwoods, the results are interesting as many of the tree species and most of the bird species are common to both. It is important to remember, however, that individual birds of the same species may use habitat differently in different parts of their range (Welsh 1987).

The value of a mix of tree species is apparent from the relative densities of birds in mixedwoods compared with their densities in less complex stands. Crawford and Titterington (1979) suggested that the degree of hardwood admixture with softwoods is a key factor determining bird populations in spruce–fir forests.

James (1984c) stated that the greatest potential damage to bird populations in boreal forest regions would occur through the loss of eastern hemlock (Tsuga candadensis [L.] Carr.) and balsam fir trees, because of their extraordinary value as habitat. In contrast to this, Crawford (1985) suggested that stands of fir, with little admixture of hardwood and sparse understory growth, are some of the poorest bird habitat in North America. Similarly, Crawford and Titterington (1979) found that stands composed primarily of balsam fir contained an impoverished avifauna, with an average of only 128 breeding pairs/40 ha and a total of 20 bird species. Stands of spruce and fir averaged 190 pairs/40 ha and 26 species. An admixture of hardwoods increased population to 231 pairs/40 ha and 24 species. Crawford and Titterington (1979) believe that spruce stands, with more foliage and limb area than fir stands, support greater populations of endemic insects that are valuable for foliage-gleaning birds. DeGraaf et al. (1993) found little difference in bird species composition between mature stands of spruce-fir and balsam fir in New England.

Apparent avifaunal preferences for a particular tree species are perhaps a result of the insects associated with that tree. Spruce budworm, for example, is one boreal forest insect to which many bird species are ecologically linked.

Table 1. An interpretation of habitat ordination results from breeding bird communities of mixedwood forests in Wisconsin. *From* Temple et al. (1979).

Alterations of vegetation within a stand	Bird species that are likely to become more abundant	
1. Increasing abundance of pine	Sharp-shinned hawk, red-breasted nuthatch, hermit thrush, redstart, blackburnian warbler, Nashville warbler, pine warbler	
2. Increasing abundance of hemlock	Pileated woodpecker, yellow-bellied sapsucker, yellow-bellied flycatcher	
3. Increasing abundance of spruce or fir	Cedar waxwing, yellow-bellied flycatcher, swainson's thrush, redstart, parula warbler, blackburnian warbler	
Increasing abundance of yellow birch and sugar maple	Black-billed cuckoo, downy woodpecker, woodpewee, least flycatcher, crow, brown creeper, veery, robin, warbling vireo, red-eyed vireo, Connecticut warbler, chestnut-sided warbler, black-throated green warbler, black and white warbler, Tennessee warbler, indigo bunting, rufous-sided towhee, rosebreasted grosbeak	
5. Increasing abundance of aspen	Yellow-shafted flicker, hairy woodpecker, house wren, veery, yellowthroat, mourning warbler, chestnut-sided warbler, song sparrow, white-throated sparrow	
6. Increasing average basal area of trees	Pileated woodpecker, solitary vireo	
7. Increasing density of trees per unit area	Scarlet tanager, ovenbird	
8. Increasing density of understory	Veery, black-throated blue warbler, Canada warbler	

4.1.4 Eastern Spruce Budworm

The role that mixedwoods serve as "habitat" for spruce budworm also enhances their importance as habitat for many species of songbirds. At least 15 species of these, mostly warblers and all common to boreal mixedwoods, increase in population as a result of increases in endemic numbers of budworm (Kendeigh 1947, Crawford 1985). During budworm epidemics, the diets of insectivorous birds can be made up almost entirely of this insect.

Much has been written about the value of birds in controlling budworm populations (Kendeigh 1947, Takekawa et al. 1982, Torgersen and Campbell 1982, Crawford et al. 1983, Crawford 1985, Langelier and Garton 1986). Birds can reduce budworm numbers by 70-87 percent in a single summer (Torgersen and Campbell 1982, Crawford 1985) when populations are not at epidemic levels. Diamond (1993) suggested a parallel between severe declines in populations of Tennessee warblers (Vermivora peregrina) in Saskatchewan and recent increases in outbreaks of spruce budworm in areas formerly much more densely populated by this bird. The beneficial effect of songbird predation is not in eliminating epidemics, but in preventing or dampening epidemics that do occur. Once populations are epidemic, bird predation has little effect (Crawford 1985).

Langelier and Garton (1986) suggested the following silvicultural and management guidelines for creating habitat favorable for birds that prey upon western spruce budworm:

- · plan for horizontal and vertical diversity;
- · avoid clear-cuts larger than 16 ha;
- · provide edge habitat;
- · avoid high-grading;
- · avoid homogenous, plantation-like stands;
- · leave some slash after harvesting operations;
- · avoid herbicide use; and
- · provide snags for cavity-nesting birds.

4.2 Neotropical Migrants

Neotropical migrant birds overwinter in Central or South America. Approximately 60–70 percent of the bird species that breed in boreal mixedwoods are neotropical migrants, with warblers, vireos, thrushes, and flycatchers being the most numerous species. There is evidence that populations of many of these birds are declining (Terborgh 1989, Hussell et al. 1992, Johnston and Hagan 1992, Robbins et al. 1993, Smith et al. 1993), although regional variations make it difficult to extrapolate to broad areas for some species (Sauer and Droege 1992, Robbins et al. 1993).

While much of the attention and research on neotropical migratory bird populations has originated in the United States, there is evidence that population declines are also occurring in Canada and Ontario. Of 33 species of neotropical migrants (including many which nest in boreal mixedwoods) monitored at the Long Point (Ontario) Bird Observatory from 1961-88, 29 species showed negative rates of change (Hussell et al. 1992). The declines were statistically significant (p < 0.05) for 15 of these species. Species that suffered the most precipitous declines included the wood thrush (Hylocichla mustelina) (-6.0 percent per year), yellow-bellied flycatcher (-5.4 percent per year), and northern waterthrush (Seiurus noveboraceusis) (-4.0 percent per year). (A population of 100 individuals in 1961, suffering a 6 percent decline per year, would be reduced to 19 individuals by 1988. A population decline of 4 percent per year would leave 33 individuals.)

Although much attention has focused on the loss of tropical forests as a primary reason for these declines, the actual situation may well be more complex. Cox (1985) and Sherry and Holmes (1993) argued that migratory bird populations are limited simultaneously in summer and winter by a dynamic equilibrium between fecundity (which occurs in the summer) and mortality (which occurs mostly in the winter). Cox (1985) stated that a population whose overwinter survival was temporarily increased would expand into a greater array of breeding habitats. Conversely, improved breeding season fecundity would also, in a compensatory manner, increase the range of habitats in which individuals were found in winter. As a result, silvicultural systems and other management practices that affect the productive nature of mixedwoods (for birds) may have significant impacts on populations that are already declining and vulnerable.

As mature and overmature mixedwoods are harvested using the clear-cut system, and their areal extent decreases in proportion to younger age classes, populations of migrant species dependent on this mature habitat will also decline. Other species that are more adapted to younger, regenerating conditions may increase. However, the authors believe that it is not appropriate for biologists and foresters to presume that the net effects of mixedwood management on songbirds are negligible if overall densities or biomass of birds remain constant. The fate and importance of individual species should not be dismissed simply because "on balance" the numbers of birds do not change.

4.3 Stand-level Effects

4.3.1 Clear-cutting

Many studies have examined the effects of clear-cutting on birds (Conner and Adkisson 1975, Titterington et al. 1979, Welsh 1981, DeGraaf 1992, Yahner 1993), and although relatively few of these focus specifically on boreal mixedwoods, their findings are highly useful. The general conclusions from these and other studies are that: 1) the level of impact of clear-cutting on species present prior to harvest depends on the amount of structure left after cutting; 2) bird communities in clear-cut forests change in species composition, although changes in species diversity may not occur; 3) postharvest silvicultural practices can have a very significant effect on the songbird community; and 4) clear-cutting can reduce the value of remaining adjacent forested habitat. These effects are discussed below.

 The level of impact of clear-cutting on species present prior to harvest depends on the amount of structure left after cutting.

The effect of a silvicultural clear-cut on the preharvest bird community will be greater than the effect of a commercial clear-cut. In a mixedwood forest, a clear-cut that removes only merchantable softwoods could leave a considerable amount of vertical structure remaining. In turn, this could still provide habitat to some of the preharvest species present. Titterington et al. (1979), working in the sprucefir forests of Maine, used discriminant analyses to show that the postclearcut stand characteristics that most strongly influenced bird species distribution were the presence of remaining softwood trees, slash, and raspberries (Rubus strigosus Michx.) and the amount of hardwood regeneration. Welsh (1987) attributed the relatively constant bird density and species diversity of different-aged postharvest mixedwood stands to the fact that they had been selectively clear-cut. Mature coniferous and deciduous trees remaining provided vertical structure and budworm habitat. Some preharvest birds may continue to occupy a site after it has been harvested if the key habitat requirements of those species still remain. The greater the "sanitization" of the cut, however, the fewer preharvest characteristics will be maintained, and this will result in fewer bird species (DesGranges and Rondeau 1993a).

Much has been written on the desirability of leaving dead and downed timber and snags after cuts to provide for bird habitat (Evans and Conner 1979, Davis et al. 1983, James 1984a, DeGraaf 1987, Franklin 1989, Thompson et al. 1993). In clear-cut boreal mixedwoods, areas of bypass (allocated stands or portions of stands within a harvested area that are not harvested, usually because they contain low volumes of merchantable timber) and unmerchantable species (e.g., birch), which die after neighboring trees are harvested, often provide snag habitat for birds (although birch snags usually fall within 5–10 years after the harvest of nearby trees). Practices such as roadside delimbing and scarification with heavy equipment (which

knocks down snags) can reduce the postharvest structure and decrease the value of stands to birds. (Another factor in the removal of snags is related to health and safety regulations, which stipulate that snags that pose a possible hazard to forest workers must be removed.)

Most information on raptor management in forested areas concentrates on protecting birds and nest sites from disturbances, rather than on the protection of foraging habitat (James 1984b, Anderson 1985). Ontario Ministry of Natural Resources' guidelines for the protection of bald eagles (*Haliaeetus leucocephalus*) (Ontario Ministry of Natural Resources 1987) and osprey (*Pandion haliaetus*) (Penak 1983) focus on leaving buffer zones around nest sites. The size of the prescribed buffer zone is greatest during the nesting season.

Bird communities in clear-cut forests change in species composition, although changes in species diversity may not occur.

Many studies have shown that different songbird communities are present in an area before and after harvesting. Species that prefer open, shrub-rich, or thicket habitats are more common following harvest. Conversely, species that prefer mature forested habitats are less common. In a comparison of bird populations on clear-cut and uncut blocks in mixed boreal forests in northwestern Ontario, Kendeigh (1947) found that logged areas had 27 species per 100 acres (40.5 ha), compared with an average of 35 species per 100 acres in uncut blocks. In the mature forest warblers were the dominant group, but in the logged area sparrows predominated.

As noted earlier, many studies have documented an immediate decrease in species diversity following clear-cutting. Diversity increases in the following several years, although midsuccessional, pole-sized stands seem to be less diverse than are young, mature, or overmature stands. The work of DeGraaf et al. (1993) in the spruce-fir forests of New England provides a good illustration of this.

A significant finding made by Noon et al. (1979) in their examination of previous work by Webb et al. (1977) and of bird communities of successional habitats in New England, was that although there were not great differences in species diversity between old and young habitats, rare species and guilds were much more likely to occur in mature undisturbed habitats than in young successional habitats. They attributed this to the fact that rare species have more stringent habitat requirements than do common ones, and that older forests are more likely to contain the critical habitat elements. This is consistent with Telfer's (1993) explanation of why old boreal forests have high species diversity in proportion to their areal extent.

3. Postharvest silvicultural practices can have a very significant effect on the songbird community.

Clear-cutting a mixedwood stand is often followed by a wide range of silvicultural techniques designed to regenerate, tend, or protect the new forest. A review of the effects on songbirds of all the various silvicultural techniques is beyond the scope of this review, although some key points merit discussion.

Some silvicultural practices, such as heavy scarification, have an immediate effect on the quality of songbird habitat; other practices, such as direct seeding, are benign when considered in the short term. However, the authors believe that it is inappropriate to consider only the shortterm effects of silvicultural practices, when long-term effects could have a more significant influence on the quality of a site as bird habitat. Similarly, it is difficult to consider the effects of a silvicultural practice in isolation from the larger objectives of which it is a part. For example, the short-term effect of planting jack pine on a mixedwood site is negligible. However, when considered in the context of an overall plantation program that may include heavy scarification to prepare the site and herbicide application to reduce hardwood competition, the effect on songbirds would be very significant.

The short-term effects of planting or seeding may be negligible as neither has a significant immediate impact on the nature of a site. The long-term effects, however, can be far-reaching. As noted earlier, planting in the context of maintaining a softwood component in a mixedwood stand is a practice beneficial to many bird species, because it maintains the plant species and structural diversity over time. (Following the clear-cutting of mixedwood sites, hardwoods often dominate unless steps are taken to encourage conifers.) From a bird habitat perspective, conversion of mixedwood sites to conifers, which is still considered a legitimate objective for some mixedwood and hardwood sites (Arnup et al. 1988), is a situation analogous to postcutting hardwood domination. Plantations of a single species provide less structural diversity, and poorer songbird habitat than do natural mixed species communities (James 1984c, Hunter 1990, Dickson et al. 1993, Thompson et al. 1993). In coniferous plantations, songbirds are often associated with remnant hardwoods (Thompson et al. 1993).

From a timber management perspective, herbicide application, whether for site preparation or tending, has the objective of controlling competing deciduous vegetation. From a wildlife perspective, herbicide application reduces the diversity of vegetation on a site. Although one would expect this to have a short-term effect on songbirds, there is limited experimental evidence to support this assumption. Lautenschlager (1993) reviewed the results of eight

studies that examined the effects of herbicide application on songbird species diversity and abundance. Most of the studies noted a decline in species that prefer brushy deciduous cover and an increase in species that favor open areas. The studies noted little change in overall species abundance or diversity, although there were some notable exceptions. Mackinnon and Freedman (1993, *in* Lautenschlager 1993) found songbird abundance to be 5–19 times greater in an untreated plot as compared to plots treated with glyphosate.

While the studies noted above examined the short-term effects of herbicide application, their long-term consequences are likely more important from a songbird perspective. Although it is often necessary to conduct multiple herbicide applications over a number of years to establish successful conifer plantations on mixedwood sites (Scarratt 1992), the authors do not know of any studies examining the effects of this treatment on songbirds. However, this treatment would simplify the structure of a forest on a mixedwood site, and could be detrimental to songbird habitat diversity. If, on the other hand, the use of herbicides is essential for maintaining the softwood component of previously mixedwood forest, their effect may well be positive.

The short-term effects of mechanical scarification can be either detrimental or neutral for songbirds. Light scarification, such as passive disc-trenching, has little effect. Heavy scarification, such as blading and windrowing, is probably detrimental. Such practices remove slash from significant portions of the cutover area and thereby eliminate an important habitat element for many bird species (Hunter 1990). Some site preparation practices result in the intentional or incidental destruction of snags or remnant trees, and this is detrimental to songbirds. Generally, the use of mechanically prepared sites by birds is inversely related to the intensity of the scarification (Crawford and Titterington 1979).

The long-term effects of mechanical site preparation, as noted above, depend upon the larger forest management context. If the objectives are to establish a pine plantation on what was a mixedwood site, then the effects of scarification in that context are detrimental. If the objectives are to prepare the site for spruce underplanting beneath a deciduous canopy, the effect may be beneficial to many bird species.

 Clear-cutting can reduce the value of remaining adjacent forested habitat.

Studies from the United States suggest that forest fragmentation often leads to increased brood parasitism by cowbirds on nesting birds in the remaining woodlots (Brittingham and Temple 1983, Terborgh 1989, Robinson 1992, Robinson et al. 1993). As such, parasitism no doubt plays an important role in decreasing the productivity of some species of forest-nesting songbirds (Robinson et al. 1993). However, although cowbirds are present in boreal Ontario, they are mainly confined to towns and agricultural areas (Cadman et al. 1987), and apparently do not pose the same threat as they do in the more southern parts of their range (D. Welsh, ³ pers. comm.).

Nest predation is much higher in the edges created by clear-cutting than in the interior forest zones (Yahner and Scott 1988). This may affect populations of migratory birds in woodlots and disjunct forested areas (Wilcove 1985, Martin 1992). The species most often identified as nest predators include blue jays (Cyanocitta cristata), crows (Corvus spp.), feral cats (Felis catus), red foxes (Vulpes vulpes), raccoons (Procyon lotor), and skunks (Mephitis mephitis) (Wilcove 1985, Terborgh 1989). Migratory songbirds are thought to be at a greater risk of nest predation because they generally attempt to raise fewer broods in a season than do resident songbirds (Terborgh 1989, Martin 1992). Most research on nest depredation associated with forest fragmentation and forestry practices has taken place in the United States, particularly in the midwest and northeast. Of the 32 studies that examined nesting success reviewed by Martin (1992), only four took place in Canada. Of those, none were in a forest management context.

One study that may be relevant to the boreal forest is that of Small and Hunter (1988). These authors examined nest predation in eight forests, ranging in size from 20–1 040 ha, in several counties of forests in midcoastal Maine. Here, forests comprise 66–90 percent of the land. They found that while the size of the forest was related to predation rates, distance to the edge was not a factor. The predators responsible for nest depredation were red fox, red squirrel (*Tamiasciurus hudsonicus*), skunk, and raccoon. They suggested that roads, rights-of-way, and fields provide increased opportunity for predators associated with open areas to invade forests. This study indicated that even in heavily forested areas, the creation of open spaces may cause increased nest depredation.

4.3.2 Alternative Silvicultural Systems

Selection Harvesting

The selection system is likely to cause the least disruption of the bird community in a mixedwood forest. Single-tree selection develops maximum vertical diversity (Frank and Bjorkbom 1973) and provides more canopy layers per

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unit area than does any other silvicultural system (Crawford and Titterington 1979). Vertical diversity is actually increased using the selection system, because the canopy openings create an environment suitable for regenerating trees while still maintaining a mature canopy. Hunter (1990) states that: "To manage a forest stand for vertical diversity, one should implement the kind of fine-scale uneven-aged management that produces uneven-height forests; in other words, selection harvesting."

The presence of well developed vegetation levels and a more complex habitat structure results in higher withinstand bird species diversity than exits in stands managed using an evenaged system (Crawford and Titterington 1979, Thompson et al. 1993). The effects of selection harvesting on the bird community in a mixedwood forest could be expected to include:

- forest interior and area-sensitive species, such as pileated woodpecker (*Dryocopus pileatus*) and cape may warbler (*Dendroica tigrina*), may persist;
- species associated with the forest canopy would likely remain, although there would be fewer mature trees and the upper canopy might not support as many birds;
- the canopies of the low and midstory trees would support more low canopy species such as the Canada warbler (Wilsonia canadensis); and
- ground-feeding species, such as dark-eyed junco (Junco hyemalis), may be found in small openings (Crawford and Titterington 1979, Temple et al. 1979, DeGraaf et al. 1993, Thompson et al. 1993).

Very few studies have been conducted on the effects of the selection system on birds, although many authors have extrapolated effects based on an understanding of the habitat needs of individual species. Of the little field work that has been carried out, Medin (1985) and Medin and Booth (1989) examined the effects of selection harvesting in alpine and mixed forests in the western United States. They found that in some logged stands, bark foraging and foliage gleaning species decreased and that some ground and shrub foraging species increased, as compared with unharvested stands.

While the selection system provides a degree of consistency of habitat and bird species stability beyond that of other silvicultural systems, it does not provide the same level of habitat for birds that prefer open and shrubby areas. Species such as Lincoln's sparrow (*Melospiza lincolnii*), which may find a small amount of habitat in the gaps created by selection harvesting, would prosper much better in open areas created by clear-cutting or natural disturbances.

The continuum of tree removal from single-tree selection to group selection could be expected to produce a range of effects on bird habitat. In group selection, the removal of a group of neighboring trees lessens the continuity of vertical habitat diversity, but increases horizontal diversity. These larger openings produce more understory vegetation than do single-tree openings. This, in turn, creates more habitat for birds that depend on stand openings but decreases habitat for crown-dependent species. The size and number of openings influence the diversity of bird species in the stand. With a greater number of large openings, the number of birds dependent upon low-growing vegetation increases, while birds dependent on overstory habitat will decrease (Crawford and Titterington 1979, Yahner 1986, Crawford and Frank 1987).

Several authors (Brittingham and Temple 1983, DesGranges and Rondeau 1993b, Thompson et al. 1993) warn that even small openings in the forest, such as those created by group selection, may be attractive to cowbirds and avian predators like blue jays and crows. Based upon a computer model simulating a hardwood forest in the central United States, Thompson et al. (1993) suggested that if edge effects occur around group selection openings, they could drive a local population of forest interior birds to extinction. Even though the openings are small, they could be much more numerous and widely dispersed than those created by clear-cutting.

In contrast to these concerns, Crawford (1985) suggested that group selection is the best harvesting system for creating habitat for those songbirds that prey upon spruce budworm. He described this habitat as a mature coniferous forest with a mixture of overstory species, managed for well-distributed, small openings containing regeneration of different ages.

Before the effects of the group selection system on bird communities in boreal mixedwoods can be fully understood, a more thorough understanding of the likelihood of detrimental edge effects on interior forest songbirds, must be reached.

Shelterwood

The authors know of no studies of the effects of the shelterwood system on birds in boreal mixedwoods, although a few have examined effects in other forest types. However, several authors have attempted to extrapolate effects on birds based on an understanding of the effects of shelterwood harvesting on forest structure.

As the shelterwood system is an even-aged one, it can be compared with clear-cutting, although the loss of vertical structure associated with a shelterwood harvest is not as great as with a clear-cut harvest. After the first cut in a two-cut system, while understory regeneration is developing,

there is considerable vertical structure in a shelterwood stand. When the last cut removes the remaining overstory, advance reproduction is well established.

Crawford and Frank (1987) stated that shelterwoods provide better bird habitat than do clear-cuts. Because part of the canopy is retained for a number of years, habitat is provided for overstory-dwelling species. However, as overmature or weakened trees are removed during the first harvest, it is unlikely that cavity nesters would be provided for unless specific measures were taken to preserve such trees or to provide for new nesting sites in future stands. Regeneration beneath the overstory provides a degree of vertical diversity and habitat for birds that require low vegetation. Upper- and lower-canopy birds lose their habitat at this time. Shrub and sapling birds, such as the magnolia warbler, and bramble-herbaceous birds, such as the common yellowthroat (Geothlypis trichas), will have improved habitat (Crawford and Titterington 1979). As the trees grow, the shrub and sapling strata diminishes and conditions once again become favorable for canopy dwelling species. Crawford and Frank (1987) advocated a three-stage rather than a twostage shelterwood system approach as this retains vertical structure for a longer time, and creates an additional vertical layer. For boreal mixedwoods, however, it is doubtful that a three-stage approach would be practical (Wedeles et al. 1995).

Webb et al. (1977) examined the effects of three levels of diameter-limit cutting and clearcutting on bird communities in the hardwood forests of New York. Of the 26 indicator species, which they monitored for up to 10 years after harvesting, they concluded that none was so sensitive to habitat disturbance as to be "driven out" by logging, and that species diversity actually increased slightly with logging intensity. Six species associated with mature forests (blackthroated green warbler [Dendroica virens], ovenbird, winter wren [Troglodytes troglodytes], blackburnian warbler [Dendroica fusca], least flycatcher [Empidonax minimum], and wood thrush) declined in abundance with increases in logging intensity, and five species (chestnutsided warbler, American redstart, white-throated sparrow, Canada warbler, veery, and black and white warbler) showed an increasing trend. However, their general conclusion that the forest has a breeding bird fauna of constant composition under all canopy conditions, as well as some of their specific conclusions, were vehemently questioned by Noon et al. (1979), based on the population census and analytical techniques used.

In summary, the key feature aspect of the shelterwood system for birds is the continuity of vertical structure provided. At no time does the stand change abruptly from a mature forest to, for example, a very young successional forest or a clear site.

Seed-tree

The impact of a seed-tree system is very similar to the impact of clear-cutting, except, of course, that some residual vertical and horizontal structure is provided by the seed trees. In Ontario's boreal mixedwoods, the most practical use of the seed-tree method is for white spruce regeneration (Lyon and Robinson 1977, Wedeles et al. 1995). Mature white spruce trees provide a significant amount of bird habitat compared with individual trees of other species, although it is doubtful that a scattering of single trees across a cutover would provide habitat to support more than "casual" use by birds. However, if group seed trees are used and the groups are sufficiently large and numerous, they may provide more attractive habitat.

Two-pass System

In a classical application of the two-pass system (Brace Forest Services 1992, Sauder 1992), mature hardwoods are removed from a mixedwood stand and advance regeneration of softwoods is left undisturbed as an understory, or in patches as they occur throughout the stand. Some mature hardwoods may be left unharvested if accessing them would cause damage to understory softwoods.

Clearly, a considerable degree of vertical structure could remain in a stand after the first harvest. In addition, some horizontal structure or interspersion would also exist if patches of softwood trees remained. The authors believe that the degrees of vertical and horizontal structure would be greater than that provided by the clear-cutting, seed-tree, or shelterwood systems.

This method of harvesting may provide habitat for a wide range of bird species. Those associated with open areas may find habitat in patches that previously contained little advance regeneration; species associated with shrubs and saplings may find habitat in the remaining advance regeneration and understory vegetation; species associated with canopy may find habitat in the hardwood trees that remain standing. Those species that require extensive canopy would likely not find habitat in these stands, nor would species requiring snags or cavities.

The second pass of the two-pass system will normally remove all of the trees from a stand in a single clear-cut (Sauder 1992, Wedeles et al. 1995). After this second cut, therefore, bird habitat will follow that of the clear-cutting model.

4.4 Large-scale Effects

Although individual birds of many species may be significantly influenced by harvesting operations at the stand level (songbird home ranges are generally 0.5–5.0 ha), the effects on populations, which represent the real interest of biologists, are related more to the manner in which

harvesting occurs across a forest or forested landscape. A large body of literature exists on the effects of fragmentation in temperate forest and in areas where forest patches are interspersed with open areas, as in rural agricultural settings (Robbins 1979, Wilcove 1985, Freemark and Collins 1992, Litwin and Smith 1992, Faaborg et al. 1993). However, there is much less literature on the effects of fragmentation in boreal forested areas. Although there is some information from Scandinavia (Helle 1985, 1986; Helle and Järvinen 1986), there is no information based on empirical work from boreal Canada.

In temperate regions, fragmentation is believed to have detrimental effects on bird populations. Specifically, fragmentation exposes breeding birds to increased risk of predation and nest parasitism; provides insufficient habitat to meet territorial and food requirements; and makes local populations susceptible to extinction through natural stochastic population fluctuations (Terborgh 1989, Freemark and Collins 1992, Hunter 1992, Faaborg et al. 1993). Fragmentation in boreal forests may occur as a result of even-aged management in concert with the network of forest access roads necessary for harvesting and silvicultural activities. Clear-cutting is the most obvious silvicultural system that may contribute to fragmentation in boreal forests.

Boreal mixedwoods are fragmented not just by the harvest blocks themselves, but by the access roads created to conduct management operations. The minimum right-of-way suggested for forest access roads in Ontario is 20 m (Ontario Ministry of Natural Resources 1990). Roads of this width may provide corridors for pest and predator species to access forested areas, and may be impediments to movement for interior-dwelling species (Greig et al. 1991b). For all alternative systems, less wood is harvested per unit area per harvest operation than in traditional clear-cutting. Therefore, more stands need to be accessed to provide the same amount of wood compared with clear-cutting, and a larger road network is needed to support alternative silvicultural systems. This larger road network may lead to increased fragmentation effects.

Because so little work has been done on this topic in boreal forests, and because the type of fragmentation that has occurred in most areas where it has been studied differs from what occurs in boreal forests (i.e., interspersion of forested areas with agricultural and rural areas), it is difficult to extrapolate with confidence from temperate forest conditions. However, the possible effects of fragmentation in boreal forests cannot be disregarded (Hunter 1992). Hunter cited Helle's (1985, 1986) conclusions that long-term declines in forest bird populations, particularly

cavity nesting, nonmigratory species of northern Finland, are due to fragmentation. As such, this represents a cause for concern in boreal Canada. Small and Hunter's (1988) work in extensively forested areas in Maine showed that predation risk was significantly correlated with forest patch size. This also implies that fragmentation may have detrimental effects on birds in the boreal forest.

A thought-provoking study on the potential impact of fragmentation was published by Helle (1986). He studied birds in a 70-km² national park surrounded by commercial forestry operations in Finland and found that although fragmentation had not taken place inside the park, bird population trends there mirrored those that occurred in the surrounding heavily commercialized forest. He suggested that population trends caused by fragmentation may spill over from fragmented to nonfragmented areas. If this is so, the effects of fragmentation may extend well beyond a fragmented forest and may have serious implications for forested, but unharvested areas. (An alternate conclusion for Helle's [1986] results may be that the trends he measured were not the result of fragmentation, but of other off-site factors [K. Abraham, 4 pers. comm.].)

Although some scientists believe there is reason for concern regarding the effects of fragmentation in boreal forests, others believe it is an ephemeral phenomenon, equivalent to shortterm habitat loss (I. Thompson, 5 pers. comm.). In agricultural and more populated environments, forest harvesting often results in permanent, or at least long-term loss of habitat, with forested areas present only in relatively small patches scattered over the landscape. In boreal forests, a harvested area (usually) returns to forest and does not remain permanently cleared. Key questions regarding fragmentation effects in the boreal forest include: 1) Do fragmentation-like effects occur in areas that experience short-term habitat loss (i.e. harvesting)?, and 2) What is the duration of the effects? If harvesting effects do exist and are long-lasting, then differentiating between fragmentation and boreal forest harvesting may be a semantic rather than a real difference. If, on the other hand, boreal forest harvesting effects do not occur or are ephemeral, then the distinction is likely relevant.

One potentially detrimental effect of forest management on birds that is constantly voiced relates to the removal of snags (Evans and Conner 1979, Thompson et al. 1993). Although this issue is most often raised in the context of clear-cutting, it applies also to alternative harvesting systems. In the selection, shelterwood, seed-tree, and two-pass systems, the interests of the manager concerned with short-term timber production appear to be best served

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when dead trees are removed. In this way growing space can be provided for regenerating stock. For example, if an equal amount of timber is to be harvested in two operations, one using clear-cutting and the other using shelterwood cutting, the area to be cut using the shelterwood system would be larger as less timber is available per unit area during a single harvest operation. Therefore, a greater area would suffer from the loss of snags. Although forest interior-like conditions may be maintained with some alternative systems, there may be significant effects on resident birds if snags are removed.

It is probably unrealistic to suppose that the forests of a boreal landscape could be managed using only alternative silvicultural systems. In fact, this would be an extremely undesirable state for birds. Such a landscape would (perhaps with the exception of seed-tree areas) contain no large disturbed areas dominated by the early successional stages needed by many birds. DeGraaf et al. (1993) suggested that it is unwise to maximize within-stand structural diversity at the expense of landscape diversity when managing for neotropical migratory bird diversity. A better approach would be to use a mix of silvicultural systems.

Much recent attention has been devoted to designing forest management approaches and practices that mimic natural disturbance regimes (Hunter 1993, Thompson and Welsh 1993). The rationale for doing so is that since native wildlife and landscapes evolved and persist under conditions that include wildfire, insect infestations, windthrow, and other disturbances, forest management that mimics these conditions should have minimal effects. (Or, more reasonably, forest management which attempts to mimic these conditions will likely have fewer negative impacts than will forest management that does not.) Thompson and Welsh (1993) stated that to mimic natural process "will necessarily involve the broader use of partial cuts, diameter limits, 3pass systems over an extended period of time, increased use of shelterwood cutting even in boreal types (e.g., in mixed woods)...". For birds in boreal mixedwoods, a landscape mosaic that includes clearcutting and a mixture of alternative systems with uncut areas could closely represent a natural disturbance regime and provide habitat for many, if not all, native species.

5.0 EFFECTS ON SMALL MAMMALS

The contribution of small mammals to forest ecology has often been unappreciated, even though they play useful roles in controlling insect pests, providing food for furbearers, and diverting predatory pressures from game species (Hamilton and Cook 1940). As well, small mammals contribute to tree growth by aerating soil and transferring mycorrhizac spores (Maser et al. 1978). More

commonly, they are viewed as pests, because they consume tree seeds, girdle trees, and generally interfere with forest regeneration (Cayford and Haig 1961, Ahlgren 1966, Radvanyi 1970, Sims and Buckner 1972).

Small mammals of boreal mixedwoods belong to four groups: rodents, insectivores, bats, and rabbits. Rodents and insectivores are the most abundant small mammals in Ontario's forests. In fact, the term "small mammals" is a near synonym for mice, shrews, and voles. Hares and rabbits (Lagomorpha spp.) in boreal mixedwoods are represented only by the snowshoe hare (Lepus americanus). There are six bat species (order Chiroptera) in Ontario's boreal forest range. However, because bat research is generally limited to behavioral studies and does not address their role in the ecology of boreal mixedwoods, bats are not discussed in this review. Common names used in the literature for small mammals can be confusing. A partial list of common native rodents (nonfurbearers) and insectivores found across the range of boreal mixedwoods in Ontario is provided in Table 2.

Recent developments in tracking small animals by using radio transmitters have greatly improved the understanding of home range size and habitat use (Koehler et al. 1987). Despite technological advances, however, these indirect observations of mammal populations can be rife with sampling error. A long-standing concern in small mammal studies is how sampling techniques might alter animal behavior in ways that contribute to random error of population estimates (Young 1952, Jones 1983). Different trapping methods also make comparative work difficult (Fowle and Edwards 1954). For this reason, empirical evidence should be weighed against general theories of animal behavior.

Based upon relevant literature, it is the impression of the authors that theoretical and empirical research remain distinct despite some important advances within both fields. Quite often, empirical evidence is explained through speculation. With this cautionary note, the following generalizations of habitat requirements reflect the current state of knowledge.

5.1 Habitat Affiliations

It is generally accepted that greater floristic and structural diversity will lead to an increased abundance and variety of small mammals (Miller and Getz 1977, Parker 1989). This was demonstrated by a recent survey of small mammals in the Lake Superior Provincial Park, where the more diverse mixedwoods of the southern portion of the park supported a greater variety and number of mammals than did the boreal mixedwoods in the northern portion (Pasitschiniak-Arts and Gibson 1989).

Table 2. Scientific and common names of boreal forest small mammals.

	Scientific Name	Common Name
ORDER RODENTIA		
Family Cricetidae	Peromyscus maniculatus	Deer mouse
	Microtus pennsylvanicus	Meadow mouse
	Clethrionomys gapperi	Red-backed vole
	Clethrionomys rutilus	Northern red-backed vole
	otom tonomys rantas	Northern red-backed vote
Family Zapodidae	Zapus hudsonius	Meadow jumping mouse
	Napaeozapus insignis	Woodland jumping mouse
	7 - 7 8	woodiand jumping mouse
Family Sciuridae	Tamiasciurus hudsonicus	Red squirrel
	Tamias striatus	Eastern chipmunk
	Eutamias minimus	Least chipmunk
	Glaucomys sabrinus	Northern flying squirrel
	Marmota monax	Woodchuck
		Woodender
Family Erethizontidae	Erethizon dorsatum	Porcupine
ODDED WASSESSA	De e	pan energy of Economics
ORDER INSECTOVORA	5 2 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3 3	
Family Soricicidae	Sorex cinereus	Masked shrew
	S. fumeus	Smoky shrew
	S. arcticus	Saddle-backed shrew
	S. palustris	Water shrew
	Microsorex hoyi	Pigmy shrew
	Blarina brevicauda	Mole or short-tailed shrew
	Condylura cristata	Star-nosed mole

One could infer that mixedwoods should harbor more abundant and diverse communities of small mammals than would other boreal forest types. Work by Parker (1989) in New Brunswick revealed that small mammal species diversity was lowest in 15- to 17-year-old plantations, when compared to mature forests and naturally regenerated areas. The authors speculate that spruce plantations in New Brunswick that are intensively managed on old fields might have the lowest structural and florisitic diversity of all boreal forest cover types.

Preliminary results of a small mammal habitat study in northeastern Ontario show that some small mammals have an affinity with certain Forest Ecosystem Classification site types (D'Eon and Watt 1994). This study revealed that three common mice and three shrew species were found in greater abundance on the floristically diverse mixedwood types, as compared with dry or wet spruce dominated habitats.

Thompson (1988) found that small mammal biomass decreased in young stands (less than 35 years old) following clear-cutting and selective cutting, relative to a mature uncut mixedwood stand. His observations were based upon a small number of stands at different stages of development. Although all of these stands were clear-cut, differences in preharvest stand structure, variable levels of utilization, and different types of silvicultural treatments create habitats of different value to wildlife. Martell

(1983) found that species diversity and abundance drops only in young, closed canopy stands and then increases to levels similar to those of mature forests. Parker (1989) noted that immediately after harvest shrews dominate, and small mammal density increases to levels exceeding those of the precut. Mice become dominant after grass and forbs become established. Red-backed voles remain present in all stages of stand development.

5.1.1 Shrews

Shrews (*Sorex* spp.) require a moist surface soil and abundant forest litter to provide food and cover. Although most of their diet consists of insects (Ryan 1986), shrews are omnivorous and eat a variety of insects, worms, plants, frogs, and even mice (Dagg 1974).

Shrews control populations of insects that spend part of their life cycle on the forest floor. For example, research by Holling (1959) showed that shrews in a southern Ontario pine forest ate as many as 101 pine sawfly (*Neodiprion sertifer* Geoff) cocoons per day. This is equivalent to consuming one-half of the estimated cocoons per unit area per season.

Jennings et al. (1991) conducted stomach analysis of pit trapped small animals in a budworm-infested forest of Maine. The masked shrew (*Sorex cinereus*), along with salamanders and toads, fed upon the late instar larva of the spruce budworm. The sparse literature concerning the role

of shrews and other small mammals in regulating spruce budworm or pine weevil (*Pissodes strobi* Peck) populations suggests that this may be an important area for further research (*see* Bellocq and Smith 1994).

Peters (1986) used a variety of published and unpublished data on body weights to predict density and home range size of animal groups. He found that herbivorous mammals have a home range defined by the predictive equation $Y = 0.032W^{1.00}$ and a population density defined by $Y = 1/(0.0046W^{0.61})$, where Y is the area in km² and W is the weight in kilograms. Thus, a 20-gram shrew should have a population density of about 25 animals per hectare (D'eon and Watt 1994). This is four to ten times greater than the often reported range of two to five shrews per hectare (Sullivan and Sullivan 1982). Unfortunately, with the exception of Bergstrom (1988), an examination of the literature revealed little about small mammal body weight and its relation to population estimates in other empirical studies.

Given their generalist behavior, shrews are found in a broad array of forest habitats. While studies by D'eon and Watt (1994) found the short-tailed shrew only on mixedwood sites, smoky shrews were less specific in their habitat affinities and masked shrews were ubiquitous.

It is difficult to predict shrew response to forest harvesting. Although studies from northeastern North America observed an increase in shrew populations immediately following forest removal (Monthey and Soutiere 1985, Parker 1989), the opposite trend is reported in northwestern North America (Sullivan and Sullivan 1982). Fowle et al. (1958) found that shrew populations increased following clear-cutting in boreal mixedwoods, while Martell (1984) reported that shrew numbers could either increase or decrease following fire in black spruce and mixedwood stands depending upon the season of the burn.

5.1.2 Mice and Voles

Mice and voles are sometimes classified as grazers (e.g., red-backed voles [Clethrionomys gapperri] and deer mice [Peromyscus maniculatus]) or as granivores—omnivores (meadow mice [Microtus pennsylvanicus], meadow jumping mice [Zapus hudsonius], and woodland jumping mice [Napaeozapus insignis]). The grazers are the most common small mammals of boreal mixedwoods. These species are important as food for other animals in the boreal forest (Thompson 1988), and are known to distribute hypogeous fungi that form beneficial mycorrhiza on tree roots in the Pacific Northwest (Maser et al. 1978) and in Germany (Blaschke and Baumler 1989). Voles feed upon the fungi in late summer and transfer fungal spores from their feces and fur to sites throughout the forest. Unfortunately, mice and voles also feed on conifer seeds and are

viewed by some foresters as pests (Cayford and Haig 1961, Radvanyi 1970).

Red-backed voles are not associated with open fields and recent clearings (Martell 1981, Thompson 1988), presumably because their preferred late summer foods of lichen and fungi are scarce in these environments (Martell 1981) and there is inadequate cover.

In the western United States, red-backed voles are associated with mature forest and oldgrowth conifers because they require large decaying logs for cover. This has generated considerable interest in the study of this species and its close relative the California redback vole *C. californiaus* (Hayes and Cross 1987, Nordyke and Buskirk 1991). In eastern North America, on the other hand, red-backed voles are common in all forest types across all age classes (Verme and Ozoga 1981, Monthey and Soutiere 1985, Probst and Rakstad 1987, Parker 1989), and are abundant in Ontario's boreal mixedwoods (Fowle et al. 1958, Krefting and Ahlgren 1974, Pasitschiniak-Arts and Gibson 1989, D'eon and Watt 1994).

In Ontario, red-backed voles do not appear to consume large quantities of tree seeds (Martell 1981). This is in direct contrast to Radvanyi's (1971) observations in Alberta. The geographic variation in feeding behavior of Swedish voles (Hansson 1986) might explain differences between Alberta and Ontario.

Deer mice live in the same forest types as do red-backed voles; however, they also inhabit clearings and old fields (Parker 1989). Meadow mice and jumping mice, on the other hand, are most closely associated with clearings. Wolff and Dueser (1986) found that deer mice and red-backed voles coexist without displays of aggression, likely because they do not compete for the same food. D'eon and Watt (1994) observed that deer mice were common to dry sites, but absent from wetter spruce sites. DeGraaf et al. (1991) found deer mice to be more closely associated with upland conifer stands than with other habitats, probably because conifer seeds are an important part of their diet (Ahlgren 1966, Martell 1979).

Although observations of mice and vole feeding behavior do not extend into the winter months in Ontario (Martell 1981), lichens, insect larva, and seeds should remain plentiful beneath the snow. Feeding by voles on the inner bark beneath the snow-line interfered with forest regeneration in Sweden (Hansson 1986) and in conifer plantations in Manitoba (Cayford and Haig 1961).

Abbott (1962), in a laboratory feeding trial, concluded that red-backed voles and meadow mice consistently rejected balsam fir seeds in favor of spruce seeds. Presumably, resin in the balsam fir seed coat is unpalatable (Smith

1970). In fact, white spruce seed was favored 70 to 1, which could explain the difficulty in regenerating spruce in boreal mixedwoods. A later study by Hart et al. (1968) attempted to test this hypothesis by establishing enclosures in a Maritime spruce–fir–hardwood forest. Although they found no differences in spruce regeneration between enclosed and open plots, the authors felt that the nature of the plots and enclosures may have altered small mammal feeding behavior and thus made their results suspect. This is an important area for future study in the boreal mixedwoods.

5.1.3 Squirrels

Squirrels, like all small mammals, are an important source of food for furbearers. They are found in all forested habitats of North America.

Red squirrels feed primarily upon the seed of spruce trees, but also forage for pine seeds, fungi, buds, insects, and occasionally mice (Brink and Dean 1966, Smith 1970, Wolff and Zasada 1975, Maser et al. 1978, Wooding 1982, Obbard 1987). They have also been reported to feed on spruce budworm larva, but their impact on population numbers appears to be minimal (Jennings and Crawford 1989).

Flying squirrels (*Glaucomys sabrinus*) rely less upon conifer seed for food (Brink and Dean 1966) than do red squirrels, and are less frequently encountered in the boreal forest because they are nocturnal and not as aggressive (Wooding 1982).

Squirrels cache seed and fungi for winter feeding (Wooding 1982). Red squirrels favor white spruce over black spruce for both food and nesting sites (Brink and Dean 1966, Fancy 1980). Individual body weights of red squirrels were recorded to be higher in conifer habitat than in hardwood habitat in a study conducted in Alberta (Rusch et al. 1982). Thus, it appears that squirrels prefer boreal conifer forests to hardwoods or mixedwoods.

Gurnell (1984) found that the home range of red squirrels in lodgepole pine was remarkably small (0.6 ha). Although the serotinous cones of this tree species are hard to open (Smith 1970), they do provide an abundant and reliable source of food. The home range of red squirrels in Ontario can range from 0.5 to 2 ha depending upon the density and maturity of conifer trees. European red squirrels (*S. vulgaris*) that live in conifer forests have considerably smaller home ranges than do those that live in hardwood forests. Wauters and Dhondt (1992) suggest this is because food is more plentiful in conifer forests.

Eastern chipmunks (*Tamias striatus*) are found in more open forest conditions and are less arboreal in their habits than are red squirrels (Wooding 1982). It is estimated that

their home ranges vary from .04 to 1.26 ha (Bergstrom 1988). Bowers et al. (1990) observed that water scarcity resulted in larger eastern chipmunk home ranges, and Trombulak (1985) argued that interspecific competition between two western chipmunks (*E. amoenus* and *E. townsendi*) was a factor that increased home range size.

5.1.4 Rabbits

Radvanyi (1987) conducted a comprehensive literature review and problem analysis of snowshoe hares and forest plantations. He concluded that the primary habitat requirement for hare is low, dense woody cover to provide winter browse and protection from predators. This is a structural attribute of 10-to15-year-old conifer plantations (Parker 1984), and of some mixedwood stands with dense conifer understories. Small hardwood trees and shrubs also provide important winter browse (Koehler and Brittell 1990). Summer foods of forbs and leaves are rarely in limited supply.

The relationship between stand structure and snowshoe hare populations appears to be so strong that Fox (1978) felt that fire cycles created waves of suitable habitat. This is but one explanation of the generally observed cyclical nature of hare and lynx (*Felix lynx*) populations. However, fire history records and trap returns of lynx over the last 100 years in Canada support his theory. The same large-scale effects may explain fluctuations in ungulate populations. This theory deserves closer scrutiny and further testing.

High populations of hare in young tree plantations can cause considerable damage. Rodgers et al. (1993) reported a preference by hare for nursery grown white spruce over naturally regenerated white spruce. They suggested that the elevated nitrogen content and depressed concentrations of distasteful camphor in the tissue of nursery stock might explain their observations.

5.1.5 Porcupines

Porcupine (*Erethizon dorsatum*) feed on tree and shrub leaves in summer and rely upon the inner bark of trees during winter (Brander 1973). For this reason, Curtis (1944) identified the porcupine as causing the most significant damage to trees. The many articles written on porcupine in the 1940s address control methods such as bounties, den poisoning (Reeks 1942), and electric fencing (Spencer 1948). Cook and Hamilton (1957) suggested that the reintroduction of fisher (*Martes pennanti*) should help control porcupine populations in the northeastern United States.

Since the 1950s, much less literature has been written on porcupine from either a control or ecological perspective in eastern North America. Wooding (1982) stated that their numbers have been drastically reduced and that their low fecundity places them at risk.

Personal observations around Thunder Bay and in other parts of northern Ontario create the impression that they are common inhabitants of the boreal forest, and densities have been estimated to be around one animal for every 2–5 ha of woodland. They feed on cedar, jack pine, balsam fir, and white birch, but only rarely on black spruce or white spruce.

5.2 Stand-level Effects

Essential habitat requirements of small mammals are summarized in Table 3 as the basis for the subsequent discussion of stand-level effects. This table is a broad interpretation of the literature cited above, and takes into account the specified or implied characteristics of the study areas. Characteristics chosen are those altered or affected by the application of silvicultural systems.

Shrews, voles, and mice will be affected most by the type of site preparation used within a silvicultural system. Slash aligning or piling from blading and trenching concentrates cover, and thus small mammals themselves, into discrete areas. This could cause increased predator success, territory modification, and mating behavior changes. Over time it could significantly reduce small mammal populations (Rodd and Boonstra 1984). However, no work has been done to test whether site preparation causes an initial concentration and subsequent reduction of small mammal populations.

Intermittent patch scarification does not align slash, yet still creates suitable microsites for planted seedlings. As such, it may by neutral in its effects upon small mammals. Patch treatments might be preferred over broadcast operations so as to retain the benefits of small mammals on the site while still protecting the immediate environment of regenerating trees from small mammal damage.

Prescribed burns will have variable effects on small mammals, depending on the intensity and timing of the burn. Presumably, very hot fires would destroy cover for small mammals until grasses and forbs reestablish on the site. In support of this theory, Martell (1984) reported that small mammal population patterns changed depending upon the season of fire. If a burn occurred when mice were nesting, the effect on populations was greater than at other times. West et al. (1980) noted that red-backed voles moved from a burned area to adjacent forest one winter after the burn, probably as a result of the lack of ground cover.

Logically, because herbicides reduce both food and cover from predators, they would temporarily decrease the numbers of small mammals, especially those of deer mice. While Clough (1987) and Santillo et al. (1989) reported a drop in small mammal populations after applying herbicides, D'Anieri et al. (1987) did not observe this to be the case. The amount and distribution of woody debris remaining on the site are probably more important determining factors than are the effects of herbicides in the short term. Over the long term, the effects of herbicides in shifting species composition and stand development patterns may have significant impacts upon small mammal communities. These could lead to temporary losses in numbers and diversity at the 15- to 17-year-old stage of conifer plantations, as reported by Parker (1989).

Effects from any cutting pattern of the forest overstory on mice, shrews, and voles can be mitigated by leaving woody debris and litter layers intact. "New forestry"

Table 3. Habitat requirements within stands that are affected by the application of silvicultural systems.

Small mammal	Habitat requirements	
Shrews	Fairly deep forest litter layers for protection and as a source of insects and other animals for food. Woody debris would probably provide useful cover. These conditions can occur within a wide range of forest cover types and densities.	
Red-backed voles	Coarse woody debris is important for cover unless rocks and boulders are available. Lichen and fungi are important for food. These conditions can occur within a wide range of forest cover types and densities.	
Deer mice	Grass and forb cover is important. Open areas or open forest canopies are required to develop grass and forb cover. Conifer tree seeds can be important foods.	
Squirrels	Cone-bearing conifer trees (especially white spruce) are critical for both food and nesting sites.	
Snowshoe hare	Low dense cover provided from young conifers. Young hardwood shrubs and trees can provide important winter browse.	

places emphasis on practices that leave woody debris and green trees as part of the biological legacy across generations of trees by a variety of plant–animal and plant–plant interactions (Franklin 1989). Bellocq and Smith (1994) suggested that woody debris may prove to be a useful strategy for reducing pine weevil damage by enabling small mammal predation of over-wintering larva.

Cut-to-length logging systems (Jewiss 1992) that distribute slash across the operating area will benefit small mammals more than tree-length logging. Harvest scheduling of oldest-first stands almost guarantees woody debris on the site regardless of the logging system used. If scheduling strategies changed and alternative silvicultural systems were employed in younger stands, operating practices that leave some woody debris may be an important consideration.

Sites prone to drying will have shallow litter layers. In such cases, complete overstory removal may temporarily eliminate small mammal habitat regardless of the amount of debris left on the site. Whereas ground disturbance and woody debris have significant impacts on small mammals, such as mice, shrews, voles, and chipmunks, they are of little consequence to squirrels or rabbits, which depend more upon shrub and tree layer structures.

Changes in the densities of conifers that are small enough to have branches in close contact with the ground will have the greatest impact upon rabbits. Changes in the density and distribution of cone-bearing conifer trees will affect red squirrels, and cutting spruce trees could result in a decrease in red squirrel and flying squirrel densities. Wolff and Zasada (1975) observed that clearcut white spruce forests in Alaska were vacated by red squirrels. Chipmunks are not as vulnerable to forest disturbances as are squirrels, because they are less arboreal in their habits. In fact, Scott et al. (1982) reported increased densities of western chipmunks on clear-cut areas in Colorado.

One of the better comparative studies of classical silvicultural systems was completed by West et al. (1980) in a white spruce forest in Alaska. Small blocks within a homogeneous stand were clear-cut or shelterwood cut. Ground cover was less disturbed in the shelterwood blocks, thereby resulting in higher northern red-backed vole (C. rutilus) population densities. In a similar study, Wolff and Zasada (1975) found that shelterwood cutting decreased squirrel density (and hence increased home range) from 1.4 squirrels per hectare in the uncut area to 0.5 squirrels per hectare in the shelterwood. Hare populations should increase as the conifer understory develops beneath a shelterwood. Two-pass cutting should also maintain hare and small mammal habitat if woody debris is left behind.

Selection systems can provide suitable habitat for most small mammals if care is taken to leave litter, snags, and woody debris relatively intact on the site. An exception might occur for deer mice, if canopy densities remain high enough to reduce grass and forb cover. Medin and Booth (1989) studied small mammal changes caused by the application of single-tree selection systems in Idaho. They recorded significant variation within and between logged and unlogged portions of stands of Douglas fir (Pseudotsuga menziesii [Mirb.] Franco) and ponderosa pine (Pinus ponderosa Laws.) over a 4-year period. Although red-backed voles declined, chipmunks increased and shrews seemed to disappear in the logged stands. However, few conclusions can be drawn from their observations about the relationship between selection cutting and small mammals because few details were given about forest floor conditions.

Measures to mitigate impacts upon small mammals may hinder natural regeneration of spruce because of seed predation by small mammals. Indeed, with seed-tree, shelterwood, and selection systems depending upon natural regeneration, ways may need to be found to discourage these animals. For example, intense site preparation could be used to reduce the numbers of small mammals. In addition, tree and seed shelters (Dominy and Wood 1986) might be used to protect conifer regeneration from small mammals.

5.3 Large-scale Effects

There is little discussion in the literature of the large-scale effects of forest management practices on small mammals. Their fecundities and high densities (relative to other mammals) may provide buffers to the large-scale impacts of forest management practices. Small mammals are likely affected by large-scale effects in indirect ways, because their ecological processes work at small (standlevel) scales as a function of their small body size and related home range (Peters 1986).

Forest structure, as affected by fire or large-scale clearcutting, may influence metapopulation cycles of hare and their main predator, the lynx (Fox 1978). However, details of these interactions remain uncertain. Once again, it seems that a forest with a diverse structure and employing a range of silvicultural systems and patch sizes is the best approach for management in such a climate of uncertainty (Hunter 1990).

Roads may be an important large-scale influence on small mammals. All-weather roads are barriers to the movement of mice and voles, presumably because small mammals fear predation in open spaces (Burnett 1992). Douglass (1977) reported that winter roads created a meadow-like environment that favored mice. While all-weather roads

reduce the rate at which small mammals repopulate a disturbed site, it is not known if road densities pose a critical threat. Although alternative silvicultural systems increase road density, the authors expect that resulting reductions in resident small mammal populations should be less than those created by clear-cutting.

6.0 EFFECTS ON UNGULATES

Three ungulates, (moose, woodland caribou [Rangifer tarandus caribou], and white-tailed deer [Odocoiles virginianus]), live within the boreal forests of Ontario. Moose are the predominant ungulate, with an estimated population of about 120 000 animals (H. Smith, pers. comm.). Caribou in Ontario's commercial boreal forest south of 50° N latitude are limited to about 1 800 animals occurring in isolated bands. Some researchers believe that these small populations are threatened (Cumming and Beange 1993). Deer also occur along the southern margins of the boreal forest. Although their numbers are also small, they represent the northern edge of a large population of the white-tailed deer subspecies O. v. borealis. The range of this subspecies stretches from the midwest to the eastern seaboard of the United States and north to southeastern Canada (Baker 1984). Thus, deer have a healthy, unthreatened population.

The ubiquitous moose and locally threatened caribou are the focus of this review. However, greater emphasis is given to moose, because caribou make relatively little use of boreal mixedwoods. White-tailed deer are not discussed.

6.1 Moose

Moose are important both economically and as a featured species in Ontario's boreal forest. Provincial statistics show that 115 000 moose hunting licenses were sold in 1993, with an estimated \$55 million generated in tourism revenue from this activity (H. Smith, pers. comm.). By managing habitat for moose as a featured species, it is assumed that habitat requirements for 70 percent of the boreal vertebrate species are accommodated, although this assumption is untested (Baker and Euler 1989, Wedeles et al. 1991).

Moose are circumpolar in their distribution across the northern hemisphere. Lack of thermal cover and woody browse for winter feeding appear to limit their range in the far north. Periods of extended hot summer temperatures (+27° C) and a parasite (*Parelaphostrongylus tenuis*) carried by deer is thought to limit their southern range (Timmermann and McNicol 1988).

There are seven recognized races of moose; two of these occur in Ontario's boreal forest. The range of *A. a. americana* lies to the east of Lake Nipigon and the range of *A. a. andersoni* extends from west of Lake Nipigon to Alaska (Peterson 1974). As there is no comparative work to indicate behavioral differences between the two races, habitat requirements are considered consistent across Ontario's boreal forest.

6.1.1 Moose Habitat Needs

Timmermann and McNicol (1988) provided a comprehensive review of the literature on moose habitat requirements as the foundation for the OMNR's *Guidelines for the Provision of Moose Habitat in Ontario* (Ontario Ministry of Natural Resources 1988a). Jackson et al. (1991) produced a companion document to these guidelines entitled *Moose Habitat Interpretation in Ontario*. The following generalizations are drawn from their work and updated from current literature.

Home range size estimates for moose vary from 26–168 km². Males use larger ranges than do females. Crête's (1988) summary of published literature suggested that the summer range of moose in eastern Canada was 20–40 km², while migrating Alaskan moose range over as much as 300 km².

Home-range area is related to both animal size and the carrying capacity of the range. Carrying capacity is related to site productivity, which is in turn a function of climate, lithology, topography, and forest cover type. Moose population density is a function of carrying capacity and predatory pressure among other external forces, such as weather. Average moose densities in North America vary from 0.2–2.0 animals/km². Moose may occasionally congregate to densities as high as 15 /km² (Timmermann and McNicol 1988), but this occurs only under unusual circumstances.

Danell et al. (1991b) studied moose consumption of Scots pine biomass in Sweden to prove the importance of site productivity for habitat quality and carrying capacity. They found that although moose consumption of Scots pine was greater on nutrient-rich sites compared with poor ones, the damage to pine was greater on the poor sites. On these, plants could not recover from browsing. As such, these sites were considered to be of less value than the rich ones, even though the plant communities were very similar otherwise.

Mixedwood sites, among the most productive in the boreal forest, support browse that is both preferred by moose and that can recover quickly from browsing damage.

7 Ibid.

⁶ Provincial Big-game Biologist, Ontario Ministry of Natural Resources, Toronto, Ontario.

Danell et al.'s (1991b) work suggested that moose carrying capacity would be higher on mixedwood sites on deep, fresh, well-drained, fine-textured soils (e.g., V17, Sims et al. 1989) as compared with mixedwoods and other cover types occurring on poorer soils.

Although moose browse of crop trees is not viewed as a widespread concern in Ontario, localized problems can occur in areas under intensive timber management. In Newfoundland, for example, Thompson and Curran (1989) found that thinned stands of balsam fir had larger twigs with greater nutritional value and thus were preferred over twigs from unthinned stands. Martinsson et al. (1983) observed that Scots pine from seed orchards suffered more from damage by moose and other agents than did natural Scots pine. Surprisingly, exotic lodgepole pine fared better than both natural and planted Scots pine in the same study.

The effects of moose browsing on stand development in Canada's boreal forest are not particularly well understood. Bedard et al. (1978) studied plant species composition in a balsam fir—yellow birch stand in the Gaspé region of Quebec. Moose browsing tended to maintain a shrub layer longer and favored the development of beaked hazel over mountain maple when compared to fence-enclosed areas.

These observations contrast with previously published work at Isle Royale where no browsing effects upon plant species composition were noted (Bedard et al. 1978). More recent work on Isle Royal, where moose densities are well above average because of the absence of predators, revealed that moose browsing outside fenced exclosures increased the abundance of spruce and decreased hardwood and shrub species (Pastor et al. 1993). Presumably, the lower densities of moose in Ontario should have little effect upon plant communities in the province's boreal forest.

Despite being considered a generalist species, moose use specific habitat types within their home range on a seasonal basis. Habitat types and use differ for moose between summer (growing season), early winter (fall to period of deep snow), and late winter (deep snow to start of growing season). Boreal mixedwoods provide habitat during each of these seasons.

Summer Habitat

In summer, moose prefer habitat that provides a combination of terrestrial forage, aquatic plants, and lowland conifer stands to escape summer heat. Ideally, these requirements should be met within a small area to allow the animals to conserve energy (which is of particular concern to cows with calves). Terrestrial forage consists primarily of leaves stripped from hardwood shrubs and young hardwood trees. A variety of plant species seems to be preferred over one single species. Beaked hazel, willow (Salix spp.), dogwood (Cornus spp.), mountain maple, and American mountain-ash (Sorbus americana) are common moose foods. Young aspen and birch trees also provide summer forage.

Terrestrial forage is most abundant in recently logged or burned mixedwoods and hardwoods. In Ontario, food does not seem to be a limiting factor in summer, although summer feeding is critical if moose are to accumulate fat and other reserves essential to their overwinter survival. Shortened growing seasons or an absence of young (5–15 years) forest cover may limit summer forage and threaten moose overwinter survival.

Although moose can feed on young conifer branches and a variety of herbs and grasses, these plants do not form a significant part of their diet in Ontario. In other regions, such as Newfoundland and parts of Quebec, balsam fir is an important dietary component (Thompson and Curran 1989).

Aquatic plants provide important nutrients, particularly sodium, but account for only 25 percent of the summer diet. The remainder consists of terrestrial forage. Aquatic plants favored by moose include pond weed (*Potamogeton* spp.), yellow pond lily (*Nuphar microphyllum* L.), bulrush (*Scirpus* spp.), eelgrass (*Vallisneria americana* Michx.), and horsetail (*Equisetum* spp.). Most occur in shallow, still waters commonly found near spruce lowlands.

Shelter from extreme heat allows moose to conserve energy and store resources for the winter. For this reason, black spruce forests growing along water bodies are particularly important.

Early Winter Habitat

Early winter habitat typically consists of open mixedwood forests (stocking less than 60 percent). Cutover or burn edges where young hardwoods are juxtaposed with mature forest having a conifer component provide a similar mix of food and cover. Clear-cuts, where some residual tree cover of unmerchantable species remains standing (i.e., selective cuts), can provide suitable early winter habitat.

After leaf fall, moose browse heavily on the current year's twigs of shrubs and young hardwood trees. (The word "moose", in fact, is derived from the Algonquian expression for "twig eater".) As temperatures drop and snow accumulates, moose congregate and favor mixedwood stands on south-facing slopes near dense conifer cover.

Topographically discrete, upland old-growth mixedwood sites traditionally used by moose at the onset of winter are known as concentration areas. Here, moose densities can be as high as 10/km². Abundant browse is available from thick beaked hazel and alder (*Alnus* spp.) growth beneath the poorly stocked canopy. Occasional large conifer trees provide useful cover.

Late Winter Habitat

Late winter habitat consists of significant amounts of dense conifers distributed horizontally and vertically to intercept snow and provide thermal cover. Conifer cover controls the loss of body heat on cold days, and provides protection from overheating on sunny days in early spring. Vertical structure within a stand also provides cover from predators.

Moose actively search for late winter habitat. Cover seems more important at this time than does the availability of browse. Snow accumulations of 60–90 cm can begin to restrict moose movement, depending upon snow density and texture. When snow depths exceed 90 cm, moose remain confined to dense conifer cover. In late winter, moose home-range sizes are estimated to be 2–8 km².

Ideally, late winter cover is close to hardwood and shrub browse in adjacent stands or openings. Allen et al. (1991) suggested that browse within 100 m of cover creates an ideal habitat situation. Surveys by Thompson and Vukelich (1981) demonstrated that cows with calves move less than 60 m from shelter. The energy balance requirements of this social class deserve special attention given their impact upon population dynamics. Small cutovers and irregular shapes to improve the quantity of "edge" are preferred over large cutovers.

Conifer cover is important for snow interception. Racey and Racey (1991) measured snow depth beneath four conifer species at three inter-tree spacings (1.8 m, 2.7 m, and 3.6 m) in a randomized complete block design near Thunder Bay, Ontario. Narrowly spaced conifers (1.8 m) had 60 percent less snow cover than did adjacent open fields. This compared to 20–50 percent reductions in snow depth at wider spacings. Although black spruce intercepted most snow at narrow spacings, red pine intercepted more snow than did black spruce at the wider spacings. This demonstrates that the density at which a stand effectively intercepts snow is speciesdependent.

Stands more than 6 m in height and with more than 70 percent conifer content can intercept snow and provide important cover. Thus, some boreal mixedwoods can provide important late winter habitat depending upon the quantity and arrangement of the conifer trees. The importance of these mixedwood stands is relative to the occurrence, size, and distribution of upland conifer stands.

Specialized Habitat

In addition to general or seasonal habitat requirements, moose also have special habitat requirements. To avoid predation, calving sites are frequently found on peninsulas or on islands in large lakes and rivers. Natural salt licks are found in swampy areas located sporadically throughout the boreal forest. These habitats and winter concentration areas often receive special consideration in forest management planning. Typically, they are identified as areas of concern in the timber management planning process and are excluded from harvest and protected by buffers (Ontario Ministry of Natural Resources 1988a).

Habitat Interpretations

Racey et al. (1989) provided moose habitat interpretations for northwestern Ontario's Forest Ecosystem Classification (FEC). They described summer feeding, early winter, late winter, and thermoregulating habitats based on the characteristics of the 38 vegetation types identified by the FEC. The FEC is one of many tools useful for identifying moose habitat, although most interpretations come from Forest Resource Inventory (FRI) maps and aerial photographs (Jackson et al. 1991).

The majority of moose habitat preference work has been based upon aerial surveys supported by feeding studies. In aerial surveys, the observed patterns of moose movement are correlated to forest cover (Thompson and Vukelich 1981). Feeding studies consist of winter browse ground surveys, dissection of killed animals, and field observations; however, some work on captive moose has been done (Schwartz et al. 1988, Renecker and Hudson 1989). Over the last few years, radio telemetry studies and satellite imagery have been used to improve the understanding of moose habitat requirements (R. Rempel, pers. comm.).

A recent empirical study of moose habitat requirements was conducted by Allen et al. (1991). A matrix of 26 tree and shrub cover species by ten density size classes was assigned a food suitability index from 0 to 1, with 1 representing the optimum. A similar scoring of cover suitability was applied to the cover-type matrix. Optimum interspersion of cover and food was defined as the area within a 100-m overlap between stands with good food and stands with good cover (Index > 0.5). Three seasons of winter aerial surveys were used to plot locations of observed cow moose on a Geographic Information System (GIS) with the cover type and habitat suitability index

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information. A series of circular plots radiating outward from the recorded location of the cow moose were then compared with random point circular plots for habitat suitability index scores. Moose were found in open mixedwoods in early winter and in coniferdominated stands in late winter significantly more than could be accounted for by chance alone. A convincing relationship between observed moose and cover types was demonstrated through an analysis that supported these habitat suitability scores.

Allen et al.'s (1991) preferred early and late winter habitat classes are in agreement with generalizations made by Jackson et al. (1991). The method used by Allen et al. (1991) is a promising way to move from the general to the specific habitat requirements for moose within a specific management unit or forest region.

Naylor et al. (1992) tested Allen et al.'s (1991) suitability indices in Ontario's Great Lakes—St. Lawrence Forest Region. A modified index explained 48 percent of the variation in observed moose densities. This justifies the use of these modified indices for Habitat Supply Analysis (HSA) of various forest management strategies, including alternative silvicultural systems. HSA uses forest inventory, growth projections, and GIS to forecast habitat supply under various management scenarios (Greig et al. 1991a). Further calibration and testing of these indices will be required before they may be used in Ontario's boreal forest.

6.1.2 Stand-level Effects

Application of the Guidelines

Because most harvesting of boreal forests involves clearcutting, OMNR Guidelines focus upon ways of altering cut size and shape to produce edge (Ontario Ministry of Natural Resources 1988a). Edge is emphasized because although clear-cut core areas can produce abundant browse, they offer little cover. Edges of clear-cut areas that are not sprayed with herbicides provide favorable mixtures of food and cover for moose. Allocation of harvest blocks to balance food and cover are emphasized in the guidelines, as is the retention of buffers and corridors of mature conifer to break up cutovers and protect special habitat areas (Ontario Ministry of Natural Resources 1988a).

Modified clear-cutting, such as strip cutting, should benefit moose by providing browse within short distances of cover. Observations in the boreal forest in northwestern Ontario support this hypothesis. Track aggregates and moose densities were greater in the areas where clear-cutting was modified to improve edge and cover in two of the three case studies examined by Payne et al. (1988).

Furthermore, observations by Brusnyk and Gilbert (1983), Todesco (1988), and Mastenbrook and Cumming (1989), confirm the utility of conifer residual cover provided as an objective of implementing the current guidelines. Moose use these areas more than cutovers in late winter and show a strong preference for the browse found within 90 m of the edge. These results agree with those of Thompson and Vukelich (1981) and Hamilton et al. (1980).

Effects of Alternative Silvicultural Systems

The authors know of no studies that examine the effects of alternative silvicultural systems on moose habitat. However, one can predict the potential effects of different systems based upon a general understanding of their characteristics (see Wedeles et al. 1995).

The selection system is not considered practical within the guidelines (Ontario Ministry of Natural Resources 1988a), because it would not create large enough gaps in the canopy to allow for development of browse in the understory. However, selectively cutting large conifers from shelter patches or in mature conifer stands to create openings might improve (or at least not degrade) habitat.

The selection system will maintain forest cover for very long periods of time in corridors or buffers of strategic value. Vertical diversity is greatest with this system, which provides cover and browse in relative abundance depending upon species composition.

As noted earlier, vegetation species composition in a selection forest is a function of initial stand structure and the means used to regulate the application of the system. For example, residual basal area, ratio of diameter classes, maximum diameter, and cutting cycle are variables that regulate the cutting in ways that can increase or decrease the amount of disturbance and overstory removal, thereby creating conditions to favor one species over another. While it should be possible to produce sufficient browse using the selection system, the shelterwood system could probably achieve similar results and can be applied more easily.

Shelterwood systems are briefly mentioned in the guidelines as a means of creating desirable habitat. Shelterwood systems extend the life of forest cover and often develop stratified mixtures that can create good early- and latewinter habitat. Again, the nature of these mixtures depends upon initial stand conditions and the cumulative effects of various silvicultural activities.

Both shelterwood and selection forests can create withinstand mixtures of cover and browse that may be lacking in naturally occurring mixedwoods. This may provide moose with superior energy balances, and observations by McNicol and Gilbert (1980) tend to support this idea. Selective cutting of hardwoods or two-pass cutting should maintain the early winter and late winter habitat value of boreal mixedwoods with well developed conifer understories. Clear-cutting of mixedwoods in the 1960s, without subsequent scarification, created conditions similar to two-pass cutting on some sites. McNicol and Gilbert (1980) found that moose preferred these conditions in winter, when compared to scarified areas regenerating to jack pine or open cutovers where no residual trees were left.

Moose habitat management strategies that involve silvicultural systems depend upon the nature of the forest structure and forest management objectives. Consider a forest consisting of a mosaic of fully stocked, even-aged stands 30–60 years old, and resulting from one or two large fires. Early winter habitat would be scarce. If the area was scheduled for early harvest to achieve other forest use objectives, inexpensive natural regeneration and moose habitat improvement might be achieved simultaneously if the shelterwood system was used.

6.1.3 Large-scale Effects

Moose habitat management guidelines have been applied only during the last 10 years. Today, cut block sizes are smaller and reserves and corridors are common features in the commercially exploited boreal forest as a result of the introduction of these guidelines.

Higgelke (1994) found that GIS-simulated applications of the guidelines projected more early- and late-winter habitat for moose, but had no effect upon summer habitat when compared to progressive clear-cutting. Within some base maps and in certain time periods, the increase in estimated moose carrying capacity was three times greater under the guidelines than under unmodified clear-cutting. However, no work has been done to test these projections or to demonstrate a relationship between these use patterns and moose populations at a regional scale.

Clearly, the current guidelines are of some benefit to moose. However, it has been questioned whether the costs of modified harvesting practices as outlined in the guidelines are justified by the value of increased moose habitat. Payne et al. (1988) noted that some of the extra costs are in road construction, opportunity costs of wood lost to windthrow in reserve strips, and marginal costs associated with finding additional sources of wood to replace the wood left for moose shelter. The quandary is that the response of moose to various forest operations is more difficult to quantify with the same level of certainty as are increases in operating costs. There is no guarantee that improving habitat will increase the moose population,

particularly in view of nonhabitat factors such as predation, hunting, and weather.

Twenty years ago moose populations in North America were thought to be completely limited by habitat availability (Franzmann 1978). This is not the current view. Work by Crête and Jordan (1982) found that food quantity and quality are not a limiting factor in southwestern Quebec, and these results are believed to apply equally well to Ontario. It seems that managing habitat to produce cover is more important than managing habitat to produce food. However, cover is rarely limited at a forest or regional scale in Ontario, and moose populations are typically well below estimated habitat carrying capacity (Higgelke 1994).

Predation can also have a significant impact on moose populations. Predation by man and wolves (*Canis lupus*) increases as a result of higher road densities, which are often required when using alternative silvicultural systems (Hamilton et al. 1980, McNicol and Gilbert 1980). Black bear (*Ursus americanus*) predation has recently been considered an important factor in Ontario. In Alaska, Schwartz and Franzmann (1991) estimated that four to six moose calves are consumed per bear each spring.

One could speculate that the arrangement of conifer cover into residual strips under the current guidelines might increase the effectiveness of bear predation upon calves. Shelterwood systems could provide equivalent wood recovery and create identical habitat carrying capacity to modified clear-cutting. However, the dispersed cover may reduce bear predation and result in superior moose population growth. These relationships are difficult to assess because predator—prey interactions of moose will be confounded with other elements of the physical environment (including habitat).

The development and testing of practical habitat supply analysis methods similar to Allen et al. (1991) is underway in Ontario (Naylor et al. 1992). The next step is the development of population models that account for important prey-predator-environment interactions.

As an example, Schuerholz et al. (1988) described the development and application of an ungulate population model in British Columbia. The model considered the relationship between cover, snow depth, animal weight, and survival, among other variables, to estimate ungulate populations within a watershed. Their analysis predicted an increase in the ungulate population in the context of a beetle-killed timber salvage operation. Although these population models provide the required framework for trade-off analysis between moose and timber values and the role that alternative silviculture systems can play, they remain to be empirically tested.

6.2 Caribou

Woodland caribou (Rangifer tarandus caribou) represent one of six caribou subspecies native to North America (Bergerud 1978). Although only approximately 1 800 animals live within the commercial boreal forest, Ontario's population of caribou is estimated to be 15 000–16 000. The majority of these animals live on the Hudson's Bay Lowlands (Bergerud 1978, Cumming and Beange 1993). Woodland caribou also inhabit the high elevation forests of central British Columbia, the lowlands of Northern Québec, and the boreal forests of Labrador and Newfoundland.

Effective breeding populations are exceedingly low in Ontario's commercial forests. The small, isolated numbers on the Slate Islands of Lake Superior, the islands of Lake Nipigon, and the Armstrong area are of particular concern (Cumming and Beange 1993). The low fecundity of caribou relative to other ungulates also contributes to their vulnerability to changes in their environment (Racey et al. 1991).

At the turn of the century, the range of woodland caribou extended from coast to coast in Canada and encompassed all of Ontario north of the French River. Most of their range coincided with that of black spruce (Hosie 1975, Bergerud 1978). Due to active logging and settlement of the region, however, caribou have disappeared from the southern boreal forests. Four interrelated hypotheses have been put forward to explain the disappearance of caribou in the south. These include: 1) direct habitat loss from logging; 2) influx of predators following the expanding range of moose and deer; 3) parasitism from "meningeal worm" carried by deer; and 4) disturbances caused by logging, road building, and settlement (Bergerud 1978, Hristienko 1985, Ontario Ministry of Natural Resources 1985, Cumming and Beange 1993). It would appear that the cumulative effects of these impacts are responsible for the disappearance of southern bands (Racey et al. 1991). Industrial sulphur dioxide emissions may also have reduced the abundance of caribou's preferred winter food of ground and bark lichens. This industrial expansion coincides with the settlement and logging of the region.

Ferguson et al. (1988) studied the characteristics of a southern caribou herd on Pic Island in Lake Superior. There are no wolves or bears on this island. These researchers concluded that predation by wolves is probably one of the most important factors contributing to the decline of southern caribou bands. Wolf numbers increase with moose and deer populations and wolves move freely along roads associated with the commercial development of forested areas.

Caribou in the commercial boreal forests of northwestern Ontario seem to favor spruce swamps in summer and early winter. In late winter they prefer mature, dry, jack pine sites (and occasionally open mixedwoods) supporting mosses, arboreal lichens, and ground lichens. Since they do not browse on twigs, lichen is extremely important during the late winter months. Caribou dig or "crater" for lichen in the winter and conifer cover is important to intercept snow. Abundant, fast-growing green plants provide forage for caribou in the early to late summer months.

Unlike moose, which prefer some vertical heterogeneity with conifers providing hiding cover, caribou prefer mature conifer stands with less vertical structure. These conditions favor the development of ground lichen, and probably allow caribou to spot predators (OMNR 1985, Racey et al. 1991).

Caribou have special habitat requirements for calving and seem to prefer the points and islands of large lakes (OMNR 1985, Racey et al. 1991, Cumming and Beange 1993). Summer is spent either in solitude or in cow/calf pairs, but the animals congregate during winter in small groups of 8–15 animals.

Surveys in Ontario found that logging of winter habitat completely displaces caribou. Aside from actual displacement, the small bands of caribou may become victims of poachers and wolves that use access roads into the area (Cumming and Beange 1993).

A comprehensive study in Newfoundland on woodland caribou and clear-cutting found that radio-collared females with calves moved 8 to 14 kms away from logging operations. Male caribou are less likely to be displaced by such activity. Displacement is greatest during active logging, but caribou are slow to return (Chubbs et al. 1993). This study on caribou movement also confirmed a preference by caribou for mature conifer habitat.

Selective and shelterwood cutting has been attempted in British Columbia as a means of developing more lichen within a stand by allowing increased light to reach the forest floor (Hristrienko 1985). The decline of British Columbia's caribou populations suggest that these measures have not been successful. Attempts to use modified clear-cutting in Ontario have not been successful either (Cumming and Beange 1993). Some of these failures can be attributed to the small population size of the bands in question. Chubbs et al. (1993) gave no indication that the displacement of caribou by logging threatens the animal's survival in Newfoundland.

Explicitly managing for moose, which take advantage of recently disturbed forest cover, is at odds with caribou requirements for older, undisturbed open conifer forests.

Ontario's new habitat management guidelines for the conservation of woodland caribou take into account the large temporal and spatial dimensions of caribou habitat supply requirements for the provision of cover, food, and a means of escape or maintaining distance from predators (Ontario Ministry of Natural Resources 1994). Under these guidelines, traditional winter use areas will be identified and evenaged forests of 100 km² will be set aside across the landscape until other forest areas develop suitable habitat qualities (i.e., older conifer forest with abundant lichen). When a winter area is cut, large clearcuts followed by prescribed burning or other means of stand replacement are the preferred option. The idea is to mimic fire disturbance patterns. Two-kilometre-wide travel corridors are to be maintained between winter habitat and calving sites, 3-km buffers are to surround winter use areas, and 1-km buffers are to surround calving sites.

It remains to be seen if these measures can save the small bands of caribou that inhabit the commercial boreal forests. Until new theories of caribou behavior are advanced and tested in Ontario, however, it seems that there is no role for the application of alternative silvicultural systems for the conservation of caribou.

7.0 FURBEARERS

Very little background information is available regarding the effects of alternative silvicultural systems on furbearers. In fact, studies on this topic are virtually nonexistent (although there are a few studies on the effects of traditional forest management [see Thompson 1988]). Even the habitat requirements of several boreal furbearers are poorly understood. In this section, therefore, most of the discussed effects are extrapolations based on an understanding of habitat needs.

Boreal mixedwoods, as noted in previous sections, are biologically rich environments compared with other boreal communities. A common theme of this chapter is that the manner in which forest management affects furbearers will, to some extent, mirror the way in which forest management affects their prey.

However, the large home range size of many furbearers and their need for cover, make it impossible to extrapolate such effects with complete certainty.

The amount of area over which an animal ranges will, to a large extent, determine how that animal is affected by forestry operations. Individuals of species with relatively small home ranges, such as ermine (*Mustela erminea*), which require approximately 10–25 ha (Fagerstone 1987), may be drastically affected by a single stand-level operation. In the boreal forest, where commercial clear-cuts generally range from 80–260 ha, a single harvesting

operation may encompass an individual's entire home range. On the other hand, some furbearers have very large home ranges. Wolves, for example, may range over 128–1 280 km² in boreal environments (Mech 1970). The effects of forest management on large-ranged species must, therefore, be considered in context. The availability of small-mammal prey in a harvested stand may change dramatically, although the importance of the food provided by any single stand may not be significant to large predators. Furthermore, virtually all species with large home ranges are either habitat generalists or are very capable of crossing various types of forest habitat to reach the types they prefer (Hunter 1990). While it may be illogical to consider stand-level effects on some species, it is entirely appropriate to consider forest-level effects.

In this section the authors have classified furbearers into three groups. The first contains those species with home ranges that are so small that all, or most, of an individual's range could be encompassed by a "normal" sized clear-cut. The second group includes those species whose home ranges are of an intermediate size. A single, traditional clear-cut would not encompass the complete home range of any individual, although it may cover a significant portion. Over several years, contiguous clear-cuts could encompass all of an individual's home range. The third group contains those species with home ranges of such a large size that the area encompassed by a single clear-cut would represent a relatively small portion of an individual's home range.

Furbearers in the first group include red squirrel, weasels (Mustela spp.), beaver (Castor canadensis), and muskrat (Ondatra zibethicus). The second group is comprised of red fox, fisher, marten (Martes americana), mink (Mustela vision), river otter (Lutra canadensis), and skunk. The third group includes coyote (Canis latrans), wolf, black bear, and wolverine (Gulo gulo). Figure 1 shows the approximate home range sizes of boreal forest furbearers.

This grouping is not intended to imply that forest-level effects are insignificant in the ecology of species with small home ranges. As with songbirds, which usually have very small home ranges, forest-level effects may be important in the ecology of some furbearers. This grouping does suggest, however, that it may be inappropriate to consider stand-level effects for large-ranged furbearers.

Forestry operations will not affect all species within a group in the same way. Some furbearers are primarily aquatic. Individuals of those species will be affected by harvesting operations and approaches in a very different manner than will terrestrial, forest-dwelling furbearers. Emphasis in this section is on the later of these.

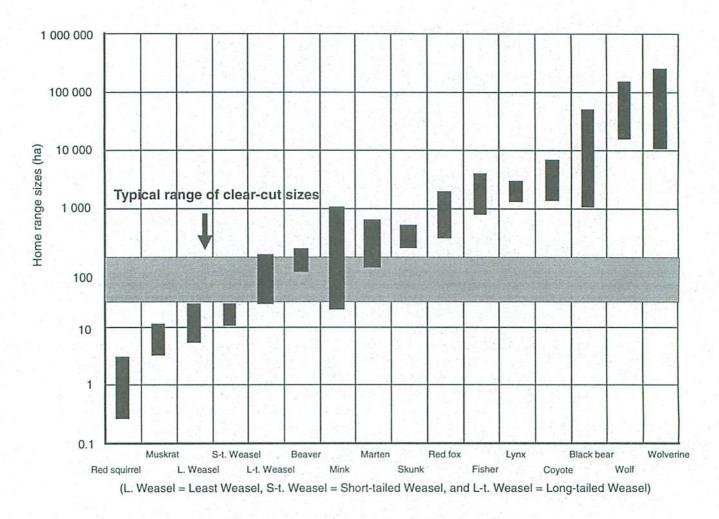


Figure 1. Home range sizes of boreal furbearers and approximate size of a typical clear-cut

7.1 Habitat Affiliations

A comprehensive discussion of the habitat affiliations of all boreal forest furbearers is well beyond the scope of this document. In this section, the authors concentrate on the role of boreal mixedwoods in providing habitat to furbearers. For more detailed information, readers are referred to the much more extensive works cited here.

7.1.1 Furbearers with Small Home Ranges

The habitat affinities of weasels are poorly understood. Drawing upon Soper (1946), Fagerstone (1987) concluded that ermine avoid dense forests and settle in successional or forestedge habitats, and are common in spruce—aspen parklands of the midwest. Simms (1979) found that ermine prefer early successional communities such as grasslands and shrubs. Long-tailed weasels (Mustela frenata) occur only sporadically in boreal regions, as this is the northern edge of their distribution (Fagerstone 1987). Least weasels (Mustela nivalis) occur in northern regions in open areas such as tundra, mead-

ows, and river bottoms. Of the three members of the weasel family, therefore, boreal mixedwoods are most important to ermine.

Beaver and muskrat use aquatic habitats within the boreal forest. Inasmuch as their aquatic and riparian habitats abut or pass through mixedwood forests, they use boreal mixedwoods to some extent. Beaver, for example, feed extensively upon aspen trees, which may be growing on mixedwood sites close to the lakes or ponds they inhabit. However, the primary aspect of the habitat affiliations for beaver and muskrat is the aquatic environment. The home ranges of individuals of these species are often linear in shape, particularly if they are inhabiting streams or slowmoving rivers. In the subjective categorization scheme considered in this report, a case could be made for including them in the group of furbearers with intermediate sized home ranges. In some instances only a portion of an individual's home range would occur near a single forest management operation.

7.1.2 Furbearers with Intermediate Home Ranges

Of all boreal forest furbearers, the most extensively studied in a forest management context is the pine marten. The habitat requirements of marten often put them at odds with traditional forest management oriented at liquidating mature and overmature softwood stands. The habitat needs and affiliations of marten have been well studied and documented by de Vos (1951), Soutière (1979), Steventon and Major (1982), Snyder and Bissonette (1987), Thompson (1988, 1991, 1994), Bissonette et al. (1991), Buskirk and Powell (1994), and Thompson and Colgan (1994).

Marten have consistently been found in close associations with mesic coniferous forests having complex physical structures, most often in mature and overmature stands (de Vos 1951; Thompson 1988, 1991, 1994; Buskirk 1992; Buskirk and Powell 1994; and Thompson and Colgan 1994). The complex structure (i.e., living branches, logs, and other coarse woody debris) is important to marten, particularly in winter, because it protects them from predators and harsh environmental conditions, and gives them access to spaces beneath the snow where prey animals live (Buskirk 1992). Buskirk and Powell (1994) state that it is not clear whether marten prefer cover types occupied by prey whose behavior makes them easy to catch, or cover types with a physical structure that renders prey more vulnerable.

High densities of marten may also be found in uncut boreal mixedwoods, as Thompson (1988, 1994) found near Manitouwadge, Ontario. If the mixedwoods supply the same important habitat elements that conifer stands do, they may be capable of providing winter habitat. Boyd (1978) contended that use by marten of mixedwood stands in winter depends on the proportion of conifer present. Marten have been found to use a broader variety of habitats during the summer, including young hardwood, mixedwood stands, and recent clear-cuts (Boyd 1978, Thompson 1988). However, all studies on marten habitat have stressed that old forested habitats with a significant conifer component are crucial to the animal's survival during the winter.

Fisher also appear to have an affinity for old forests, although it seems that they are not as dependent on them as are marten (de Vos 1951, Ontario Ministry of Natural Resources 1986, Douglas and Strickland 1987, Buskirk and Powell 1994). Kelly (1977, *in* Allen 1987) reported that fishers in New Hampshire selectively used forest stands with 80–100 percent canopy coverage, and used sparsely stocked stands only when adjacent to preferred dense cover. Arthur et al. (1989) concluded from a radiotracking study in Maine that fisher used dense conifer habitats mostly in winter, but that prime fisher habitat

encompassed a mix of forest types, including some openings. In boreal forests, mixedwood types are a very important component of fisher habitat (Boyd 1978, Douglas and Strickland 1987). Trappers in the Algonquin region of Ontario, surveyed on the winter habitat preference of furbearers, indicated the following use by fishers: wetlands 23 percent, old mixed hardwood/conifer 21 percent, young mixed hardwood-conifer 21 percent, old hardwood forest 11 percent, old conifer forest 8 percent, young hardwood forest 8 percent, young conifer forest 6 percent, and other 2 percent (Strickland and Douglas 1984, in Douglas and Strickland 1987). Based on a series of track transects, Thomasma et al. (1994) found that fishers use mixed forests with greater than 50 percent conifer closure in much greater proportion to their availability than any other habitat type in the Ottawa National Forest of the upper peninsula of Michigan.

Although fisher seem better able to use early successional forest that do marten, the provision of overhead cover and physical structure are clearly important habitat elements (Allen 1987).

Mink are closely associated with aquatic habitats (Eagle and Whitman 1987). However, Thompson (1988) sheds doubt upon the assertion that forested areas do not provide important habitat for mink. He noted that Gilbert and Nancekivell (1982) found a high occurrence of hare and microtine rodents in mink diets in northern Alberta and deduced that mink spend considerable time beyond the riparian zone. Thompson (1988) also reported several instances in which mink were found in forested habitats hundreds of meters away from riparian areas. The role of boreal mixedwoods as habitat for mink is difficult to differentiate from the role of other forest types, given the general lack of information on mink ecology in such areas.

As lynx rely heavily on snowshoe hares for food (Quinn and Parker 1987, Thompson 1988), their habitat preferences are influenced by those of their prey. As noted earlier, prime hare habitat includes a high density of shrubs and saplings above the local snow depth, young trees and/or low shrubs that provide twigs, and cover from predators and thermal stress. Thompson (1988) cited several studies that noted heavy use of 10- to 20-year-old successional stands by snowshoe hares and lynx. During years of high snowshoe hare populations, their habitat preference broadens (Boyd 1978); during years of low populations, hares survive in core areas of optimal habitat. These areas provide a choice mix of food and cover, and are also important for lynx. Young boreal mixedwood and deciduous forests are thus very important as hare and lynx habitats.

Lynx need more than young forests to meet their habitat needs. Mature conifer forests, or mixedwoods with a high

proportion of conifer, are used for denning, cover, and as travel corridors (Boyd 1978, Parker et al. 1983, Quinn and Parker 1987). Parker et al. (1983) suggested that ideal lynx habitat would contain up to 50 percent mature conifer, although this seems somewhat high in light of lynx's preference for hare (Thompson 1988).

The red fox has a worldwide distribution and thrives in many habitats, ranging from lowarctic to subtropical. Also, it is able to survive in wilderness, rural, and urban surroundings (Henry 1986, Voigt 1987). Many studies (Soper 1942, Ables 1975) have found that foxes prefer habitats that contain a mosaic of cover types, including mixed forests, meadows, valleys, etc., and that they avoid large expanses of unbroken habitats. However, very little work has been done on foxes in the boreal forest. Wedeles (1984) found that red foxes used mature and young mixedwood stands in excess of their relative abundance compared with other cover types in a very heterogenous environment in the southwestern Yukon. He attributed this to their affinity for snowshoe hares, which showed similar habitat patterns. In boreal Saskatchewan, Henry (1986) found that red foxes prefer edges between regenerating stands that support high populations of voles and hare. Foxes seem to avoid large, unbroken expanses of mature forest (Wedeles 1984, Ontario Ministry of Natural Resources 1986, Allen 1987). In boreal forests, foxes may use mixedwood habitats at least in proportion to the amount of prey they consume.

Skunks are found throughout boreal Ontario, although their numbers are higher in the south. In general, skunks use open areas or forest edges and seldom enhabit unbroken forests (Rosatte 1987). However, Thompson⁹ (pers. comm.) reported trapping many skunks in 30- to 40-year-old aspen dominated mixed forests near Manitouwadge, Ontario, during his studies on marten habitat.

River otters inhabit riparian areas, marshes, and small lakes. Key habitat features for these animals include abundant riparian vegetation, submerged trees, and other physical structures (Melquist and Dronkert 1987). Their use of upland sites appears limited, although little such investigation has been conducted in boreal areas.

7.1.3 Furbearers with Large Home Ranges

As noted earlier, wolves may range over hundreds of square kilometers. The presence of wolves in an area and their habitat use is dictated by the availability of prey. Boreal mixedwoods are undoubtedly important habitat for wolves, given that they provide significant habitat for moose, a very important prey species. Since wolves are

opportunistic feeders, the habitat affinities of other prey also influence their use of an area. Wolf densities are smaller in areas where prey is relatively sparsely distributed, such as the arctic tundra, than where it is relatively abundant, as in the southern boreal forests (Mech 1970). Habitat *per se* is likely not a limiting factor in wolf ecology; prey distribution and their incompatibility with humans are probably more important.

Coyotes are relatively recent immigrants to Ontario, having arrived here in the 1920s and 1930s as part of a continentwide eastward migration from the Great Plains and western states (Kolenosky et al. 1978). This migration is thought to have occurred because of the extirpation of the wolves from large parts of their range (Mech 1970). In Ontario, coyotes are present in boreal regions (Kolenosky et al. 1978), but are restricted mainly to farmlands and rural areas and only rarely occur in forests (D. Voigt, ¹⁰ pers. comm). As such, they are not affected by commercial forestry operations.

Black bears, found throughout boreal Ontario, are very dependent upon forests. Generally a mix of forest communities, with a variety of tree and shrub species of varying ages, provides optimum habitat (Kolenosky and Strathearn 1987). Densities are usually greatest in highly diverse forests at a relatively early stage of development. Mixedwood forests are also important black bear habitat.

Wolverines are now present only in the very northern part of Ontario (Hash 1987), although their historical range extended south through Ontario into the northeastern United States. While they undoubtedly inhabited boreal mixedwood forests in Ontario, as they still do in the more westerly parts of their range, the importance of this forest type to wolverines is difficult to determine in hindsight. Given the very large home ranges of wolverines (100–1 000 km²), the significance of boreal mixedwoods may have been proportional to the size of the home range that it comprised for any individual.

7.2 Stand-level Effects

7.2.1 Furbearers with Small Home Ranges

As noted earlier, issues related to boreal mixedwood forestry are most relevant to ermine, but very little ecological information is available on this species. Food habit studies suggest that voles, followed by mice, are their main prey. However, they eat a variety of food ranging from insects to snowshoe hares (Banfield 1974, Fagerstone 1987).

The effects of clear-cutting on voles and mice depend upon the postharvesting silvicultural activities that take

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¹⁰ Wildlife Research Scientist, Ontario Ministry of Natural Resources, Maple, Ontario.

place. In instances where prey populations remain high, there may be no deleterious effects on ermine. Prey populations are most likely to remain high when woody debris remains on a site following harvesting and silvicultural activities. Dead and downed material provides habitat for prey species, and cover for ermine. Ermine are well adapted to snow, and its increased accumulation on clearcut sites may not present an impediment to use of these areas.

Where heavy site preparation is used (e.g., clearing debris to expose mineral soil), prey populations may decline, thereby causing a related decline in ermine populations. This might also result in an increase in ermine home range size, which varies according to prey abundance. If ermine remain in a clear-cut area in which prey populations are reduced, they may expand their home ranges. It might be speculated that this could lead to increased intraspecific strife, and perhaps range abandonment.

Although beavers are largely aquatic, they depend on terrestrial resources (i.e., shrubs and trees) for food. Beavers eat many species of trees, but where they occur, trembling aspen are preferred. They also eat herbs and shrubs, with alder (*Alnus* spp.) and willow being the most important species for them in the boreal forest.

Given the preference for aspen by beaver, mixedwood forestry can have significant effects on this species. Beavers generally forage on land within 50 m of the water's edge (Novak 1987). In typical forestry operations in Ontario, uncut buffers from 30-90 m are left around most water bodies (Ontario Ministry of Natural Resources 1988b). The extent of the buffer depends upon the species of fish inhabiting the water body, and on the grade of slope leading to the water's edge. This combination of leaving buffers and the beaver's own "selective" harvesting of aspen, will decrease the abundance of aspen in shoreline mixedwoods over time. Thompson (1988) suggests that aspen communities may represent only transient beaver habitat for similar reasons. If beaverinhabited waterbodies in mixedwood forests were cut to the water's edge, aspen reproduction would likely occur. Therefore, not leaving buffers may be beneficial to beavers in some instances, particularly in circumstances where harvesting was to take place on only part of the area abutting the water body. The uncut portion could provide food until the harvested section begins to regenerate.

The OMNR permits the use of alternative harvesting systems in lakeshore buffers (Ontario Ministry of Natural Resources 1988b), although few forestry companies exercise this right. Shelterwood or selection systems, which would preserve the shading of water bodies and impede erosion, are generally not conducive to aspen regenera-

tion, and so might not enhance beaver habitat. From a beaver habitat perspective, however, this would be no worse than simply leaving the buffer.

Muskrats rarely leave the water and are fairly oblivious to nearby human activity. Forestry operations should have little, if any, effect on muskrat populations, assuming that water quality is protected (Thompson 1988).

7.2.2 Furbearers with Intermediate Home Ranges

Relative to other furbearers, the effects of forestry on marten have been relatively well studied. Based on winter track transects and live trapping, Snyder and Bissonette (1987) found that use by marten of commercially clear-cut spruce-fir forests in western Newfoundland was about one-third that of uncut forests. They also found that marten used young clear-cuts (< 8 yrs old) considerably less than expected, and did not use older clear-cuts (16-23 years) at all. The authors suggested that decreased prey abundance and a lack of woody structure impeded use of the older clear-cuts, and that 23 years was insufficient time for postcutting habitat to be adequate. Soutiere (1979) found that marten densities in commercially clear-cut mixedwoods in Maine were one-third of those in unlogged forests. Steventon and Major (1982) found that three radio-collared marten used clear-cut areas in mixedwood forests in Maine at a rate much less than their proportional presence. Thompson (1994) found marten density indices 88–95 percent higher in uncut forests than in logged areas in mixedwood and coniferous habitats near Manitouwadge, Ontario.

There are some indications that the effects of forest harvesting on marten can be mitigated by using certain alternative systems. Soutiere (1979) found that marten densities and track abundance were only slightly less in selectively cut (i.e., high-graded) mixedwood forests than in uncut mixedwood forests in Maine. The selective harvesting reduced average cover to 60 percent, with a residual basal area of 20–25 m²/ha. Campbell (1979, in Allen 1987) concluded that silvicultural prescriptions that resulted in less than 57 percent removal of harvestable trees had relatively minor impacts on marten habitat quality in Wyoming. No comparable studies have been done in Ontario. However, these studies suggest that selection harvesting, two-pass harvesting, and perhaps shelterwood harvesting may not have the same detrimental effect on marten as does clear-cutting. Selection harvesting may have almost no effect, depending on the amount of cover remaining after the harvest. The Ontario Ministry of Natural Resources (1986) suggested that selection harvesting, which leaves 30–40 percent of the forest canopy, will have minimal impact on marten and fisher. For the two-pass and shelterwood harvesting systems, the forest may remain useful to marten after the first cut, but the time interval between the first and second cut will influence the ultimate utility of the stand. A short time interval would render the stand of little value, although the period of time in this low-value state is less than that of clear-cut sites.

In a generic model of marten habitat management, Thompson and Harestad (1994) suggest that: "Selective logging, including using a shelterwood system, will not reduce a habitat's carrying capacity for American marten if removals are kept below 30 percent of the stem basal area every 50 years in boreal and montane forests..."

The studies of Soutiere (1979), Steventon and Major (1982), and Snyder and Bissonette (1987) also indicated that marten use residual overmature stands to much the same extent that they use larger uncut forests, although they travel through clear-cut areas somewhat "reluctantly" to access them. In a stripcutting scenario, uncut patches or strips should continue to be of use to marten after the first cut. The utility of the area would decrease after the second cut, as the time period for seedlings to become established (generally 3–10 years) is much less than the time for a stand to return to a useful state for marten. The Ontario Ministry of Natural Resources has suggested that "a few" small clear-cuts may not be detrimental to marten and fisher (Ontario Ministry of Natural Resources 1986).

Another aspect of the effect of forestry on marten relates to rotation age. The physical characteristics of a stand that make it appealing for marten — an abundance of dead and downed wood material, snags, etc., — are common in very old stands. In commercial forestry terms, overmature stands are beyond rotation age and losing volume with time. It is not common forestry practice to allow mixed-wood stands (or other stands) to age to the point where they naturally have these features. However, forest and wildlife managers can foster the presence of these features using alternative systems. The selection system is most conducive to retaining complex physical structure within stands, although it may also be possible to some extent with two-pass and shelterwood harvesting.

The authors know of only one empirical study that examines the effects of forest management on fisher (Buck et al. 1994). In this study, the use of sites subjected to "heavy" harvesting was compared with that of "lightly" harvested sites in fir dominated forests in northern California. Heavily harvested stands were more open and had a greater hardwood component that did the lightly harvested stands. Based on comparisons of habitat use and mortality in the two areas, Buck et al. (1994) concluded that heavily harvested sites were poorer fisher habitat, and that the loss of conifers had a significant influence on habitat quality. It is unclear whether these results would hold true in boreal

mixedwoods, given the habitat preferences of fishers. Clear-cutting would be as detrimental to fisher as it is to marten, although given the fisher's somewhat more elastic habitat requirements, the detrimental effect may not be as severe nor as long-lasting. The use of alternative systems will influence the quality of fisher habitat in a manner similar to its effect on marten habitat. Ontario Ministry of Natural Resources (1986) assumed this to be the case, as their harvesting guidelines for protection of marten and fisher habitat are identical.

Lynx's affinity for snowshoe hares suggests that young successional forests should provide good habitat. Clear-cutting, which creates young successional forest, may benefit lynx in this context. However, this does not imply that there are no concerns about the effects of forestry on lynx. Snowshoe hares do not colonize boreal clear-cuts for 6–7 years after harvesting, and it often takes 10–30 years for their densities to peak (Telfer 1974, Thompson 1988, Koehler and Brittell 1990). For several years following a clear-cut, a site is of little value to lynx.

If clear-cut mixedwood sites are left to regenerate naturally, they should contain an abundance of preferred hare food; namely aspen and deciduous shrubs. However, while aspen marketability is increasing (Wedeles et al. 1995), conifer regeneration is generally more desirable from a commercial perspective. Considerable expertise exists in Ontario for converting mixedwood sites to conifer plantations; and although this is expensive, it is not an uncommon practice. The application of herbicides, which is usually required to achieve such a conversion to conifers (Scarratt 1992), eliminates valuable browse for hares and decreases the value of these sites for hare and lynx. In instances where conversion is not attempted, regenerating mixedwood sites commonly contain more aspen and deciduous shrubs than they did prior to harvest (Jovic 1981, Matiece 1981, Scarratt 1992).

As noted earlier, lynx do not rely entirely upon young forests for their habitat needs, as they use mature mixed-woods and conifer forests for den sites and cover. Since mature forests support few snowshoe hares, it is important that denning areas for lynx be close to prey habitat (Koehler and Brittell 1990).

An optimal forest management scenario for lynx may be similar to that typified by the OMNR moose guidelines (Ontario Ministry of Natural Resources 1988a): namely, moderate sized clear-cuts (approximately 80–200 ha) interspersed with mature forest. Koehler and Britell (1990) suggested that clear-cuts should not exceed 100 m in width as lynx are reluctant to cross large openings. However, if sufficient travel corridors exist, this may not be a problem.

Because of the lack of empirical evidence on the effects of alternative silvicultural systems on lynx, as in many other instances the authors are left to hypothesize about these. Selection harvesting, which stimulates growth of the understory, may provide habitat for hares and lynx, although compared with clear-cutting it would not be as productive in this respect. However, selection stands may be useful in maintaining cover and denning sites. Shelterwood systems may also provide young growth suitable for hare and lynx, but similarly, would not do so to the same extent as would clear-cutting. Strip cuts and patch cuts would provide both young successional stands and mature cover for lynx. When the uncut strips are harvested, the first-cut strips should be regenerated enough to provide snowshoe hare browse, depending on the type of regeneration fostered.

The issue of rotation age is also relevant for lynx, although perhaps not to the extent that it is for marten. Lynx's preference for den sites in older forests suggests that the removal of overmature stands may be detrimental. The use of alternative systems, which maintain the physical characteristics of overmature stands, may be useful in providing lynx cover and denning habitat.

Given foxes' opportunistic and generalized manner of habitat and food use, traditional forest management may not be detrimental to them. Thompson (1988) suggested that traditional forestry practices could affect red foxes in much the same manner as they do lynx, particularly in instances where snowshoe hare is a major component of their diet. In instances where their diet is more generalized than that of lynx, they may attain medium densities in the shrub stage and maximum densities in sapling and young stands (Thompson 1988). Naturally regenerating, clearcut mixedwood stands may be an important element of fox habitat in boreal areas.

Similarly, alternative harvesting systems should affect fox habitat in much the same manner as they affect lynx habitat. The need for old forests may not be as important for fox as for lynx, marten, or fisher, except that they would add an element of heterogeneity to a forest if interspersed with other stand types.

Thompson (1988) stated that, because few data exist on the distance that mink will move from aquatic and riparian habitats, predicting the effects of logging on them is entirely speculative. If shoreline reserves continue to maintain small rodents, and if mink are not dependent upon food that is beyond the boundaries of buffers, then forestry effects on mink may be negligible (Thompson 1988). The Ontario Ministry of Natural Resources (1986) suggested that timber operations along shorelines should maintain structural diversity, such as snags and wood debris, to provide habitat for mink prey.

7.2.3 Furbearers with Large Home Ranges

Although the prey of furbearers with large home ranges may be affected by stand-level forestry operations, furbearers of this group are generally so wide-ranging that it is difficult, and perhaps inappropriate, to consider standlevel effects on them.

7.3 Large-scale Effects

7.3.1 Furbearers with Small Home Ranges

The authors know of no studies examining large-scale effects on small furbearers, but perhaps some parallels exist with birds and small mammals. For birds, one concern about the effects of fragmentation is that they may suffer increased predation, thereby leading to population-level effects. Red squirrels, like birds, are eaten by virtually every species of carnivore that inhabits the boreal forest (Obbard 1987). Could red squirrels in remaining mature forest stands suffer increased mortality because of higher populations of red foxes and lynx (species that would thrive in a mosaic of recently clear-cut stands) or from marten, which have less area in which to forage because of lost habitat?

At present there is no known empirical evidence to suggest that forestry operations have large-scale effects on any furbearers in this group. However, before this assessment is accepted as fact, further investigations are required.

7.3.2 Furbearers with Intermediate Home Ranges

Some furbearers with intermediate-sized home ranges may be in an ecologically interesting and perhaps precarious situation. The home ranges of marten, for example, are sufficiently small that stand-level perturbations can affect individuals. Marten's home ranges are small enough that a decrease in the value of one portion of the area that they occupy cannot be "absorbed" or compensated for by increasing use of another portion of their range. Furthermore, some of these species (e.g., marten, fisher, lynx) have distinct habitat affiliations, unlike most larger furbearers that are habitat generalists. Finally, species in this intermediate category are neither as dense in population nor as fecund as are small mammals, and thus are not able to recover as rapidly from local population-level effects.

In essence, this group of furbearers may be caught between having the ability to respond to habitat disturbances by virtue of dense populations and high fecundity, or by virtue of being habitat generalists with large home ranges. This may explain why many furbearers in this group are susceptible to the impacts of habitat change caused by forest management practices.

As noted earlier, forest- or landscape-level implementation of alternative silvicultural systems is not a realistic

scenario in boreal mixedwoods. Yet, a broader implementation of some alternative systems may be reasonable in some situations. If, for instance, marten and fisher population management was given a high profile in a commercially valuable forest, it might be possible to integrate alternative silvicultural systems with traditional systems in a manner that maintained their habitat. In one rotation. a portion of the forest could be harvested using clearcutting, another portion harvested using selection harvesting, and other portions not harvested at all. During the next cutting cycle, a portion of the remaining uncut forest could be clear-cut, and another portion harvested using the selection method. Eventually, all of the commercial forest area would experience some type of harvest, yet a portion of the forest (higher than would be the case if only clearcutting was used) would always be available for marten and fisher habitat. This is a simplified scenario, but the point is that implementation of selection harvesting in this manner would assist in preserving marten and fisher habitat over a landscape and yet still permit commercial timber harvesting. (This scenario is based on the premise that selection harvesting does not seriously degrade marten habitat — a premise that is untested in Ontario's boreal forest.)

7.3.3 Furbearers with Large Home Ranges

While there has been a considerable amount written on the effects of habitat fragmentation on large predators and furbearers (Harris 1984, Morrison et al. 1992), relatively little of this work has been done in boreal settings. Most work has examined the effects of habitat fragmentation where sites do not return to their initial conditions (e.g., clearing land for agriculture). In boreal Ontario, most of the forested land harvested is designated to return to forest, so fragmentation effects from agricultural areas would not be analogous.

As noted earlier, large furbearers are habitat generalists and range over large areas. They use many habitat types and can travel through or ignore those that are of little value. Thus, they are well adapted to natural, large-scale disturbances that change the nature of extensive tracts of forest. As such, forestry operations that foster the return of harvested areas to original or natural conditions may not have a significant impact on large furbearers (although there are important differences between the effects of fire and commercial forestry [Thompson 1993]).

Some mixedwood forestry practices may change the value of the forest for large furbearers. For example, conifer plantations are of less value for many prey species than are mixedwood forests. Similarly, conversion of mixedwood stands to conifer stands over large areas may have a cumulative effect of lowering the capacity of the forest for large furbearers.

It is difficult to speculate on the role that alternative silvicultural systems might play in landscape-level effects on large furbearers. Selection harvesting, which often mimics small-scale natural disturbances, may produce pockets of high quality habitat for some prey species and therefore be beneficial. On the other hand, this may be counterbalanced by the greater network of roads required to extract a comparable amount of wood using some alternative systems compared with conventional clear-cutting. Roads remove a portion of the land base from forest production. (In northern Ontario, estimates for the amount of forest removed from production due to roads and landings generally range from 4-8 percent.) Loss of this productive land may lower the carrying capacity of the forest for large furbearers and other animals. Creating access also increases the susceptibility of large furbearers to hunting and trapping (Boyd 1978, Thompson 1988).

Forests are important habitat for this group of furbearers. However, for wolves and wolverines, at least, forests are not essential. Wolves were formerly found throughout the prairies, and wolverines occur in the treeless areas of the far north. They do occur in nonforested habitats further south, not because of the lack of forests, but because of their inability to coexist with humans (and vice versa). The influence of silvicultural systems *per se* on large furbearers may not be significant. The encroachment of human habitation, which usually accompanies forest management, is by far the more significant influence in wild forested areas.

8.0 CONCLUSIONS

Predicting the effects of alternative silvicultural systems on wildlife is difficult for the following reasons:

- most harvesting experience in boreal mixedwoods has been with either selective cutting of softwoods or commercial clear-cutting;
- little experimentation has taken place to examine the effects of silvicultural systems on wildlife; and
- the basic habitat requirements of many wildlifespecies in boreal settings are not well known.

In a survey of the literature, the authors found few examples of classical scientific experiments that tested hypotheses about the manner in which wildlife species react to different harvesting systems or scenarios. (The literature is richer on this topic for birds, albeit in other forest types, and for moose and marten than for other genera.) Given that clear-cutting is the most common harvesting system used in boreal forests, it would be reasonable to expect that studies on the effects of clear-cutting on wildlife would be available. Again, for many species, such studies do not exist.

In many instances it is difficult to conduct hypotheticodeductive experiments on the effects of alternative silvicultural systems on many species of wildlife. The logistics of such experiments are difficult, particularly for examining larger scale effects, and the costs are high. This has two significant implications: 1) biologists and foresters need to use inductive reasoning to predict effects until hypothesis-testing experiments can be done; and 2) adaptive management approaches (see Holling 1978, Walters 1986, Lee 1993, Ontario Forest Policy Panel 1993) should be used to learn about the effects of alternative silvicultural systems on wildlife.

Inductive reasoning relies upon knowledge of habitat affinities and relationships at small and large scales to predict effects. While such literature is more extensive than it is for hypothetico-deductive experiments, for many species, particularly furbearers (see Thompson 1988), it is still inadequate to predict effects with much confidence.

Adaptive management involves specially designed, builtin learning processes. It also explicitly recognizes the dilemma of having to manage large ecosystems, or portions of them, given a lack of essential knowledge on how human actions affect ecological structures and processes. It rests on the principle that the knowledge needed for natural resource management can best come from experimentation with real scale elements of the managed system itself. It is not simply learning from trial and error as forests are managed—most forest managers and biologists are doing that. For adaptive management to be valid, explicit forecasts of the expected behavior of specific ecosystem components must be compared with actual measurements of the same components, in search of contrasts and the reasons for it. Baskerville (1985) has laid out protocols of adaptive management for application to forests.

Section 2.0 of this report discussed, among other things, the manner in which coevolution between plants and animals may have influenced the ecology of some species in the boreal forest. Understanding coevolution, while interesting from a theoretical viewpoint, also has a practical aspect. It requires an intimate knowledge of species habitat affinities, and will contribute to an understanding of how silvicultural systems may affect wildlife (and ultimately the vegetation with which they coevolved). In the sequence of proceeding from general to specific knowledge, however, information about the general habitat affinities of wildlife species must be available prior to the development of hypotheses or understanding about coevolution.

8.1 Birds

As noted earlier, the use of any silvicultural system will be to the benefit of some birds and the detriment of others. However, this should not be used as a rationalization for marginalizing the detrimental effects on some species. Traditional forest management (i.e., clear-cutting) would, in the short term, typically favor species affiliated with open areas and shrub sites and negatively affect those species that prefer old forests. Alternative systems, such as selection harvesting and two-pass harvesting, may provide means for extracting commercial harvests, but not negatively affect interior-dwelling species that prefer old forests.

Although the habitat affiliations of birds have been well studied, little published information is available from boreal mixedwoods. As birds often show different habitat affinities in different regions, it may not always be accurate to extrapolate from other forest types to mixedwoods (Welsh 1987). Some interesting work to address this need is being carried out. Researchers from the Canadian Wildlife Service (CWS) are attempting to map boreal songbird habitat preferences onto the FEC edaphic grid based on several hundred census points in Ontario's boreal mixedwoods (Welsh 1993). Also, researchers from the OMNR are comparing the effects of some partial harvesting scenarios on bird species diversity and relative abundance in boreal mixedwoods (K. Abraham, 11 pers. comm.). Work of this nature will provide biologists with some of the information needed to predict effects of silvicultural operations on songbirds.

A key unknown in boreal birdecology is whether fragmentation effects may occur in managed forest landscapes. Although most research on the effects of forest fragmentation has been carried out in settled and agricultural environments, some work from heavily forested areas in Maine (Small and Hunter 1988) and Finland (Helle 1985, Helle and Järvinen 1986) suggests that such effects may exist in forested landscapes and that the issue is worthy of further investigation. If fragmentation effects do occur they may be of particular consequence for neotropical migrants, which are under increasing pressure from incompatible land use practices in their overwintering habitats.

Fragmentation effects must be understood in conjunction with the habitat preferences of songbirds. In the near future, through work such as that being carried out by the CWS and the OMNR, habitat preferences of boreal mixed-wood songbirds may be used to identify habitat types and mixtures of habitat types that should be fostered, and to recommend silvicultural systems that could be used to

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establish them. However, should this lead to the retention of small blocks of habitat of a preferred type, the net effect may be detrimental to the species it was intended to benefit. If the species are susceptible to fragmentation effects, the small blocks of habitat may act as population sinks with negative net productivity. This scenario underscores not only the need to understand whether fragmentation effects occur in forested boreal landscapes and the extent of these, but the need to understand the relationships between songbird habitat preferences and productivity.

Although it might seem that habitats with more birds censused are more productive (i.e., produce more birds than other habitats), this is not necessarily so (Martin 1992). If censuses are conducted at times of high populations, less productive habitats may be as fully occupied as are more productive ones. Species might be present or even more abundant in marginal or unsuitable habitats because of limited availability of preferred habitat. In conjunction with this, the territorial nature of birds could restrict occupancy of prime productive habitats even during times of moderate or low populations. The productivity of prime habitats may be essential for maintenance of populations (Martin 1992). It may be for some species that management efforts should be focused on prime, nonfragmented habitats. At present, however, biologists and foresters are working with insufficient information on habitat affinities, fragmentation effects, and habitat-productivity relationships.

8.2 Small Mammals

As with birds, it is impossible to evaluate simultaneously the effects on all small mammals without differentiating between the effects on different species. Further, it is often assumed that small mammals are ubiquitous and will always be present in spite of forest management practices. However, this view is being tempered, given the broadening recognition of the importance of small mammals in forest ecosystems.

Habitat affinities of squirrels and snowshoe hare are better understood than those of other small mammals. Mature conifers are required by red squirrels, and hares need low, dense woody cover.

The literature on small mammals contains apparent contradictions about the effects of silvicultural systems on small mammals. However, these contradictions diminish when interpreted in the light of silvicultural techniques, rather than systems. The potential effects of clear-cutting on red-backed voles, for example, may be either positive or negative depending on the intensity of the site preparation treatments that follow the cutting.

Some of the detrimental effects on small mammals associated with any cutting pattern can likely be mitigated by leaving woody debris and litter layers intact. Such practices are more common with alternative systems (although they can also be accomplished with clear-cut systems and careful logging techniques). Selection systems should provide habitat suitable for all of the small mammals, with the exception of deer mice, if canopy densities remain high enough to reduce grass and forb cover.

Although some of the general relationships between small mammals and forests have been explored over the last few decades, research is still required to answer specific questions. For example: How much woody debris is required for a healthy vole population? What are their foraging strategies and preferences? How critical are they in controlling insect outbreaks?

8.3 Ungulates

Existing moose habitat guidelines (Ontario Ministry of Natural Resources 1988a) make scant mention of harvesting systems other than clear-cutting. While alternative systems may, in some circumstances, improve the quality of moose habitat, the incremental improvements in habitat may not be sufficient to warrant their use. If, on the other hand, the use of alternatives systems is meant to foster other forest values, these alternative systems may also benefit moose habitat.

As described in this report, the effects of alternative systems on moose are based largely on extrapolation from an understanding of the animals' habitat needs and the effects of alternative systems on forest cover. In the past, with clear-cutting being the traditional forest management approach, there has been little impetus to investigate the effects of alternative systems on moose. However, as the use of alternative systems gains popularity in boreal mixedwoods, there may be a higher priority to use adaptive management approaches and hypothetico-deductive experimentation to investigate the effects of such systems.

Topical issues in moose management are the relative roles of habitat and predation (including hunting) in limiting animal populations. In Ontario, moose populations are typically below the estimated carrying capacity of the habitat. Management efforts devoted to increasing moose carrying capacity may be frustrated when influences other than habitat are responsible for limiting populations. In Ontario, the increase in provincial moose populations co-incident with the implementation of the moose selective harvesting system (H. Smith, ¹² pers. comm.), suggests that hunting pressure, not habitat, has limited moose populations.

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More sophisticated ungulate population models are required to undertake trade-off analyses of forest management activities for different outcomes. These models can provide the required framework for adaptive management, which is a sensible strategy given the difficulty in designing controlled experiments with animals having such large home ranges and versatile behavior.

Although moose can be accommodated under a variety of silvicultural systems, woodland caribou appear to be sensitive to cutting of any kind. A proposed strategy of large clear-cuts and long delays between return harvests may be a reasonable starting point in commercial forests with significant caribou numbers (Ontario Ministry of Natural Resources 1994). Temporary protection in the form of large reserves seems prudent until the outcome of the proposed strategy is evaluated.

8.4 Furbearers

There is less information on the habitat needs and effects of forest management on furbearers than on any of the other groups of wildlife discussed in this report. Given the central role that furbearers play as predators in forest ecosystems, there is an obvious and significant need for further research.

In this review, the authors identify furbearers with intermediate-sized home ranges (those whose home ranges are of approximately the same size, or somewhat larger than a typical clearcut) as potentially the most vulnerable to the effects of forest management. The home ranges of these animals are sufficiently small that stand-level perturbations can have a significant effect on individuals. However, their home ranges are not so large that a decrease in the value of one portion of the area they occupy can be compensated for by an increased use of another portion of their range. These species also have distinct habitat affinities, unlike most larger furbearers that tend to be habitat generalists, and are neither as dense in population nor as fecund as small mammals.

Although some work has been conducted elsewhere on this group of furbearers, little has been done in Ontario's boreal mixedwoods. Whereas selection harvesting may not cause deleterious effects on marten (as clear-cutting does), this has not yet been investigated in Ontario. With marten about to become a provincially featured species (Koven and Martel 1994), this is an uncertainty of obvious importance. Similar investigations on fisher are also conspicuous in their absence.

Few studies investigate the effects of large-scale forest management on furbearers. Undoubtedly, this is a very difficult topic to study given the size of areas involved, the difficulties of working with elusive animals, the costs, and other logistics. For large furbearers, there is a tendency to assume that the size of home ranges buffers the effects of forest fragmentation. However, this assumption can and should be challenged. A key question is: Do cumulative effects exist? If silvicultural systems affect the densities of prey species, even in a minor way, at many sites throughout the forest, will these changes eventually combine to produce a cumulative effect on predator species?

Nonhabitat related effects may also be important in influencing furbearers. Road networks (which may be more extensive with increased use of alternative systems) have the potential to increase human contact with furbearers to the eventual detriment of their populations. The possible significance of these changes is unknown.

8.5 Closing Comments — Ecosystem Management, Species Management, and Alternative Silvicultural Systems

Heightened awareness of the value of wildlife, while a positive step in the evolution toward responsible stewardship, has increased the complexity of forest managers' jobs. When commercial forestry operations began in boreal Ontario, and throughout the 1950s and 1960s when the use of fast-paced harvesting machinery became common, emphasis was placed only on managing forests for the commercial value of the timber they contained. In the 1970s and 1980s, wildlife species of economic and recreational value (such as moose and sportfish) were considered in forest management. Recent years have witnessed rapid changes in the evolution of society's values, leading to the current belief that all wildlife species should be accounted for in forest management. Foresters and biologists face great challenges in meeting these demands.

While a forest may be able to provide habitat for all native wildlife species, an individual stand cannot. Discussions of the beneficial or detrimental effects on wildlife usually lack meaning when used in a general context (such as "this harvesting system is good for wildlife"). Without reference to specific species or sites, these generic phrases serve only to hinder understanding and communication. Some species benefit, and others suffer, from the use of any silvicultural system. It is impossible, therefore, to meet the habitat needs of all species with any single silvicultural system. To achieve this goal, a range of systems or methods is needed.

A management philosophy that addresses this issue and is gaining acceptance uses the metaphor of coarse and fine filters (Hunter 1990). The coarse-filter approach involves maintaining a variety of ecosystems, and assumes that a representative selection of ecosystems will in turn maintain a diversity of species. For example, one might choose to manage a forested ecosystem such that a historical (or

"natural") distribution of Forest Ecosystem Classification (FEC) types is always maintained across the stands of a landscape. One then assumes that other species, such as understorey vegetation, moose, and birds, will also be maintained at their historical levels across this same landscape.

The problem with this approach, however, is that some species will inevitably pass through the coarse filter. This is where the fine-filter approach can be applied. A species, such as the woodland caribou, that may have additional requirements that are not met through the coarse-filter management approach, can be specifically managed for in certain parts of the ecosystem. However, the use of a fine-filter approach is generally expensive and requires a great deal of information. As a result, a combination of coarse-and fine-filter management is the best approach for most ecosystems. In this way most of the species are preserved through the coarse-filter approach, but some of the more prominent species that may be missed with the coarse filter are managed for specifically (Hunter 1990).

One way of applying the coarse-filter approach is to manage so as to mimic natural disturbance patterns (Hunter 1990, 1993) (i.e., mimic the disturbance patterns in which boreal forest biota persisted prior to human interventions). Given that the biota have persisted there, the assumption is that mimicking natural disturbance patterns should not have deleterious effects.

In boreal Ontario, this approach is being attempted on the White River Forest on the north shore of Lake Superior (Domtar Forest Products 1993). Guidelines have been developed that address both stand and forest-level issues. Specific stand level management measures have been identified that address concerns related to: forest composition (FEC types are not to decline below a given amount from a preindustrial harvesting baseline level); stand age (some stands are to be retained past rotation age); stocking (understocked and overstocked are to be created); structure (several mechanisms are present to preserve and manage for structural elements); and productivity (measures that guard against long-term site degradation are included). Forest-level measures are centered around managing for landscape patterns (mimicking the size, shape, and frequency distribution of natural disturbances, and patterns within disturbances).

In boreal Ontario, large natural disturbances are most frequently caused by fire. Largescale clear-cutting can be used to mimic such disturbance, provided it is modified to incorporate all characteristics of a fire. Alternative silvicultural systems can also play a role in implementing new forest management philosophies. For example, a great number of natural disturbances in boreal forests are relatively small; group selection harvesting can usefully mimic

these disturbances as part of a coarse-filter approach. As noted above, this approach alone is likely insufficient to accommodate the needs and concerns of all species. For species such as pine marten a fine-filter approach, consisting of selection harvesting, is needed.

Throughout much of this report, the most apparent effects are those dealing with species that use old or mature forests, and that require large undisturbed areas. The natural tendency to which the authors have conformed is to document or discuss concerns related to these species. Species that thrive in disturbed environments do not appear at risk because clear-cutting practices will continue in boreal mixedwoods (although the extent of these practices may decrease somewhat). Species that require old or mature forest habitats are most affected by traditional harvesting practices, are at greater risk, and are most likely to benefit from alternative harvesting systems.

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