



NATIONAL COUNCIL FOR AIR AND STREAM IMPROVEMENT

**DEFINING OLD-GROWTH IN CANADA
AND IDENTIFYING WILDLIFE HABITAT IN
OLD-GROWTH BOREAL FOREST STANDS**

TECHNICAL BULLETIN NO. 909

DECEMBER 2005

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PRESIDENT'S NOTE

In Canada, as elsewhere, there is concern about the impact of forestry operations on old-growth forest ecosystems. Land managers are engaged in complex technical issues such as defining and delineating old growth stands and developing conservation plans for wildlife species that use old growth habitats. This technical bulletin provides a literature review of old-growth forest definitions used in all the forest regions of Canada. It also reviews relationships between wildlife species and old growth stands in the Boreal Forest Region.

There are two main approaches to defining old growth. One is to include all stands that are older than some age limit such as 100 or 150 years. The other is to define old growth in terms of physical characteristics and ecological functions. While some proposals have been made to consider a universal definition of old-growth forest, at this time no universal definition has gained widespread acceptance. Instead, most managers and government regulators use definitions they have developed for the forest region in which they work.

Several wildlife species in the Boreal Forest Region are more abundant in mature and old growth stands than in younger age classes. Physical characteristics of older forests that are important to these species may include presence of dead and downed woody debris, complex structure in the arboreal component, and protection from severe weather conditions. Effects of older-forest characteristics on species abundance may be direct (e.g., use of dead trees as den sites) or indirect (e.g., effects of physical characteristics on predator-prey relationships).

Mechanisms responsible for statistical relationships between older-forest characteristics and species abundance are not well defined for most species. Presence of older-forest characteristics in many different stand types may explain why few if any wildlife species in the Boreal Forest Region are found exclusively in old growth stands. Additional explanations include imprecise definitions of old growth and variability in habitat requirements across species ranges.

More work is needed to understand how stand and landscape management techniques can be used to create conditions in managed forests that contribute to conservation objectives for wildlife species associated with mature and old growth forests. For some species, it appears that the actual age of the forest is less important than the physical structure of the vegetation; understanding these functional relationships would enhance our understanding of how to manage forest landscapes for timber and biodiversity conservation in the long term.



Ronald A. Yeske

December 2005

MOT DU PRÉSIDENT

Au Canada, comme ailleurs, on se préoccupe de l'impact des opérations forestières sur les écosystèmes des forêts anciennes. Les gestionnaires de territoire s'occupent des questions techniques complexes telles que l'identification et la délimitation des peuplements et élaborent des plans de conservation sur les espèces fauniques qui peuplent les habitats des vieilles forêts. Le présent Bulletin technique présente les résultats d'une revue de la littérature sur les définitions utilisées dans toutes les régions forestières du Canada concernant les forêts anciennes. Il examine également les relations entre les espèces fauniques et les peuplements anciens de la région forestière boréale.

Il existe deux grandes approches dans la façon de caractériser une forêt ancienne. La première consiste à inclure tous les peuplements dont l'âge dépasse une certaine limite, par exemple 100 ou 150 ans. L'autre consiste à définir les forêts anciennes en termes de caractéristiques physiques et de fonctions écologiques. Présentement, il n'existe pas de définition universelle de la forêt ancienne qui soit reconnue par tous malgré les quelques propositions faites dans ce sens. Plutôt, la plupart des gestionnaires et des responsables de la réglementation se servent de définitions qu'ils ont conçues pour leur propre territoire de travail.

Plusieurs espèces fauniques de la région forestière boréale sont plus abondantes dans des peuplements anciens ou matures que dans des peuplements dont la classe d'âge est plus jeune. Les caractéristiques physiques des vieilles forêts, importantes pour ces espèces, peuvent comprendre la présence de débris ligneux morts et abattus, une structure complexe au sein de la composante arboricole et une protection contre les conditions météorologiques particulièrement violentes. L'influence des caractéristiques des forêts anciennes sur l'abondance des espèces peut être directe (par ex, l'utilisation d'arbres morts comme tanière) ou indirecte (par ex, l'influence des caractéristiques physiques sur les relations entre le prédateur et sa proie).

Les mécanismes responsables des relations statistiques entre les caractéristiques physiques des forêts plus vieilles et l'abondance des espèces fauniques ne sont pas bien connus pour la plupart des espèces. La présence des caractéristiques des forêts plus vieilles dans de nombreux types de peuplements peut expliquer la raison pour laquelle il y a peu ou pas d'espèces fauniques de la région forestière boréale occupant exclusivement un peuplement ancien. Les définitions imprécises de la forêt ancienne et la variabilité des besoins en matière d'habitat pour chacune des espèces constituent d'autres explications.

D'autres études sont nécessaires pour comprendre comment utiliser les techniques de gestion du paysage et des peuplements pour créer, dans les forêts aménagés, les conditions qui contribueront aux objectifs de conservation des espèces fauniques associées aux forêts anciennes ou matures. Pour certaines espèces, il semble que l'âge réel de la forêt soit moins important que la structure physique de la végétation. Comprendre ces relations fonctionnelles nous permettrait de mieux saisir comment gérer à long terme les territoires forestiers pour conserver à la fois la matière ligneuse et la biodiversité.



Ronald A. Yeske

Décembre 2005

DEFINING OLD-GROWTH IN CANADA AND IDENTIFYING WILDLIFE HABITAT IN OLD-GROWTH BOREAL FOREST STANDS

TECHNICAL BULLETIN NO. 909
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ABSTRACT

In Canada, as elsewhere, there is concern about the impact of forestry operations on species that may depend on old-growth forest. However, during debates on old forest, a distinction is not always made between wildlife that require “mature and older” forest and those that need only true “old-growth.” This is challenging for the forest industry, in terms of providing appropriate amounts of “mature and older” forest on the landscape versus providing strictly “old-growth.” This technical bulletin provides a literature review of old-growth forest definitions used in all the forest regions of Canada as well as a review of the relationship between wildlife species and old-growth stands in the Boreal Forest Region. Over 300 papers and books were reviewed and approximately 170 are cited in this report.

Fundamentally, there are two approaches to defining old-growth forest stands. The first approach uses age-specific definitions. In this approach, stands, trees, or ecological sites are designated old-growth when they reach a specific age. This type of definition is common across Canada and is useful in preparing forest management plans because it is clear and the information is available in forest inventories. However, the diversity and complexity of forests in Canada means that old-growth conditions may occur at different ages, even for the same tree species, depending on the local conditions. This has led some to define old-growth to be when physical characteristics or the ecological function of the stand reaches a certain point. These process-based definitions can be vague, or can be more complex and require more sophisticated measurements than age-specific definitions. This type of definition has the advantage of being more relevant to physical structure and ecological function of a stand than simple age, but can be difficult to use in forest management planning because the information is usually not mapped. Process-based definitions have not been used extensively in forest management planning; however, both definitions play a useful role in the discussion of old-growth forests.

Several species of vertebrate wildlife find superior habitat in both mature and old-growth boreal forest stands and these stands or forests serve as source populations for them. However, the research available has not identified any wildlife species that is totally dependent on old-growth forest stands in the Boreal Forest Region. As forest stands age in this Region they become better suited to the needs of some species of wildlife. Older stands in the Boreal contain dead and downed woody debris on the ground, have a complex physical structure in the arboreal component, and provide protection from severe weather to resident wildlife. These characteristics of older forests are important habitat features to some wildlife species.

A review of the literature concerning mammal habitat in the Boreal Forest Region reveals that woodland caribou (*Rangifer tarandus spp*), American marten (*Martes americana*), and red-backed vole (*Clethrionomys gapperi*) prefer both mature and old-growth boreal forest habitat. They are commonly found in old-growth and mature forest, and thrive in these areas; however, the literature reviewed did not show a preference for old-growth over mature forest conditions. Some bats, fishers (*Martes pennanti*), red squirrels (*Tamiasciurus hudsonicus*), and flying squirrels (*Glaucomys sabrinus*) are also found in mature and old-growth forest areas, but the research available does not show that old-growth or mature forests are essential to their habitat needs. They use old-growth and mature forests, but also find important habitats in younger stands.

Studies of birds and their habitat in the boreal forest have identified some 38 species whose habitat needs were met in either mature or old-growth forest areas. Species which were identified in at least three studies as more abundant in old-growth include bay-breasted warbler (*Dendroica castanea*), Cape May warbler (*Dendroica tigrina*), red-breasted nuthatch (*Sitta canadensis*), brown creeper (*Certhia familiaris*), black-throated green warbler (*Dendroica virens*), pine siskin (*Carduelis pinus*), winter wren (*Troglodytes troglodytes*), and golden-crowned kinglet (*Regulus satrapa*). However, habitat affinities of species are not always consistent geographically and across forest types. Some bird species vary either in habitat preference or density over parts of their range in Boreal Canada. A species affiliated with thickets and early successional stages in eastern Canada may have an affinity for old growth in other parts of the Boreal.

More research is needed on amphibians and reptiles in old-growth stands of the Boreal Forest Region, although the ecology of these taxa is fairly well known in the Great Lakes-St. Lawrence Forest Region and in the coniferous forests of western Canada. More work should also be initiated to measure wildlife survival and reproduction in both mature and old-growth stands. This would help define species that find superior habitat in old-growth and advance our understanding of the relationship between wildlife and characteristics of older forest stands. For example, greater understanding of how habitat characteristics per se affect woodland caribou (as compared to hunting, predation, and human disturbance) would have important practical value in developing management plans for boreal forest landscapes in which both timber production and caribou conservation are important objectives.

KEYWORDS

Boreal Forest Region, old-growth forests, wildlife and boreal forests, wildlife and old-growth forests

RELATED NCASI PUBLICATIONS

None

LA CARACTÉRISATION DE LA FORÊT ANCIENNE AU CANADA ET L'IDENTIFICATION DES HABITATS FAUNIQUES DANS LES PEUPEMENTS ANCIENS DE LA FORÊT BORÉALE

BULLETIN TECHNIQUE NO. 909
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RÉSUMÉ

Au Canada, comme ailleurs, on se préoccupe de l'impact des opérations forestières sur les espèces possiblement tributaires de la forêt ancienne. Cependant, au cours des débats sur la forêt ancienne, on ne fait pas toujours la distinction entre les espèces fauniques qui ont besoin d'une « vieille forêt mature » et celles qui ont besoin d'une véritable « forêt ancienne ». Cette situation constitue une difficulté pour l'industrie forestière pour ce qui est de déterminer le pourcentage approprié de « vieille forêt mature » versus le pourcentage de « forêt strictement ancienne » à conserver sur le territoire. Le présent Bulletin technique présente les résultats d'une revue de la littérature sur les définitions utilisées dans toutes les régions forestières du Canada concernant les forêts anciennes de même qu'un examen des relations entre les espèces fauniques et les peuplements anciens de la région forestière boréale. La revue a porté sur plus de 300 articles et livres et le présent rapport en mentionne environ 170.

Il existe principalement deux approches pour caractériser une forêt ancienne. La première consiste à faire appel à des définitions en fonction de l'âge. Selon cette approche, on qualifie d'anciens des peuplements, des arbres ou des aires écologiques qui ont atteint un âge déterminé. Cette définition est courante au Canada et s'avère utile dans la préparation des plans d'aménagement forestier car elle est claire et l'information qui s'y rattache se trouve dans les inventaires forestiers. Cependant, la diversité et la complexité des forêts canadiennes signifient que les conditions propres aux forêts anciennes peuvent survenir à des âges différents (même pour la même essence d'arbre) en fonction des conditions locales. Cette situation a conduit certaines personnes à établir qu'une forêt est ancienne lorsque les caractéristiques physiques ou les conditions écologiques du peuplement atteignent un certain point. Ces définitions basées sur un processus peuvent être vagues, ou être plus complexes et exiger alors des évaluations plus sophistiquées que des définitions conçues en fonction de l'âge. Ce type de définition offre l'avantage de correspondre plus à la structure physique et à la fonction écologique d'un peuplement que l'âge seulement, mais peut être difficile à appliquer dans la planification d'un aménagement forestier parce que l'information n'apparaît pas sur les cartes. Les définitions basées sur un processus ne sont pas utilisées de façon généralisée dans la planification des aménagements forestiers. Toutefois, les deux définitions contribuent de façon utile à la discussion sur les forêts anciennes.

Plusieurs espèces fauniques vertébrées trouvent un excellent habitat à la fois dans les peuplements matures et dans les peuplements anciens de la forêt boréale, et ces forêts leur servent de point de départ. Cependant, la recherche actuelle n'a pas identifié d'espèces fauniques qui soient totalement dépendantes d'un peuplement ancien de la région forestière boréale. À mesure que les peuplements vieillissent dans cette région, ils répondent mieux aux besoins de certaines espèces fauniques. Les peuplements plus vieux de la forêt boréale contiennent des débris ligneux morts et abattus sur le sol, présentent une structure complexe au sein de la composante arboricole et offrent aux espèces résidentes une protection contre les conditions météorologiques particulièrement violentes. Ces caractéristiques typiques des forêts plus vieilles sont des éléments essentiels de l'habitat d'un certain nombre d'espèces fauniques.

Une revue de la littérature sur l'habitat des mammifères de la région forestière boréale révèle que le caribou des bois (*Ranifer tarandus spp*), la martre d'Amérique (*Martes americana*) et le campagnol à dos roux (*Clethrionomys gapperi*) préfèrent autant un habitat de la forêt boréale situé dans un peuplement mature que dans un peuplement ancien. Ils sont répandus autant dans les forêts matures que dans les forêts anciennes et ils croissent en abondance dans ces peuplements. Cependant, l'examen de la littérature n'a pas montré s'ils affectionnaient les conditions d'une forêt ancienne plutôt que celles d'une forêt mature. On trouve certaines chauves-souris, pékans (*Martes pennanti*), écureuils roux (*Tamiasciurus hudsonicus*) et grands polatouches (*Glaucomys sabrinus*) à la fois dans des forêts anciennes et des forêts matures, mais la recherche actuelle n'indique pas si l'une ou l'autre de ces forêts est essentielle à leurs besoins en habitat. Ils utilisent les deux types de forêts, mais trouvent aussi des habitats essentiels dans des peuplements plus jeunes.

Les études sur les oiseaux et leur habitat dans la forêt boréale identifient 38 espèces dont les besoins en habitat ont été satisfaits par un peuplement mature ou un peuplement ancien. Les espèces décrites dans au moins trois études comme étant plus abondantes dans la forêt ancienne comprennent la paruline à poitrine baie (*Dendroica castanea*), la paruline tigrée (*Dendroica tigrina*), la sittelle à poitrine rousse (*Sitta canadensis*), le grimpereau brun (*Certhia familiaris*), la paruline à gorge noire (*Dendroica virens*), le tarin des pins (*Carduelis pinus*), le troglodyte mignon (*Troglodytes troglodytes*), et le roitelet à couronne dorée (*Regulus satrapa*). Toutefois, les affinités d'une espèce avec son habitat ne sont pas toujours géographiquement les mêmes et peuvent aussi varier en fonction des types de forêts. Dans certaines parties de leur aire de répartition de la forêt boréale canadienne, certaines espèces d'oiseaux privilégient, soit l'habitat, soit la densité de peuplement. Dans l'est du Canada, une espèce associée aux fourrés et à ses premiers stades de succession végétale pourrait avoir une affinité avec la forêt ancienne dans d'autres parties de la région boréale.

D'autres études sont nécessaires sur les amphibiens et les reptiles des peuplements anciens de la région forestière boréale, bien que l'écologie de ces taxons soit relativement bien connue dans la région forestière des Grands Lacs et du St-Laurent et dans les forêts de conifères de l'ouest canadien. Il faudrait également entreprendre d'autres études pour mesurer le taux de survie de la faune et leur reproduction dans des peuplements anciens et dans des peuplements matures. Ces travaux permettraient de déterminer quelles sont les espèces qui trouvent un habitat de qualité supérieure dans les forêts anciennes et de faire progresser nos connaissances sur la relation entre la faune et les caractéristiques des peuplements anciens. Par exemple, une meilleure compréhension de l'influence des caractéristiques en soi d'un habitat sur le caribou des bois (comparativement à la chasse, à la prédation et aux perturbations humaines) aurait une valeur pratique considérable dans l'élaboration des plans d'aménagement des paysages de la forêt boréale alors que la production de la matière ligneuse et la conservation du caribou constituent d'importants objectifs.

MOTS CLÉS

faune et forêts anciennes, faune et forêts boréales, forêts anciennes, région forestière boréale

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DEFINING OLD-GROWTH IN CANADA AND IDENTIFYING WILDLIFE HABITAT IN OLD-GROWTH BOREAL FOREST STANDS

1.0 INTRODUCTION

In the current debate over environmental issues in forestry, no subject has generated more controversy than old-growth forests. From coast to coast in Canada, people have discussed old-growth forests, their management and protection. The debates, discussion and demonstrations have been vigorous, controversial and sometimes illegal. Views on old-growth are diverse. Some stakeholders advocate complete protection of all old-growth stands while others believe that old-growth should be managed as one part of an ever-changing forest which will occur, disappear, and then reoccur (Kimmins 2003). Kimmins (2003) provides a succinct summary of the debate on old-growth with the title of a recent paper in *The Forestry Chronicle*: “Old-growth forests: an ancient and stable sylvan equilibrium, or a relatively transitory ecosystem condition that offers people a visual and emotional feast? Answer—it depends.”

In that article, Kimmins explores the fact that old-growth forests are valuable for several reasons: their beauty, their contribution to wildlife habitat, their value as components of biodiversity, and the quality of the wood that can be produced from them. As well, he points out that the value people place on old-growth springs from their own perspectives as to what is best for the forest and for people who live in the forest. However, he also stated that

“there are important spiritual, aesthetic, wildlife, and environmental values associated with old forests, and the area of these forests is declining. There are many valid reasons (social, scientific, and environmental) for sustaining significant and representative areas of such forests. However, conservation of such forests, and ensuring a future supply of the values they provide, will not be achieved unless the reverential respect for such forests is matched by another meaning of respect: understanding such forests and basing our relationship with them on that understanding.”

Over the past decade, hundreds of scientific papers and thousands of articles in the popular press have been published on old-growth forests in Canada. In an effort to advance our understanding of old-growth forests, the Canadian Forest Service organized a national conference on old-growth forests in 2001 and published the results in *Environmental Reviews* (Volume 11, Supplement 1). The May-June issue of the *Forestry Chronicle* in 2003 was devoted entirely to old-growth forest issues. As this fund of knowledge increases, the values placed on old-growth should become clearer, and the understanding of the ecological processes that produce old-growth should also become clearer. Perhaps, as well, the emotional and spiritual values of old-growth will also be discussed in a common language that helps us understand why people like and value old-growth forests.

There are two purposes in writing this technical bulletin: the first is to review the definitions of old-growth in use in Canada in the current literature; the second is to gather knowledge available on species of wildlife that require old-growth boreal forests as habitat in North America. If some wildlife require old-stands and without them they would not have habitat at all, then that knowledge is important. On the other hand, if species use old-growth, but can also live elsewhere, that too is important knowledge. An additional challenge is the need to ensure that everyone understands how old-growth is defined. Without a clear definition, there is little hope of communicating how best to regard old-growth in forest management.

2.0 METHODS

This project is primarily a literature review, and the methods used were straightforward. We canvassed the literature on definitions of old-growth forests in the main forest regions in Canada and reported on how these definitions were used. In addition, we searched for studies that would illuminate the relationship between wildlife and old-growth boreal forests. We attempted to find species of wildlife that required old-growth boreal forest to maintain healthy populations. Literature was obtained at local university libraries, on the Internet, from colleagues, and from our own personal libraries.

Initially and throughout the review, we concentrated on papers published after 1990 because there is a large volume of literature on this topic and it seemed important to concentrate on the latest knowledge available. However, a few references that were published before 1990 are also included because they provide a perspective that was important to present knowledge. With a few exceptions, we restricted our review to papers published in peer-reviewed journals because they represent work that has the benefit of reviews by other scientists.

3.0 DEFINITIONS OF OLD-GROWTH

3.1 What Is Old-Growth?

In 1997 Hunter and White asserted, “It is widely accepted that it is not possible to craft a universally applicable definition of old-growth forest stands except one that is extremely general: for example, old-growth forests are relatively old and relatively undisturbed by humans” (Hunter and White 1997). The problem in defining old-growth forests is that everyone involved needs a definition for very different reasons. Forest managers require a definition that is clear and can be included in a forest management plan, with specific instructions for harvest or other management activity. Foresters, local communities and others who work with forest managers need to know about the function of old-growth ecosystems on a landscape. Are these forests the only habitat for certain wildlife species and do they provide functions at the ecosystem level that cannot be performed elsewhere? Other questions include: how much old-growth is “natural” on the landscape? and What ecological factors are most important in determining the characteristics of old-growth? Questions of this nature are difficult to answer, but they all depend on everyone having a definition that will assist, not hinder, the discussion that must occur in developing forest management plans.

An important concept in this discussion is the difference between primary forests that are old-growth because they have been undisturbed by people, and forests that have been harvested once or more and have returned to an old-growth stage. Sometimes primary forests are called “ancient” forests, if long intervals occur between catastrophic disturbances and if they contain species with great longevity, for example the Douglas fir (*Pseudotsuga menziesii*) and Sitka spruce (*Picea sitchensis*) forests of British Columbia (Wells, Lertzman, and Saunders 1998). However, primary forests can also occur in any forest type, such as in the fire-driven jack pine (*Pinus banksiana*) and black spruce (*P. mariana*) forests in central Canada. While stand-replacing fires occur in these areas, recent research indicates that many areas persist long beyond an average fire interval (Cumming, Schmiegelow, and Burton 2000) and are primary forests (Kneeshaw and Gauthier 2003; Kneeshaw and Bergeron 1998).

Environmental groups with an interest in old-growth forests sometimes define primary old-growth forests somewhat differently than governments or scientists define them. This can lead to misunderstanding in the dialogue between governments and advocacy groups interested in conservation of old-growth forest areas. In the next section, a number of definitions used in a variety of situations are discussed to illustrate different aspects of trying to understand what the term “old-growth forest” means.

3.2 Primary Old-Growth Forests

A concept raised by conservationists and international forestry organizations, such as the United Nations Food and Agriculture Organization, is that of “primary forests.” Primary forests are forests that have not been managed and in which there has been little human impact. In Canada, considerable primary forest remains, but in many other countries most primary forest has been managed or lost. Primary forests are of interest because these forests can provide information on processes and structures which can be used in managed landscapes to help managers develop strategies to emulate natural disturbances. Primary old-growth forests provide benchmarks in terms of dead wood, plant cover, fungi, gene repositories, and functional relationships and so are of value to managers by providing a living example of ecosystems to eventually emulate.

The Convention on Biological Diversity provides a definition of primary forests and distinguishes them from old-growth as follows:

Primary Forests – “A forest that has never been logged and has developed following natural disturbances and under natural processes, regardless of its age.”¹ Included in the definition of primary are “... forests that are used inconsequentially by indigenous and local communities living traditional life styles relevant for the conservation and sustainable use of biological diversity.”

Old-Growth Forests – “Old-growth stands are stands in primary or secondary forests that have developed the structures and species normally associated with old primary forests of that type that have sufficiently accumulated to act as a forest ecosystem distinct from any younger age class.”²

The Food and Agriculture Organization of the United Nations defines primary forests as

“forests that have never been clear cut and that have little or no evidence of past human activity. Such forests may have been grazed, experienced limited exploitation of valuable tree species, and their floors may have been burned by Amerindians and European colonists.”³

Part of the dialogue that occurs on this topic can lead to misunderstanding if people differentiate between old-growth and primary forests without clear definitions of both concepts. In the Canadian boreal forest, few studies have attempted to distinguish ecological characteristics between forests that could be called primary and those called old-growth. As work proceeds on the “pre-settlement” forests of North America, we expect more detailed knowledge of the characteristics of these forests.

3.3 Process-Based and Age-Specific Definitions

The need for a definition of old-growth that will help in understanding and communication has led to different approaches to defining old-growth forests. Some people believe that a definition based on ecological function or the physical structure of a stand of trees is the best way to define old-growth. Others, perhaps because they need very clear and specific guidance to develop a management plan, want something that is unambiguous, even if it has limitations based on ecological function or physical structure. Two broad approaches to defining old-growth are available: the age-specific definition and the process-based definition.

¹ <http://www.biodiv.org/programmes/areas/forest/definitions/.asp>

² <http://www.biodiv.org/programmes/areas/forest/definitions/.asp>

³ Lund, H. Gyde. 2002. Definitions of old-growth, pristine, climax, ancient forests, and similar terms. [Online publication], Gainesville, VA: Forest Information Services. Misc. pagination. <http://home.comcast.net/~gyde/lundpub.htm> (accessed December 12, 2005).

3.3.1 Examples of Age-Specific Definitions

A good example of age-specific definitions is from Ontario where 59 different definitions are provided, based on specific ecotypes (Uhlig et al. 2003). Forests in Ontario are categorized into ecosites, based on specific soil and drainage characteristics, and the expected forest type that would normally grow on those sites. Each site has a description of the common soil and site characteristics present and a specific age at which old-growth commences and an estimate of the duration of that forest type. Table 3.1 lists five examples from Ontario to illustrate the pattern of the definitions provided.

Table 3.1 Examples of Age-Specific Old-Growth Definitions (Uhlig et al. 2003)

Ecosite Type	General Species Association	Common Soil and Site Description	Vegetation and Stand Structure Characteristics	Old-Growth Age of Onset (years)	Old-Growth Stand Duration (years)
ES 13 Boreal West	Jack pine	Dry to moderately fresh, rapidly to well drained, coarse to fine sandy soils	Conifer dominated, often even-aged, ground cover of mosses	110	70
ES 23 Boreal West	Trembling aspen (Po), white birch (Bw), balsam fir (Bf)	Moist, sandy to coarse loamy soils	Dominated by aspen, deciduous tree component exceeds 50% of canopy	Po: 90 Bw: 100	Po: 30-60 Bw: 40
ES 11 Boreal East	Black spruce (Sb)	Wet, deep fibric, organic soils	Conifer dominated Wetlands, includes Labrador tea, leatherleaf, bog laurel and feathermosses	140	210 +
FOC 1 Deciduous Forest Region	White pine (Pw), red pine (Pr), jack pine (Pj)	Dry to fresh, shallow over bedrock, sandy to coarse loamy soils	Conifer dominated, shrubs include: blueberries, juniper, serviceberries	Pw: 120	450+
ES 11-14 Great Lakes-St. Lawrence Forest Region	White pine, red pine, poplar, jack pine, red oak (Or)	Dry to fresh, very shallow to deep, sandy to coarse loamy soils	Conifer dominated, shrubs include beaked hazel, blueberry, bush honeysuckle, et al.	ES 11: 130 ES 12: 140 ES 13: 120 ES 14: 120	ES 11: 60-120 ES 12: 60-110 ES 13: 50-100

In the detailed report by Uhlig et al. (2003), the background and the algorithms by which the decisions about old-growth composition were made are provided. The database for establishing dates of onset and duration of old-growth is based on 2,312 growth and yield plots in the boreal forest and 2,696 plots in the Great Lakes-St. Lawrence forest. This represents one of the most detailed approaches to defining old-growth available in Canada, and in the literature surveyed. These definitions and the old-growth policy that supports these definitions will be implemented in forest management plans in Ontario starting in 2006.

The Ontario old-growth policy also has a more generic definition that illustrates the concept of old-growth that was used before the age-specific definitions were developed. The policy states that “old-growth features and characteristics typically include the following:

- a complex forest and stand structure
- large dead standing trees (snags), accumulations of downed woody material, up-turned stumps, root and soil mounds, and accelerating tree mortality, and
- ecosystem functions (e.g. stand productivity, nutrient cycling, and wildlife habitat) that are different from earlier stages of forest succession.”

Perhaps because of the pressure to be specific, the Canadian federal government produced a poster that defines old-growth forests as in Table 3.2, using age-specific definitions.

Table 3.2 Definitions of Old-Growth Forests in Canada from the Canadian Federal Government⁴

Forest Region	Old-growth starts at about:	Oldest trees live to approximately:
West Coast (Temperate)	150 years	1000 years
Montane (B.C.)	100 years	350 years
Great Lakes-St. Lawrence	150 years	400 years
Boreal (dry)	100 years	250 years
Boreal (wet)	100 years	250 years
Acadian	150 years	400 years

Scientists who study old-growth forest often specify a definition of old-growth for purposes of their study. In interior British Columbia, for example, Bartemucci et al. (2002) defined old-growth as older than 120 years. Schaefer and Pruitt (1991), working in jack pine stands in Manitoba, defined old-growth as older than 90 years. In the balsam fir (*Abies balsamifera*) forests of Newfoundland, Thompson, Larson, and Monteverchi (2003) suggested that old-growth starts at about 80 years in those forests. Acadian Forest old-growth starts at about 150 years, based on the experience of Mosseler, Lynds, and Major (2003).

Age-specific definitions are limited by the fact that forests are very different and exist on a variety of soils with complex moisture and nutrient conditions. Age-specific definitions assume that forests age in consistent processes along relatively well-defined successional pathways. Under this assumption, an old-growth forest will have characteristics that are consistent over a range of time and environmental conditions. However, there is much variety in forests in Canada, and they evolve along

⁴ available at http://www.nrcan.gc.ca/cfs-scf/NFW/index_e.html

different pathways, even though it may appear that the soil and moisture conditions are similar. Wildfire and insect defoliation, for example, may exert influences on successional pathways that override the simple concept that a forest is old because it has been a long time since it was disturbed. To deal with this issue, a second approach has been used to define old-growth, the process-based definition. The process-based definition defines old-growth by the key characteristics that are present in old-growth, regardless of the age.

3.3.2 *The Process-Based Definition*

A typical definition of old-growth, based on process, is “a stand of trees that is in the last stage of succession or development” (Frelich and Reich 2003). A similar process-based definition is “the stage in stand development when single tree replacement has a greater influence than past stand-level disturbance events”; or “the start of old-growth is peak of tree basal area” (Harper et al. 2003). Kneeshaw and Gauthier (2003) believe that old-growth starts in the boreal when the original cohort starts to die and is replaced by new individuals.

As Kimmins points out, there is a strong tendency for people to classify forest stands in a dichotomous way: a forest is either old-growth or it is not (Kimmins 2003). He suggests that old-growth should be considered “a phase of stand development in which the surviving individuals of the initial cohort are approaching maximum longevity, losing physiological vigour and becoming increasingly susceptible to disease and damage.” Old-growth stands generally have large standing dead trees, large decaying logs on the ground, a decline in overstory leaf area, and a breakup of the canopy. However, because successional processes are not rigid, there are usually overlaps with early phases of stand development and mixtures of disturbed and undisturbed areas within larger stands. Kimmins (2003) also points out that

“the possibility that relatively high-OGI [Old-growth Index] stand conditions can develop in early, mid, and late seral stages, with very different characteristics and persistence, is one reason for the difficulty in finding useful generalizations about old-growth, or reliable correlations between high-OGI stands and various measures of biodiversity, ecosystem productivity, stability and sustainability.”

Working in Quebec, Villeneuve and Brissen (2003) found that the presence of large trees, both in height and diameter, the presence of shade tolerant species like eastern hemlock (*Tsuga canadensis*) and sugar maple (*Acer saccharum*) and high structural diversity, both horizontal and vertical, were key components in identifying old-growth stands. In their study, four characteristics were used to identify old-growth: age of stand, presence of large dead trees, low cutting intensity, and the presence of shade-tolerant species.

3.3.3 *Current Thinking about Old-Growth Definitions*

At this time, most people who study old-growth, or are responsible for forest management, believe that a variety of definitions is most appropriate in our approach to old-growth forest protection and management. In a current article, Spies (2004) comments that “one implication of the multiple definitions of old-growth is that forest policies and management practices may need to be as diverse as the old-growth forests they address.” He explains that while old-growth forests have multiple meanings and values in ecological, social, and economic arenas, a consensus on the wording of an ecological definition of old-growth will never be reached and may not be desirable, given the diversity of forests. At some point in the management process, the boundary between what is and what is not old-growth forest is arbitrary. However, for forest management purposes, it is often necessary to identify an arbitrary line. Stand development is a continuous process that lacks clear threshold or abrupt changes in structure that could be considered diagnostic of the beginning of the old-growth stage (Spies 2004).

However, the suggestion by Mosseler, Thompson, and Pendrel (2003), supported by earlier work of Kimmins (1997, 2003) and Spies and Franklin (1988), that an index of “old-growthness” might be a useful tool to assist in discussion and management issues about old-growth seems promising. They explain that

“such an index would include a number of the attributes and processes associated with old-growth forest that are considered most important from a biological and ecological perspective for a given forest type or forest region. Such an index would be derived by assigning a value to and (or) weighting attributes, functions and processes for important components of the forest ecosystem so that a proportion or percent of ‘old-growthness’ could be established.”

3.4 Is There a Universal Definition?

In an interesting paper in the *Wildlife Society Bulletin*, Hayward (1991) suggested that population biology be used to defined old-growth.

“Old-growth – a stand of forest in which the rate of tree regeneration and the age structure are influenced by process in the stand rather than being correlated to the timing of a major disturbance that influenced the majority of the stand. Age structure of the stand is very broad and major discontinuities are not prominent. In particular, the forest age structure approaches a theoretical reverse J or negative exponential shape.”

This suggestion, made in 1991, has had very little attention since it was proposed and while it may be applicable over broad areas, more work would have to be completed to assess its usefulness to the discussion about old-growth.

One of the recent definitions of old-growth that is measurable and relatively consistent throughout the boreal forest, and is an index, was suggested by Kneeshaw and Gauthier (2003). They define old-growth as “the original cohort begins dying off and is replaced by the recruitment of understory stems.” They propose to measure the onset of old-growth using a cohort basal area ratio (CBAP). The CBAP is a ratio of the basal area of the replacement cohort to the total basal area of both replacement and initial post-disturbance cohorts:

$$CBAP = \frac{BA_{\text{replacement cohort}} + 0.1}{BA_{\text{replacement cohort}} + 0.1 + BA_{\text{initial cohort}}}$$

where BA is the basal area.

These authors assert that “the CBAP is thus sensitive to both mortality and recruitment processes and reflects the change from a forest stand in which dynamics have been controlled by large-scale disturbances to a stand in which small-scale disturbance influence dynamics.” Furthermore, “the old-growth cohort basal area proportion provides a method for comparing regions and forest types that, because of different species compositions, would not have the same structural attributes.”

Spies (2004) also lists ecological characteristics of old-growth that may be helpful in universal definitions of old-growth. Table 3.3 illustrates his thoughts on characteristics that may be both specific enough and general enough to develop a universal definition.

Another recent article by long-term students of old-growth also emphasized the structural complexity of old-growth forest stands that may be applicable over different forest types (Franklin and Van Pelt 2004). In old-growth stands they

“find a gradual evolution of (1) canopies from simple, top-loaded, single-layered canopies in young stands to the vertically continuous, bottom-loaded canopies in old forests; and (2) spatial heterogeneity from uniform young stands that are initially dominated by competitive processes to the fine-scale structural patchwork of old-growth forests.”

Table 3.3 Ecological Characteristics of Old-Growth (Spies 2004)

Development Time	Structure	Patch Size	Stability	Examples of Forest Types
Long	Low	Mixed	Enduring	Pinyon-juniper, subalpine white pine, dwarf black spruce
Intermediate	Moderate	Fine-grained	Enduring	Balsam fire, black spruce
Short	Moderate	Coarse-grained	Short-term, transient	Aspen, red alder, jack pine, black spruce
Intermediate	High	Coarse-grained	Long-term transient	Douglas fir, ponderosa pine, white pine, red pine, Atlantic white cedar
Intermediate	High	Fine-grained	Surface fire dependent	Ponderosa pine, oak-hickory, longleaf pine, Douglas fir-incense cedar
Intermediate	High	Fine-grained	Enduring	Beech-maple, hemlock spruce

In an attempt to find a definition of old-growth in British Columbia that would be helpful in all the forest regions there, Wells, Lertzman, and Saunders (1998) proposed definitions in three broad categories: conceptual, quantitative, and working. Conceptually, an old-growth forest is a forest “in which gap dynamics predominate.” Quantitative definitions attempt to “quantify the qualitative features of conceptual definitions.” Working definitions are basically age-based definitions that are recognizable from forest inventory information. Wells, Lertzman, and Saunders (1988) proposed working definitions for British Columbia, and suggested that the criteria that Spies and Franklin (1988) developed for their “index of old-growthness” were a useful step in defining old-growth in a more robust way.

Although a definition of old-growth has not been accepted universally, as work progresses in this area, a definition may emerge that will gain acceptance over wide areas and a variety of forest ecosystems.

3.5 The Acadian Forest

The Acadian Forest covers most of the Maritime provinces except for a small area of boreal forest in central New Brunswick (Mosseler, Lynds, and Major 2003). Much of this forest area has trees similar to those growing in the Great Lakes-St. Lawrence Forest Region, except that red spruce (*Picea rubens*) is a common component of this area. Timber has been harvested in this forest region for many centuries, first by aboriginal people, and later by European colonizers.

For the Acadian Forest, Mosseler, Lynds, and Major (2003) described old-growth as follows.

“We consider OG forests in the AFR to be forests in the ultimate or final stages of stand development, distinguished by old trees, and free of much evidence of human activity. The typical temperate-zone OG forest of the AFR has a multi-aged structure (or at least several recognizable age cohorts) and is composed of long-lived, shade-tolerant late-successional trees. These stands can approach a steady-state condition in which species composition and diameter distribution remains reasonably constant.”

The government of Nova Scotia simply states “the interim Old Forest Policy defines old-growth as ‘climax forests that are at least 125 years old.’”⁵ This simple definition is intended to apply to the Acadian Forest Region; however, Nova Scotia also established an evaluation scheme that assigns old-growth into various categories based on length of time since disturbance, age and size of trees, “primal forest value”, and other values. While the specific definition seems simple and easy to understand, assigning a specific stand to an old-growth category is complex and time-consuming.

The Nova Scotia old-growth rating system was used to document the ecological characteristics of rare Acadian forest ecosystems (Stewart et al. 2003). These researchers used four stands, two in softwood composed of hemlock, red spruce and pine (*Pinus spp*) and two in hardwood composed of sugar maple-yellow birch-beech (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*). All four stands had peak basal area representation in the 40 to 50 cm diameter classes, and volumes of dead wood ranged from 111 to 148 m³/ha in the softwood stands and 63 to 83 m³/ha in the hardwood stands. These uneven-aged stands had reference trees of 164 to 214 years. The stands all rated high on the scoring system based on stand age, primal value, number of large diameter trees, length of large-diameter dead wood, canopy structure, and understory structure (Stewart et al. 2003).

In its protected areas strategy, the New Brunswick government⁶ has set aside protected areas that include old-growth areas. A review of this strategy illustrates some of the characteristics that were used to designate old-growth (Table 3.4).

⁵ available at <http://www.gov.ns.ca/natr/forestry/planresch/oldgrowth/index.htm>

⁶ *Protected Natural Areas Our Heritage*, published by the Government Of New Brunswick (2003); available at <http://www.gnb.ca/0078/reports/>

Table 3.4 Protected Areas in New Brunswick with Characteristics Used to Describe Old-Growth Forests

Name of Area	Description of Area
Blue Mountain Protected Area	Untouched forest stand, comprised of large red pines, which probably originated after the Great Miramichi Fire of 1825
Cranberry Lake	An unusual stand of red oak mixed with red maple, individual trees are impressive in size
Freeze Lakes	Even-age, undisturbed balsam fir forest typical of the area, dense tree cover blocks the sun and only mosses can grow on the forest floor
Loch Alva I	An ancient stand of red spruce, many are roughly two centuries old, and are greater than 50 centimeters in diameter

3.6 The Great Lakes-St. Lawrence Forest

Considerable attention has been paid to old-growth forests in the Great Lakes-St. Lawrence Forest Region. From Minnesota to eastern Quebec, red (*Pinus resinosa*) and white pine forests (*P. strobus*) have been seen to represent the classic concept of old-growth in this forest region. Although many public battles have been fought over logging and management of red and white pine forests, the actual scientific basis for identifying old-growth and the ecology of pines in this Forest Region have been less clear.

The Ontario approach to old-growth identification includes 18 ecosites within the Great Lakes-St. Lawrence Region, and provides specifications for the age at which they become old-growth (Uhlir 2003). These definitions are specific and detailed. For example, ES 11-14, dominated by white and red pine, on dry to fresh, very shallow to deep, sandy to coarse loamy soils, become old-growth when the white pine are 150 years old and the red pine are 140 years old. These ecosites also reach old-growth status if the last disturbance on ES-11 is 130 years ago and 140 years ago on ES-12. In the forest management planning process, these ecosite-based definitions have been used to designate forest units that are old-growth and these units are useful in preparing management plans.

Carleton (2003) measured five main features of red and white pine forests in Ontario in a chronosequence on four different soil site types. Perhaps surprisingly, the oldest stands did not have the most plant species diversity, the most snags, or the most coarse woody material on the ground. Those characteristics were at their highest levels in mid-succession. Total stem volume increased to about 250 years and then declined slightly to about 300 years, which were the oldest stands in this study. Stand physiognomy, the basic shape of the canopy, was variable with no clear trends in post-fire successional patterns. Carleton concluded that substrate heterogeneity in providing habitat diversity for understory plants was very important but “much which contributes to forest floor plant species diversity remains to be explained.” (Carleton 2003, p. S129). Based on his study, a reasonable conclusion is that stand age is probably one of the best criteria to identify old-growth stands in this forest region.

The Quebec government, as a part of its concern for forest biodiversity, has protected old-growth forest stands, based on a definition as follows:

“Old-growth forests are stands that have usually suffered little from the impacts of natural disturbances and human activity. They contain living trees of all ages, along with dead trees (standing or fallen) at varying stages of decomposition. The dominant trees are always old.”⁷

In an effort to provide a more specific definition of old-growth forests in this Forest Region, Villeneuve and Brisson (2003) listed some specific characteristics of old-growth forests. This effort was needed to support the biodiversity protection objectives in a legal context. The legal designation of candidate protection sites requires adopting quantitative definitions and validation criteria applicable to various environments.

Villeneuve and Brisson (2003) listed 23 different definitions based on tree species, forest cover type, minimum age, minimum dbh, (diameter at breast height) and a minimum height. As in Ontario, these site designations are very specific to the environmental conditions present in various parts of the region. Table 3.5 illustrates two examples of this process.

Table 3.5 Examples of Old-Growth, Specific Definitions for Old-Growth from Quebec

Bioclimatic Domain	Tree Species	Forest Cover Type	Minimum Age	Minimum dbh (cm)	Minimum Height (m)
Sugar maple-hickory and sugar maple-basswood	Yellow birch	Sugar maple and hemlock stands	165	45	25
Sugar maple Yellow birch	Eastern white pine	Pine stands	170	56	33

3.7 The Boreal Forest

As the largest forest region in Canada, and the focus of both harvesting activity and recreation, the boreal forest has been the subject of many papers that discuss and research the role of old-growth. Some have precise quantification of structural conditions, e.g., Uhlig et al. (2003), Kneeshaw and Burton (1998), while others have used a phase of stand development as a definition, e.g., Harper et al. 2003.

A descriptive account of old-growth in the boreal forest of Ontario and Quebec is provided by Harper et al. (2003).

“On clay deposits, the mostly black spruce (*Picea mariana*) forest canopy starts to break up after about 100 years following fire, when the forest is considered “old-growth.” At this time, numerous gaps appear, from either spruce budworm (*Choristoneura fumiferana*) defoliation or, more likely, wind throw. In later stages, the largest trees, although characteristic of old-growth in other forests, disappear. The moss layer becomes thicker, and the colder soil temperature and lower decomposition rates reduce productivity; as a result, newly regenerated trees produced from layering are not large. A variety of sizes of deadwood in various stages of decay become more abundant. There are also more epiphytic lichens on trees, more ericaceous shrub species in the understory, and more of the characteristic *Sphagnum* spp. on the ground.”

⁷ definition available at www.mrn.gouv.qc.ca/english

In the southern boreal mixedwood forests of Quebec, fire frequency is variable and spruce budworm outbreaks frequently occur in the absence of fire. The successional sequence following disturbance starts with aspen and white birch dominating the stands for about 100 years. As the first cohort breaks up, a second rotation of hardwoods occurs and some balsam fir and white spruce are recruited to the stand. After about 200 years, the old-growth is composed of balsam fir, black spruce, jack pine, and white spruce in various combinations (Bergeron et al. 1998; Bergeron and Harvey 1997).

“Wet boreal forests” as defined by Thompson, Larson, and Montevecchi (2003), are “conifer-dominated forests that receive sufficient moisture from precipitation and fog, especially during summer, such that fires are rare to non-existent.” The dominant tree species is balsam fir, although black spruce is present on the wetter areas. In these ecosystems, balsam fir is self-replacing and is the dominant conifer, unlike other fire-dependent boreal ecosystems where pine or spruce is the most abundant conifer, often following mixed or deciduous successional forest stages.

Thompson, Larson, and Montevecchi (2003), in a typical example of wet boreal in western Newfoundland, compared stands of balsam fir older than 80 years to younger stands, and found that these old-growth areas could be distinguished by “lower tree density, greater variance among tree heights, larger diameter trees, lower small-tree density, lower density and diversity of deciduous shrubs, greater large snag density, taller snags, greater volume of logs on the ground, and a more open canopy than either younger age class.” They also noted that the “area covered by small shrubs, all mosses, *Sphagnum* spp. mosses, and number and volume of fallen logs increased with age of stand but average log diameter and areas covered by total litter and conifer litter declined with stand age.”

The authors concluded that

“the old-forest stage, which has developed by about 80 years, provides an environment that is distinctly different from that of stands at the peak of their maturity. These old stands are distinctive in their physiology, structure, and function. Furthermore, these differences support a biodiversity that can be readily distinguished at all scales, from sites to landscapes, compared to that in younger forests, including mature forests.”

In the sub-humid boreal forests of the prairie provinces, old-growth is quite variable, ranging from 80 to over 300 years, depending on the soil and site conditions (Timoney 2003). These old-growth forests generally have lower basal area, but higher canopy heights, lower canopy cover, more microtopography, more large snags, and lower tree densities than younger stands.

A recent study questions the assumption that the amount of old-growth is dependent on the fire cycle in the boreal forest of the prairie provinces (Chipman and Johnson 2000). Because fire is the primary large-scale disturbance, the assumption is that fire is the principal determinant of diversity. However, in the Chipman and Johnson study (2000), the vascular plant diversity in the mixedwood boreal forest is primarily determined by the moisture and nutrient gradient. They write:

“This gradient is determined by the hill slope hydrology and surficial geology. Thus the primary pattern of vascular plant diversity is determined by both the hill slope shapes and the hill slope assembly between ridgelines and streams. Our results suggest that fire frequency is not the principal determinant of diversity. Instead, the hill slope (and surficial geology) is the fundamental unit of diversity together with its interaction with light and fire..”

This leads to a somewhat different understanding of how species diversity is related to old-growth. In this study, the highest diversity of plant species was not in the oldest stands. The conclusions drawn by Chipman and Johnson include:

“at the local (hill slope) scale, species richness and diversity are highest in aspen stands, moderate in mixedwood and jack pine stands and lowest in black spruce stands. Within slope

positions (i.e., canopy types), basal area (light availability) and age (time-since-fire) further determine species richness. At the landscape scale, species richness shows small scale variability, unlike the large scale pattern of time-since-fire. In short, the hill slope (and surficial geology), and not fire, is the fundamental unit of diversity.”

Another study, in the aspen forests of Alberta, illustrates that gap phase replacement may occur and when it does, the forest “may be older than we think”, based on our knowledge of succession in that region (Cumming, Schmiegelow, and Burton 2000). Aspen forests can persist for many years following fire, when individual trees die and are replaced by regeneration in the openings that occur following the death of old trees. The resulting forest is a mosaic of structural diversity, but not necessarily species diversity, and can be quite different from forests that appear to be old-growth based on the presence of older trees.

As in the Great Lakes-St. Lawrence forest, the most appropriate way to distinguish old-growth forests from forests that are not old-growth, in the Prairie boreal forest, may be to measure the time since disturbance.

3.8 The Western Coniferous Forest

The coniferous forest in western Canada includes some of the most diverse ecosystems found anywhere on Earth. Included within this category are the montane forests of western Alberta and British Columbia, the Douglas fir and western red cedar (*Thuja plicata*) ecosystems of the coastal areas, and the lodgepole pine (*Pinus contorta*) and ponderosa pine (*P. ponderosa*) areas in the interior of British Columbia. Forests in this part of Canada extend over 11° of latitude and 25° of longitude and encompass a wide range of physical variables that influence tree growth.

In a widely cited paper, Wells, Lertzman, and Saunders (1998) reported on old-growth forests for British Columbia, and discussed both suggested definitions for old-growth and the problems in establishing them. In the conclusion in that paper the authors state:

“One important conclusion we draw from this discussion of old-growth definitions is the idea that a single, precise definition of old-growth applicable to all forest types is neither possible nor desirable.” They continue, “...we propose that forests in which gap processes predominate have attained functional old-growth status. However, direct measures do not currently exist that indicate whether or not gap processes predominate in an individual stand. Therefore, we suggest that definitions of old-growth should incorporate the distinct structural character of these forests.”

This definition is difficult to apply in the field, and for practical purposes, minimum ages were suggested for broad forest-cover types, based on the literature and discussions in a public forum. Table 3.6 provides a sample of the definitions that came from these sources.

Table 3.6 Examples of Working Definitions of Old-Growth for Broad Forest-Cover Types in British Columbia (Wells, Lertzman, and Saunders 1998)

Tree Species	Common Name	Major Forested Biogeoclimatic Zone	Minimum Age (yr)
<i>Picea sitchensis</i>	Sitka spruce	Coastal western hemlock	150
<i>Tsuga heterophylla</i>	Western hemlock	Coastal western hemlock, mountain hemlock	150
<i>Pinus contorta</i>	Lodgepole pine	Widespread in all zones	120
<i>Pinus ponderosa</i>	Ponderosa pine	Interior Douglas fir and Ponderosa pine	150

Douglas fir ecosystems of western North American have been studied extensively in both Canada and the United States. Franklin and Spies (1991) proposed an old-growth index in Douglas fir forests based on crown decadence, density of Douglas fir >100 cm, density of shade-tolerant trees > 25 cm dbh, density of large snags, and log biomass. Some characteristics, e.g., density of large snags and log biomass, follow a U-shaped curve; they have high values following a disturbance, then fall for a few years and return to high values as the forest ages. Old-growth Douglas fir has high amounts of woody debris following a fire or harvest, and high amounts later as well in the old-growth stage of succession. Other attributes, e.g., average tree size, follow an S-shaped curve, with low values at the beginning and high values late in the length of time since disturbance. In their study, Franklin and Spies hypothesized “based on the high structural variability in old-growth Douglas fir forest, multiple developmental or successional routes to old-growth-like forests” (Franklin and Spies 1991, p. 68). For that reason, they preferred to find a definition of old-growth in Douglas fir as structural and functional, rather than based on age alone. In their work, Douglas fir stands began to develop old-growth characteristics on some sites as early as 200 years while it can take longer on less productive sites.

3.9 Summary

While some proposals have been made to consider a universal definition of old-growth, at this time no universal definition has gained wide-spread acceptance. Instead, most managers and government regulators use definitions they have developed for the forest region they work in. This variety is probably necessary to meet the needs of people who live and work in Canadian forests until a universal definition can be widely accepted.

One of the most important questions in the discussion of old-growth concerns the reasons why old-growth is important. Old-growth often does not contain the highest biodiversity or the most species of organisms. Old-growth may contain habitat for certain species of either plants or wildlife, and it is important to know which species and why they are constrained by old-growth forests. From a science perspective, old-growth forests provide benchmarks for understanding that cannot be obtained in other areas of the forest. Old-growth has many social and spiritual values; however, other areas in the forest also contain social and spiritual values. Before any clear understanding of why old-growth is important can be accepted, the basic ecological characteristics of old-growth, in all its ramifications, needs to be understood.

4.0 WILDLIFE DEPENDENCE ON OLD-GROWTH IN NORTH AMERICAN BOREAL FORESTS

4.1 Superior Quality Wildlife Habitat

Critical to an understanding of wildlife habitat in forested areas is the concept of the quality of the habitat. Habitat is the range of physical and environmental conditions across which a given species can be found, including food, cover from extreme weather, and escape from predators. Habitat selection is the choice by individual animals for one habitat type over another; preferred habitats are those that the animals select more than others that are available.

Population density is frequently used as an indicator of habitat quality but can be misleading. Just because a specific habitat supports relatively high populations of wildlife does not necessarily mean that the habitat is of superior quality. Some sites may be ecological traps (or sinks) in which survival and reproduction rates are too low to sustain a population over the long term in the absence of immigration from a source population where the habitat is superior. Van Horne (1983) discussed this problem and Thompson (2004) elaborated on the concept more recently. A more technical discussion of the source-sink problem is provided by Ritchie (1997). A recent study in Alberta of red squirrels (*Tamiasciurus hudsonicus*) provides an example of this mechanism (Wheatley, Larsen, and Boutin 2003). In that study, adult and juvenile immigration was more important than local juvenile production in replacing squirrel mortality in the study area. In other words, the study area was sink habitat and the population of squirrels was maintained by animals emigrating from a source habitat.

The problem of finding ways to use population parameters as indicators of habitat quality and population fitness is discussed at some length in Bock and Jones (2004). They reviewed the ornithological literature and noted that long-term demographic studies of survival and reproduction rates provide the best measures of population fitness. Nevertheless, they concluded that abundance measurements are much more practical and provide useful information for some bird species.

In Figure 4.1 (Thompson 2004), the conceptual relationship between habitat quality and “fitness” is illustrated. In this case, fitness is assumed to be proportional to the number of young produced over time in each habitat type. A healthy marten, e.g., living in its “superior quality habitat”, will produce more young over time than a marten living in “low quality or sink” habitat.

Measuring fitness is relatively rare in the ecological literature because it is time consuming and requires sophisticated science to learn about it in a field situation. Thompson (2004) provided several examples of research that provided measures of fitness to define preferred habitat. Despite the difficulty in measuring fitness, it remains a crucial concept in understanding the relationship between wildlife and habitat of all kinds. Old-growth forests may be superior quality habitat for a species, but the species may also live and reproduce in low quality habitat as well. A long-term problem arises if the entire superior habitat is gone and only low quality habitat continues to be present in a species’ range.

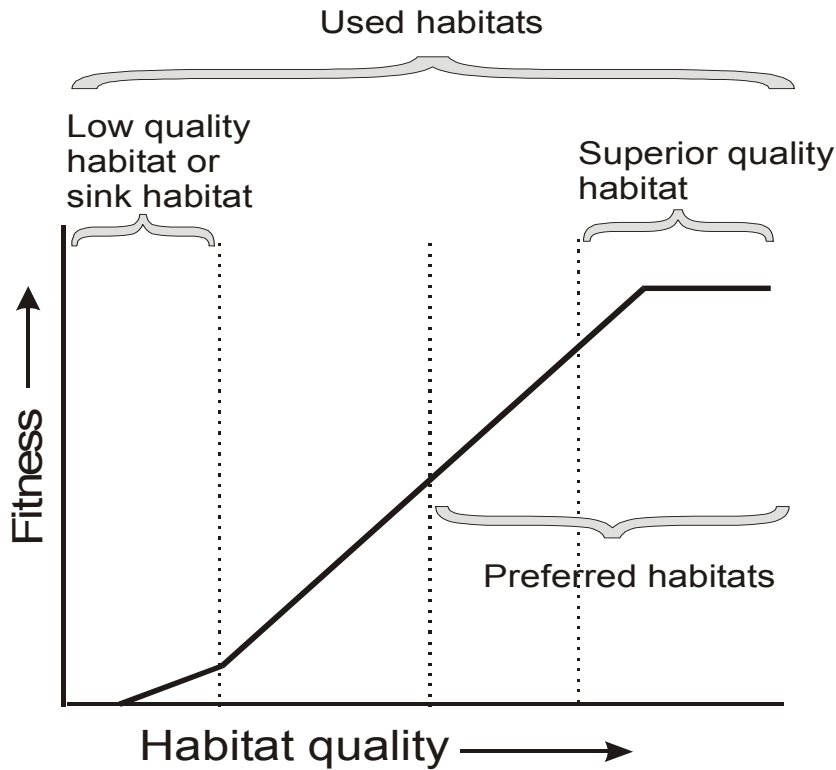


Figure 4.1 Low Quality, Preferred, and Superior Quality Habitats as Subsets of All Habitats Used by a Species (Thompson 2004)

4.2 Mammals

Extensive discussions in the forest management literature of the North American boreal forest and old-growth have concerned American marten and woodland caribou (*Rangifer tarandus spp*). However, some other residents of this forest are also linked to mature and old-growth forests, either as superior quality habitat, or as a required habitat component (Fisher and Wilkinson 2005; Sullivan et al. 2003). Other species commonly found in mature and old-growth boreal forests are the southern red-backed vole (*Clethrionomys gapperi*) on the forest floor, and the red squirrel and northern flying squirrel (*Glaucomys sabrinus*) in the forest canopy. Although there are few studies of bats in old-growth, there is evidence that some species also inhabit old-growth forests, particularly for roosting sites. Fishers (*Martes pennanti*) are recognized as old-growth forest species in some areas (Thomasma, Drummer, and Peterson 1991), but population fluctuations of their main prey species can outweigh habitat in controlling their occupancy of old-growth habitat, and snow depth may be a major factor in their distribution (Krohn, Elowe, and Boone 1995). The important question is not whether the species lives in old-growth forests, but whether or not that habitat is preferred and hence superior.

4.2.1 American Marten

Early scientific literature on the ecology of marten in the boreal forest of Canada usually stated that these mammals “prefer” older or old-growth forests de Vos (1951). More recent studies continue to

find that marten are very successful in old forests, but can survive in younger stands as well, although population levels in young stands are lower than in old, conifer-dominated stands (Potvin, Bélanger, and Lowell 2000; Poole et al. 2004; Chapin, Harrison, and Katnick 1998). Marten may be examples of animals that require the superior quality habitat, as in Figure 4.1, to thrive, but can exist at lower levels in poorer quality habitat.

Like all wildlife, marten need food and cover to survive and where those factors are most favourable, they have abundant populations. Food species include a variety of mice (*Peromyscus* spp.) and voles (*Microtus* spp.), hares (*Lepus americanus*), and ruffed grouse (*Bonasa umbellus*). Red-backed voles are taken throughout the boreal range, while other voles and mice are taken when they occur in areas occupied by marten (Thompson and Colgan 1987). Snowshoe hare can be an important part of the diet in some circumstances (Poole and Graf 1996; Thompson and Harestad 1994), but marten apparently do well in their absence.

Mature and old-growth forests, as defined by either age or physical structure, provide coarse woody debris on the ground, and abundant dead and dying trees throughout the stand, which, in turn, is favored habitat for the mice and voles that are prey items for marten. The woody debris is also important to marten as hunting structure. The diversity and abundance of overhead cover also provides protection against predators. As well, the sub-nivean (under snow) environment in older forests is diverse, and provides pathways and hiding places for both predators and prey, and marten can hunt in these areas where prey capture rates are adequate for survival. The sub-nivean environment also provides a buffer against the low temperature and winds that make winter a difficult time for survival over most of the boreal forest (Buskirk et al. 1989; Thompson and Harestad 1994; Buskirk and Powell 1994; Thompson and Colgan 1987; Wilbert, Buskirk, and Gerow 2000).

Studies of marten have often focused on parameters that may be linked to fitness, (e.g., population density, home range size, age of individuals, capture rate in traps) because of the problem of measuring fitness in field studies. The assumption behind these measurements is that the parameter has a positive relationship to fitness. Marten in superior quality habitat will generally have the smallest home ranges and the highest population density, when compared to animals in lower quality and sink habitat. The assumption that population density is related to superior habitat, however, must be considered in light of the concerns mentioned above (Wheatley, Larsen, and Boutin 2003; Thompson 2004; Van Horne 1983; Bock and Jones 2004).

In Ontario, Thompson and Colgan (1994) measured foraging success of marten in old, uncut conifer forests as compared to areas that had been logged using clear cut systems. The uncut forests were composed of black spruce, balsam fir, quaking aspen, white spruce, and white birch which had never been logged, between 150 and 250 years old. Their results supported the idea that “Marten may prefer old coniferous forests because of a greater rate of prey capture compared with that in more open habitats presented by logged forests.” In the same study area, Thompson (1994) compared marten population demography between uncut and logged boreal forests in Ontario and reported higher mean ages, more productivity, and lower daily natural and trapping mortality of martens in uncut forests. The work on comparative foraging success rates was corroborated in northwestern Ontario by Andruskiw (2003).

In a study of marten habitat in a clearcut boreal forest in Quebec, Potvin, Bélanger, and Lowell (2000) reported that marten preferred deciduous and mixed stands,

“a large proportion of which had a dense coniferous shrub layer as a result of a spruce budworm epidemic 15-20 years ago. At the landscape scale, winter home ranges differed from random mosaics because they had a larger proportion of uncut forest (>30 years), a smaller proportion of open regenerating stands, larger core areas in forest habitat and less

edge between open regeneration stands and forest. Winter home ranges usually contained < 30-35% open or closed regenerating stands and > 40-50% uncut forest.”

However, in that study, Potvin, Bélanger, and Lowell (2000) defined “deciduous” as any stand with coniferous basal area of <50%, which is a mixedwood stand by everyone else’s definition.

The clear cut technique used in this example left a landscape that had a centre dominated by a cutover matrix (60% of the block) and was surrounded by contiguous uncut forest. In this study, the animals found habitat in the uncut areas, but also were able to use some of the younger stands perhaps because of the shrub layer in the understory. Potvin, Bélanger, and Lowell (2000) recommended that $\geq 50\%$ uncut forest should be left within 10 km² management units and that <30% of the block be clearcut over a 30 year period, to provide habitat for marten.

In the low productivity environment of Labrador, Smith and Schaefer (2002) found that marten had very large home ranges, (males 45 km²; females 28 km²) and avoided bog areas and areas with sparse tree cover. They suggested that, because of the generally homogeneous nature of the forest in their study area, where nearly all stands were > 80 years old, marten habitat selection should be envisaged primarily as the use of dense canopy stands, isolated in a matrix of avoided scrub forests and bog.

The subspecies of marten found on Newfoundland (*Martes Americana atrata*) is classified as endangered and a formal recovery plan has been written. This subspecies lives primarily in balsam fir forests >80 years old and avoids forests in 40- to 60-year-old age class. Thompson and Curran (1995) tested hypotheses that the main reason these animals avoided the younger and selected the older stands was the presence of field voles (*Microtus pennsylvanicus*) in the older forest and their absence in the younger forests, as well as the increased amount of physical structure in the older forests. The data they collected on habitat use and the age of forest stands are consistent with these two hypotheses; however, an alternate hypothesis could not be ruled out. Further study is needed to consider an alternative hypothesis: “The use of second-growth forest may be limited by mortality of marten dispersing from the uncut forest into more accessible second-growth stands that are open to trapping (of furbearers other than marten) and hare-snaring.”

In the boreal forest of Maine, Chapin, Harrison, and Katnik (1998) studied marten habitat in a managed forest setting. In that study, marten did not avoid regenerating forest edges; however, home ranges were composed of more than 60% forest cover over six metres in height. In addition, “despite different spatial requirements, both males and females tolerated a median of only 20% regenerating clearcuts in their home ranges, and maximum observed values were 40% and 31% for individual males and females, respectively.” A recommendation from that study was that forest management which consolidated clearcuts and retained large residual patches would help maintain marten in extensively logged landscapes. A more recent study in the same county in Maine (Payer and Harrison 2003) listed the characteristics of habitat that marten selected. Used habitat had taller trees, higher live-tree basal areas, and greater snag volumes than unused areas regenerated 13-21 years prior to the study.

“We conclude that where horizontal structure is not limiting, forest stands regenerated by clearcutting may provide suitable habitat for resident, nonjuvenile marten when the following threshold are reached; live tree basal areas equal to or > 18 m²/ha, mean tree height equal to or > 9 m for trees with dbh equal to or > 7.6 cm and snag volume equal to or > 10 m³/ha.”

However, it is important to note that in the Payer and Harrison (2003) study area, marten density in an adjacent, uncut forest reserve was approximately 75% higher than on their study area, which is consistent with the observation that old, uncut boreal forest provides the highest quality habitat for marten but viable populations can also exist in earlier successional stages, and is consistent with the source-sink model of populations.

A study of marten in northeastern British Columbia revealed a viable population of marten living in a predominately deciduous and early successional forest area composed mostly of aspen 30 to 40 years old, with remnant stands of conifer and mixed wood (Poole et al. 2004). While the study demonstrated that marten showed a preference for mature coniferous cover (80 to 150 years old), it was not essential to maintain a moderately dense population of this species. These authors concluded “These results [of their study] are consistent with recent thinking that vertical and horizontal structure may be more important habitat attributes than overstory age or species composition...”

In summary, marten probably need three essential factors in selecting appropriate habitat: shelter against winter conditions, structure to help avoid both avian and mammalian predators, and prey animals in sufficient quantity to meet their needs for energy (Thompson and Harestad 1994). These habitat conditions are present in both old-growth and mature boreal forests. They are also present in certain younger forests, and indeed as demonstrated by Poole et al. (2004) and Payer and Harrison (2003), viable populations can exist in these areas, although it is also clear that in the latter areas, densities were lower than in old-growth forests. Based on the literature we surveyed it is not possible to know if old-growth stands are superior to mature forest stands for American marten. It does seem clear that marten can exist in immature forests, although their fitness is almost certainly lower, and they suffer much greater trapping mortality, than in mature and old-growth forests (Table 4.1).

Table 4.1 A Summary of Findings from Research Papers That Illustrate Habitat Use by American Marten in the Boreal Forest of North America

Paper	Authors’ Designation of Forest	Findings
Thompson 1994	Uncut- 150 to 250 years	Density in uncut was higher than logged forests (3-40 years)
Thompson and Colgan 1994	Uncut- 150 to 250 years	Fitness was higher in uncut forests than in logged forests (3-40 years)
Buskirk and Powell 1994	“Late successional”	Concluded that “old-growth conifer” are important to marten survival
Thompson and Harestad 1994	“Overmature”	Review article which said use of overmature was higher than predicted by availability
Chapin, Harrison, and Katnik 1998	Size of patches, tree height	Consolidated clearcuts and large residual patches with tall trees are best
Potvin, Bélanger, and Lowell 2000	Mature, overmature, uncut > 30 years	In black spruce forest, > 50% uncut within 10 km ² blocks is best
Smith and Schaefer 2002	> 80 years in low productive environment	Habitat is dense canopy conifer older than 80 years
Payer and Harrison 2003	Basal area, tree height, dbh, snag volume	Used areas had taller trees, higher live-tree basal area, greater snag volume
Poole et al. 2004	Mature coniferous 81-150 years	Preferred mature coniferous stands, 81 to 150 years old, but also appeared healthy in 30 to 40 years old stands

4.2.2 Woodland Caribou

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) has identified five subpopulations of woodland caribou (*Rangifer tarandus caribou*) in Canada. A small herd of circa 200 animals in the Gaspé region is classified as endangered due to risk from predation and habitat

loss. The boreal subpopulation ranges across most of the boreal forest region, and is “threatened from habitat loss and increased predation, the latter possibly facilitated by human activities.” A small population in the southern mountains of British Columbia and Alberta is also classified as threatened and a northern population in the Yukon, the Northwest Territories, and British Columbia is listed as Special Concern. The Newfoundland population is considered Not at Risk (COSEWIC 2002; Thomas and Gray 2002).

Declines in populations of woodland caribou in Canada are a concern (McLoughlin et al. 2003; Schaefer 2003; Courtois et al. 2004; Thomas and Gray 2002) and, although the exact causes of the decline have been vigorously discussed, a consensus on the prime reason for the decline is still emerging. Hunting, industrial development, and loss of habitat have all been proposed as possible contributing factors to the observation that woodland caribou populations are smaller now than they were 200 years ago (Dyer et al. 2001; McLoughlin et al. 2003; Schaefer 2003; Bergerud 1974, 1983). The discussion of events that have led to caribou numbers declining will probably continue for some time until a more complete understanding of the relationship of these animals to their habitat is understood.

What does seem clear from caribou habitat studies is that mature and old-growth forests play an important role in maintaining caribou populations, even if loss of this habitat is not the prime cause of their population decline. In Manitoba, Schaefer and Pruitt (1991) illustrated that caribou travel and feeding in winter were skewed towards lakes, jack pine stands 90-160 years old, bogs, and away from burned uplands. They observed that the oldest jack pine stands had less snow, more lichens (*Cladina spp*) and easier travel corridors than nearby recent burns. Rettie and Messier (2000), working in Saskatchewan with radio collared female caribou, reported that the animals “preferred peatlands and black spruce forests to all other habitat types at the daily area scale.” However, the caribou in their study area were thought to be limited by predation and seemed to be selecting habitat based on avoiding wolves (*Canus lupus*).

“The highly selective behaviour exhibited in winter maintained separation from habitat preferred by moose, and placed caribou in habitats containing protein rich sedges and horsetails as well as abundant terrestrial and arboreal lichens.”

Researchers from Quebec report that caribou preferred “mature conifer stands with or without lichens, wetlands, and areas including large waterbodies” for home range establishment (Courtois et al. 2004). Similar results were reported in northern Ontario; in winter, caribou used older stands of black spruce and jack pine, where lichens were more abundant than earlier successional stages and the shrub understory was limited (Antoniuk and Cumming 1998). In Alberta, Bradshaw et al. (1995) reported that caribou used bogs and fens, and similar low, wet habitat complexes in winter, and then as snow accumulated they moved into “denser tree stands.” Although they did not provide the age of these stands, they suggested that it was easier for caribou to move in the treed stands because the snow was less dense and less deep, compared to the more open wetland areas. Other research from Newfoundland and British Columbia reported a similar finding: woodland caribou prefer older forests in winter while their summer habitat is based on a wide variety of plant communities (Mahoney and Virgl 2003; Apps and Kinley 1998).

Bergerud (1983) suggested caribou were limited by predation through a prey switching mechanism inherent in wolves. He proposed that when a moose population increased following a burn or timber harvest, wolves also increased as this food source became more abundant. If caribou lived in the vicinity of these populations, they would also be taken by wolves, simply because they were available or perhaps because they are smaller and easier to kill than moose. If moose populations were reduced, then wolves would exert more pressure on caribou, and the caribou population would decrease. Although little evidence is available to support or reject this hypothesis, it has been accepted as the underlying mechanism, or at least the proximate cause, of caribou decline by some authors (Courtois et al. 2004; Bergerud 1985; Fuller and Keith 1980; Seip 1992).

A recent attempt to test the Bergerud hypothesis in Alberta (James et al. 2004) revealed that caribou occupied habitats that were spatially separated from the moose-wolf predator prey system.

“We monitored radiomarked caribou, moose and wolves between 1993 and 1997 and we found that selection of fen/bog complexes by caribou and selection of well-drained habitats by moose and wolves resulted in spatial separation. This spatial separation in turn reduced wolf predation pressure on caribou but did not provide a total refuge from wolves.”

However, if the spatial separation is changed by some outside factor, e.g., logging or mining, caribou will become vulnerable to predation by wolves.

A recent modeling paper, also using data from Alberta, reported on the use of a model to investigate the relationship between moose, wolves, caribou, and the food available for both ungulates (Weclaw and Hudson 2004). As expected, the interaction between and among these populations is complex and variable. The conclusion in the ecological model was that the caribou population levels are probably determined by forage availability, predation, and the combination of the two factors working together. In the complex ecology of these northern ecosystems, caribou may seek habitat that keeps them separate from wolves and moose, and provides sufficient forage (Seip 1998).

In summary, the literature on caribou ecology illustrates that caribou use old-growth, mature conifer forests, and peat or wetland complexes in winter. However, the reasons that caribou seek out these areas are less clear. They could include avoiding industrial activity, avoiding predators, finding important food supplies, finding refuge from winter weather and snow, and perhaps easier movement through snow in these areas. Furthermore, from our general knowledge of the ecology of boreal ecosystems, the causes of caribou decline and use of winter habitat is probably based on all or some of the variables mentioned and the interplay between these variables.

Based on this review of the literature, it is also not clear whether caribou select old-growth or mature conifer forest. The studies reviewed did not suggest that old-growth forest provided habitat that mature forest did not provide. The studies suggest that both mature and old-growth forests are often used in winter, along with peatland, fen, and other wetland complexes. Because woodland caribou live in disturbance-driven ecosystems with intense human activity over most of them, finding and identifying the detailed nature of habitat that allows the populations to be stable or increase will be difficult indeed.

Table 4.2 A Summary of Research Papers That Illustrate Habitat Use by Woodland Caribou in North America

Paper	Authors' Designation of Forest	Findings
Schaefer and Pruitt 1991	Jack pine 90-160 years	Winter use was skewed toward these stands
Rettie and Messier 2000	Percent canopy closure	Caribou winter habitat was in stands with high canopy closure, generally older than 100 years
Courtois et al. 2004	200 to 500 years old because of fire cycle	In winter, mature conifer, (no age specified) wetlands and areas with large water bodies are preferred
Antoniuk and Cumming 1998	Basal area, tree volume, height of trees	Areas used by caribou in winter had low basal area, low timber volume, and relatively short trees, with abundant lichens
Mahoney and Virgl 2003	Stand age	Caribou avoided stands < 40 years old, but used "mature stand" presumably 40 to over 80 years.
Apps and Kinley 1998	Stand age	Selection for stands older than 120 years

4.2.3 *Red-Backed Vole*

Red-backed voles can be found in early stages of succession, following a timber harvest or fire; however, the population density is generally higher in mature and old-growth stands. Most authors believe that these small mammals feed on the abundant fungi, seeds, and green plants in older stands and are able to use the coarse woody debris on the ground for shelter from harsh winter conditions and from both mammalian and avian predators.

In boreal forest studies, Sullivan, Lautenschlager, and Wagner (1999) and Moses and Boutin (2001) found red-back voles in clearcuts not long after timber harvest, perhaps because there was an abundance of food and coarse woody material remaining after the harvest. In interior British Columbia, Von Trebra, Lavender, and Sullivan (1998) found similar results following shelterwood cuts. However, in years following harvest, the density of these voles in clearcuts declines and eventually they are nearly absent from early successional boreal forest areas (Martell 1985; Martell and Radvanyi 1977). In a review of several studies of small mammals and timber harvest, Kirkland (1990) noted that red-backed voles had an initial positive response to clearcutting and that this initial response did not continue beyond 1 or 2 years.

Most studies in the boreal forest have found that red-backed voles are most abundant in uncut forests (Sullivan, Sullivan, and Lindgren 2000; Sullivan and Sullivan 2001; Nordyke and Buskirk 1991; Thompson and Colgan 1994; Smith and Schaefer 2002). Both flying squirrels and red-backed voles feed extensively on hypogenous and epigeous fungi that occur in older stands (Sullivan et al. 2003) and this may be part of the reason they prefer this habitat. Sullivan et al. (2005) suggested that the red vole's dependence on mesic habitats with an abundance of stumps, rotting logs, and exposed roots that help to provide a moist microclimate is likely related to its presence in old-growth forest.

Sullivan et al. (2005) investigated whether thinned stands of lodgepole pine could produce habitat conditions for these voles. They compared small mammal populations in thinned stands of lodgepole pine with results from unharvested lodgepole pine. A conclusion from their work was “reproduction, recruitment, and survival of *C. gapperi* were maintained in young managed lodgepole stands (thinned or unthinned) at levels recorded in old-growth forest.” Further,

“the results of our study suggest that abundance and diversity of forest-floor small mammals will be similar among thinned and unthinned stands of young lodgepole pine and old-growth forests at 12- to 14-years after thinning. Inherent in this community similarity will be comparable productivity of red-backed vole populations, at least in terms of reproduction, recruitment, and survival among stands. Abundance of red-backed voles should also be reasonably similar among stands except in years of high numbers. This latter difference will likely decline with time as the heavily thinned stands approach structural and compositional similarity to old-growth forest. Thus, appropriate thinning regimes that provide a variety of stand structures, either within (variable-density thinning) or between stand treatments (conventional thinning) should help manage for plant and animal diversity across forest landscapes. Old-growth attributes may be produced in perhaps decades in intensively managed young stands rather than waiting centuries with the alternative of no management intervention.”

Very few studies of this nature exist in the literature of small mammal ecology (see Table 4.3). The conclusion from the Sullivan et al. studies is that the structure of the physical environment may be one of the most important attributes of red-backed vole habitat. Food resources and predator avoidance are also important attributes and they may be linked to structure in a closely correlated relationship. While it makes common sense that red-backed voles require the food and cover in old-growth forests, they may also find their habitat needs in mature forest stands.

Table 4.3 A Summary of Research Papers That Illustrate Habitat Use by Red-Backed Voles in North America

Paper	Authors' Designation of Forest	Findings
Nordyke and Buskirk 1991	Index of old-growth based on tree dominance, density of downed logs, dbh	Numbers higher and body condition better for voles in stands with highest index of old-growth characteristics
Simon et al. 1998	Stand ages 30-150 years old	Most captures in old stands
Smith and Schaefer 2002	Mature forests were over 80 years	Higher populations in stands over 80 years
Sullivan, Sullivan, and Lindgren 2000	Stands called old-growth were 106-149 years	Highest number of animals trapped in “old-growth”
Sullivan and Sullivan 2001	Index based on % tree cover and crown volume	Highest abundance in highest index values
Sullivan et al. 2005	Old-growth was 160-200 years	Highest abundance and fitness was in old-growth

4.2.4 *Red Squirrel and Flying Squirrel*

In the boreal forest of Canada, there are relatively few studies of red squirrel and flying squirrel habitat requirements. A study in Alberta showed that red squirrels were more abundant in older forests than in younger forests (Wheatley, Larsen, and Boutin 2003) and in Ontario a similar observation was made (Thompson et al. 1989). A more general study of red squirrel habitat (Kemp and Keith 1951) concluded that older forests provided better habitat than young forests. The main nesting location for red squirrels was identified as large, old, white spruce (*Picea glauca*) trees in one brief study (Fancy 1980). However, no studies are available that conclude that there is a difference in older forests with mature seed-bearing trees and old-growth forests for these mammals.

Flying squirrels have been studied more extensively in the western coniferous forests and in Oregon in old-growth Douglas fir forests, than in the boreal (Carey 1995; Maser, Maser, and Trappe 1985). These squirrels forage extensively on highly digestible mushrooms and supplement their diet with arboreal lichens when mushrooms are unavailable, as reported in the non-boreal parts of its range (Hall 1991; Carey 1995). In one of the few studies of northern flying squirrels in the boreal forest region, Cotton and Parker (2000) found that “A significant proportion of nest trees were larger, older and taller than trees that were randomly available in the locale of nest trees.” However, the squirrels did not appear to select particular habitat characteristics at nest sites that differed from random sites and there was a wide range of tree characteristics that were suitable nesting sites. What did seem important in flying squirrel habitat was a diversity of physical structure, both of living trees and of coarse woody material on the ground. The main conclusion from this study was

“variation in habitats used by flying squirrels in the sub-boreal spruce zone of British Columbia is evidence of the ability of this animal to occupy a wide range of conditions in a region that is not typified by old-growth forests.”

A study in British Columbia for both red squirrels and flying squirrels found that second growth stands of lodgepole pine (*P. contorta*) were not different from old-growth stands as habitat for these mammals (Ransome and Sullivan 1997). Other studies from other forest regions have come to a similar conclusion (Rosenberg and Anthony 1992; Waters and Zabel 1995). More recent studies by Ransome et al. (2004) support the hypothesis that “population dynamics of *G. sabrinus* and *T. hudsonicus* would be maintained at levels recorded in old-growth forest by large-scale pre-commercial thinning of young lodgepole pine forests. Although red squirrels and flying squirrels declined in the immediate post harvest period, by 12 to 14 years following pre-commercial thinning, both abundance and population characteristics were similar to animals that live in old-growth stands.”

A recent study of lichens as nesting material for northern flying squirrels, although not in the boreal forest region, indicates that lichens are used both for nesting material and food by this species (Hayward and Rosentreter 1994). Even though the bulk of flying squirrel studies have not been in boreal ecosystems, it does seem plausible that lichens and mushrooms are important for these animals throughout their range and that older forest with lichens will probably be desirable habitat for them. Based on the studies available, however, it is not possible to differentiate flying squirrel habitat based on old-growth versus mature forest conditions.

4.2.5 *Bats*

Although there is abundant literature on bats, few studies concentrate on the use of old-growth boreal forest stands. In a recent study in Alberta, foraging by bats in cleared, thinned and unharvested boreal forest found

“*Myotis lucifugus* [little brown bat], an aerial insectivore, preferred to forage along the edge of clear-cuts, while *M. septentrionalis* [northern long-eared bat], a species that gleans prey from surfaces, did not forage in clear-cuts but preferred intact forest. The largest species in our study, *Lasionycteris noctivagans* [silver-haired bat] preferred clear-cuts and avoided intact patches.” (Patriquin and Barclay 2003)

Some species of bats prefer older trees for roosting sites and often use older conifer trees, although most of the studies that report this fact were not done in boreal forests (Crampton and Barclay 1998; Vonhof and Barclay 1996). In mixed forests in Alberta, bats preferred to roost in aspen (Crampton and Barclay 1998; Patriquin and Barclay 2003). In central Ontario, old-growth pine forests were important habitat components for bats; however, the data did not support the hypothesis that selection of old-growth stands is related to greater roost site availability (Jung, Thompson, and Titman 2004). In these pine forests, the old-growth stage may provide a more open understory and a less cluttered habitat beneath the canopy for flight and foraging (Jung, Thompson, and Titman 2004; Brigham et al. 1997). However, large old trees are important roosting sites (Jung, Thompson, and Titman 2004).

Because there are a limited number of studies of bat habitat in the boreal forest, it is not clear whether bats require old-growth stands, as distinct from mature forests, as part of their habitat. What does seem important, from studies of bat ecology in different parts of the forested regions of Canada, is that these animals use older forests, for both foraging and roosting and that without mature and old-growth forests, some species (e.g., northern long-eared bat) will be less abundant.

4.2.6 *Fisher*

Sometimes fisher are considered old-growth forest species; however, in reality they have complex habitat requirements that are influenced by snow depths and their primary prey species, as much as old-growth forest stands. While they occur in the boreal forest (for example, in Ontario their range occurs in the western part of the province in the boreal forest region) their preferred habitat seems to be in the Great Lakes-St. Lawrence Forest Region (Gibilisco 1994; Thompson 2000; Garant and Crête 1997).

Harris (1984) considered the fisher to be most closely associated with old-growth Douglas fir forests in Oregon. In a habitat suitability model developed for fisher, Allen (1983) wrote: “Dense coniferous and mixed coniferous/deciduous are the preferred habitat.” In a test of the same habitat model for fisher, Thomasma, Drummer, and Peterson (1991) concluded that the most suitable winter habitats are “dense forest stands comprised primarily of large diameter conifer trees.”

However, Krohn, Elowe, and Boone (1995) suggested that the reports of fisher needing old-growth forests come from areas where deep snow is a major factor in their habitat, e.g., the Pacific Northwest (Harris 1984) or the Great Lakes states (Thomasma, Drummer, and Peterson 1991). In other areas, these mammals may not be so dependent on old-growth. Because their diet is largely snowshoe hare and porcupine, both resident in younger and mature forests, it is logical that fisher will hunt in those areas. In their study in the Great Lakes forest region of upper Michigan, Thomasma, Drummer, and Peterson reported that fisher selected dense hemlock stands in late winter when snow was deep and their primary prey were associated with those stands in winter (Thomasma, Drummer, and Peterson 1994). Although not reported in the Michigan study, porcupines (*Erethizon dorsatum*) are an important prey item for fishers and they are often associated with hemlock stands in this region.

In their review of marten and fisher habitat, Buskirk and Powell (1994) summarized their thoughts as follows: “Do American marten and fishers require particular forest types—for example, old-growth conifers—for survival? We think they do.” However, they also were careful to put that conclusion in context.

“Although there is logic in our use of specific life needs to explain habitat selection behaviours of fisher and American martens there is also speculation and teleology involved. We and others believe that habitat selection patterns are probably most easily explained in terms of fitness or its currencies. ...Our guesses may not be correct. We offer them as hypotheses to be tested and likely rejected in the process of learning more about these species.”

In Maine, in a study that measured the use of selected habitats by fisher, Arthur, Krohn, and Gilbert (1989) found that fisher used coniferous stands of trees, but not necessarily old-growth stands. In their study, fisher dens were in hollow aspen (*Populus tremuloides*) trees found within conifer stands. These authors concluded

“because of the diversity of the fisher’s diet, it was not surprising that we found little evidence of active fisher selecting for particular forest types. The only indication of preferential use of habitats by active fishers during winter was their obvious change in behaviour when they encountered dense patches of hare tracks.”

The normal range of fisher includes the boreal forest; however, studies that link these mammals to old-growth boreal stands is lacking. As pointed out by Buskirk and Powell (1994), however, fisher are often found in coniferous forests with large trees, although the distinction between old-growth habitat and mature forest habitat is not clear for fisher.

4.3 Birds

The boreal forest provides habitat for hundreds of millions, and likely even billions of landbirds. Blancher (2003) used data from the Canadian Breeding Bird Census (Kennedy, Dilworth-Christie, and Erskine 1999) and the North American Breeding Bird Survey (reported in Blancher as Sauer, Hines, and Fallon [2002], recently updated in Sauer, Hines, and Fallon [2004]) to estimate a population of between 1.4 and 2.5 billion breeding birds. The population is considerably higher after nesting and before migration, when young-of-the-year birds are also present. Blancher (2003) estimates that there are between three and five billion birds in the forest at the end of breeding season. Most of the breeding population (> 90%) is migratory. A breakdown of breeding population by family is provided in Table 4.4.

Table 4.4 Estimated Numbers of Boreal Breeding Landbirds by Family (from Blancher 2003)

Family	Species	BB Census Population (millions)	BB Survey Population (millions)
Paurilidae (wood warblers)	27	1,000	310
Emberizidae (sparrows and allies)	26	680	460
Turdidae (thrushes)	11	270	200
Tyrannidae (flycatchers)	15	130	54
Vireonidae (vireos)	6	88	84
Regulidae (kinglets)	2	84	53
Picidae (woodpeckers)	9	51	18
Fringillidae (finches)	10	30	47
Corvidae (jays, crows and allies)	7	30	23
Phasianidae (grouse and allies)	9	25	6.7
Paridae (chickadees and allies)	4	25	14
Icteridae (blackbirds and allies)	11	20	27
Hirundinidae (swallows)	7	19	23
Troglodytidae (wrens)	4	17	25
Cardinalidae	2	7.8	1.8
25 other landbird families	54	39	34
Total		2,500	1,400

4.3.1 Birds and Old Forests

Old forests play an important role in the ecological dynamics of the boreal forest, and as habitat for many bird species. Some bird species, such as boreal chickadee (*Parus hudsonicus*) and three-toed woodpecker (*Picoides tridactylus*), are very strongly associated with old forests (Schmiegelow and Mönkkönen 2002). However, Bunnell (1999) pointed out that birds (and other animals) don't know when they are in old forests; their dependence or use of old forest may relate to the presence of structural characteristics, such as those identified by Mosseler, Thompson, and Pendrel (2003) and not to the age of the forest per se.

The hypothesis relating to the affinity of species to structural characteristics rather than stand age has prompted several authors to propose that it should be possible to create old forest characteristics in forests which are themselves not old-growth. Bunnell (1999) noted that the retention of residual forest and structure in harvested areas maintains many species assumed to be late successional species. Wedeles and Donnelly (2004) summarized several studies that showed that retention of residuals in cutovers provided habitat for some species associated with the pre-harvest forest. These can be taken as evidence supporting the notion that birds cue in on habitat and structural elements, rather than on an old forest gestalt. Hagar, McComb, and Emmingham (1996) found that several "old-growth" bird

species were consistently more abundant in thinned versus unthinned stands, leading them to suggest thinning as a means of approximating old-growth conditions. Suggestions for the retention of snags and downed woody debris (Hagan and Grove 1999b) have their basis in a similar intent.

Although some management practices can hasten the development of old-growth features, some elements, such as large live trees and snags, are a function of age, even if their presence can be encouraged by management. Old trees with rough bark are required for shelter and foraging for many resident species during the winter, and the development of cavities suitable for nesting comes with age. So although it may be that old-growth characteristics can be induced to some extent, suitable age-related conditions need to be present for this approach to be successful. This, and broader concerns related to age-class truncation and structure, has led many authors to advocate retention of large areas of old forests (Evans and Conner 1979; Schieck and Hobson 2000; Imbeau, Mönkkönen, and Desrochers 2001; Cumming and Diamond 2002; Kirk 2003) or to extend or maximize rotation ages (Evans and Conner 1979; Kirk et al. 1996; Hagan et al. 1997; Hobson and Schieck 1999; Imbeau, Savard, and Gagnon 1999).

Studies of the roles that old-growth forests play in providing habitat for songbirds have generally focused on two or three aspects: the comparative densities of birds in old forests, species richness in old forests, and the habitat affinities of individual species.

4.3.2 *Species Richness and Density*

In a study of songbird habitat use in mixedwoods near Manitouwadge in boreal Ontario, (Welsh 1987) examined bird communities in stands ranging from 1 to 220 years since last disturbance (either clearcutting or fire). He found no clear relationship between either bird densities or species richness and stand age, except that the youngest plot (1 year) had the lowest number of birds, and the highest density was in a 5-year-old plot. Old forests did not have a greater or lesser density or richness than stands as young as 6 years.

In an analysis of habitat used by birds found in the boreal forests of the prairie provinces Telfer (1993) categorized the habitat affinities of 146 species of breeding birds and compared their presence in different age-classes of forest to the predicted relative abundance of those age-classes according to a negative exponential fire frequency relationship. He found that the proportion of bird species associated with mature (51-150 yrs) and old (150+ yrs) forests exceeded the percent of land area associated with old forests, assuming a 50-year fire cycle. (A 50-year fire cycle for this region is consistent with that reported in the literature (Weir, Johnson, and Miyanishi 2000). The author interpreted this as evidence of the disproportionate ecological importance of old forests for birds.

(Schieck, Nietfeld, and Stelfox 1995) examined bird use in forests of different age (based on time since fire) in mixedwood boreal forests in Alberta. They found that species richness was highest in old (120+ years) compared to mature (51-63 years) and young (23-26 years). In addition, two-thirds of the 57 species examined had their highest abundance in old forest.

The work of Schieck, Nietfeld, and Stelfox (1995) was extended by Hobson and Bayne (2000) who, working in the same study area, collected additional data including from stands following harvest rather than fire. Working in aspen forest, they categorized the communities into three classes: young (15-25 years), mature (50-60 years), and old (80-110 years). They found that the nesting guild structure of the avian community was highly influenced by forest age, with canopy-nesting and cavity-nesting guilds most abundant in mature and old forests, with the trend strongest for cavity nesters. They also found species richness in general to be higher in mature and old stands than in young stands. The authors speculated that the greater presence of the cavity-nesting guild in old forest may be attributed to a high number of large snags (although the total number of all snags was not higher in old stands) and a greater presence of large live trees. The authors attributed the high

presence of canopy nesting birds in old stands to higher densities of coniferous trees and shrubs than in younger stands.

Thompson, Larson, and Montevecchi (2003) and Thompson, Hogan, and Montevecchi (1999) reported on songbird use in relation to stand age in balsam fir forests of western Newfoundland. They identified three strata of forest ages: 40-60 yrs, 60-80 yrs, and > 80 yrs. Of the 32 species they included in their analyses, 22 were present in all three age classes. The abundance of several species was significantly related to stand age ($p < 0.05$) and species richness was significantly greater in the 40-year-old stand than in either older age class ($p < 0.01$). Five species were significantly more common in 40- and 60-year-old stands than in old (80+ years); three species were equally abundant in 60-year and 80+ year stands, but less abundant in 40-year stands; and three species were significantly most abundant in the 80+ year forest class. Thompson, Hogan, and Montevecchi (1999) noted that the balsam fir forests of Newfoundland are relatively short-lived and lack a difference in tree species composition between young-mature and over-mature age classes. As they described it, the forests progress through a series of age classes dominated by balsam fir at decreasing densities, ranging from < 20,000 stems/ha in a shrub stage to about 2,000 trees/ha at 80+ years. The authors attribute their observed trend of declining abundance in birds with forest age to the decline in deciduous tree component and deciduous litter. They attributed the gradient of increase in abundance of some species to abundance of large diameter trees or dead trees, probably as foraging substrates.

Cumming and Diamond (2002) surveyed the bird community in boreal mixedwood stands of four age classes (50-60 years, 80-90 years, 100-110 years, and > 140 years) in central Saskatchewan. They found that the number of songbird species recorded in each habitat progressively increased with age. From youngest to oldest, the number of species was 15, 18, 22, and 26. Eleven species were not detected in the youngest forest stands, but species detected in the youngest forest also occurred in the oldest. They also found that eight species were found significantly more often in the oldest age class (see below for species). They speculated that the greater species richness and abundance was caused by greater habitat heterogeneity in old forests (although no measures of habitat heterogeneity were included in the analyses), caused by wind throw gaps, tree disease, and death, which allows for infilling with various ages and species of trees.

4.3.3 *Species Affiliations*

Welsh (1987) provided data showing the following species disproportionately, or only, in old-growth forests: golden-crowned kinglet (*Regulus satrapa*), bay-breasted warbler (*Dendroica castanea*), and ovenbird (*Seiurus aurocapillus*). He also referred to several other species as “late seral”, but no data were provided to demonstrate the habitat affiliation; these species were Cape May warbler (*Dendroica tigrina*), red-breasted nuthatch (*Sitta canadensis*), brown creeper (*Certhia familiaris*), black-throated green warbler (*Dendroica virens*), and blackburnian warbler (*Dendroica fusca*). Finally, he also documented habitat use by several species that spanned age classes and included presence in old forests.

Species with significantly greater ($p < 0.01$) presence in old forests (120+ years) compared to mature (51-63 years) and young (23-26 years) in the mixedwoods of Alberta, as found by Schieck, Nietfeld, and Stelfox (1995), included yellow-rumped warbler (*Dendroica coronata*), magnolia warbler (*Dendroica magnola*), black-throated green warbler, western tanager (*Piranga ludoviciana*), pine siskin (*Carduelis pinus*), yellow-bellied sapsucker (*Sphyrapicus varius*), hairy woodpecker (*Picoides villosus*), red-breasted nuthatch (*Sitta canadensis*), brown creeper, least flycatcher (*Empidonax minimus*), yellow warbler (*Dendroica petechia*), American redstart (*Setophaga ruticilla*), mourning warbler (*Oporornis philadelphia*), white-throated sparrow (*Zonotrichia albicollis*), winter wren (*Troglodytes troglodytes*), and Swainson’s thrush (*Catharus ustulatus*).

Of the 32 species reported on by Thompson, Larson, and Montevecchi (2003) in the balsam fir forests of western Newfoundland, the only ones that were most abundant in 80+ year old stands compared to 40-60 and 60-80 year old stands were ruby-crowned kinglet (*Regulus calendula*), black-backed woodpecker (*Picoides arcticus*), and grey-cheeked thrush (*Hylocichla minima*). Interestingly, boreal chickadee, black-throated green warbler, and pine siskin were common in 40-60 year old stands in this study, but have been reported with old-forest affiliations by other studies.

Hobson and Bayne (2000) found the following species significantly more abundant in old (80-100 years) aspen and mixedwood stands than in similar mature (50-60 yrs) and young (15-25 years) stands: bay-breasted warbler, pine siskin, white-winged crossbill (*Loxia leucoptera*), boreal chickadee, brown creeper, pileated woodpecker (*Dryocopus pileatus*), and red-breasted nuthatch.

Kirk and Hobson (2001) studied bird-habitat relations for 42 species in jack pine stands in the boreal region of north-central Saskatchewan. Of the 44 variables included in a canonical correspondence analysis, they found stand age to be the most important explanatory variable. While few bird species were restricted to particular age-classes of stands, they did find marked differences in abundance among age categories for some species. (The age classes they identified were young, immature, mature, and overmature; the age boundaries of the classes differed for each of three jack pine communities: jack pine, jack pine-black spruce mixedwood, and jack pine-aspen mixedwood.). They found several neotropical migrant songbirds were strongly associated with overmature stands containing a mix of jack pine, white spruce, and white birch. These species included Cape May warbler, bay-breasted warbler, and Tennessee warbler (*Vermivora peregrina*). Other species strongly associated with overmature stands included brown creeper, red-breasted nuthatch, alder flycatcher, and pine siskin.

Cumming and Diamond (2002) found the following species significantly more often in old forests beyond rotation age (80-90 years) in Saskatchewan boreal mixedwoods: winter wren, golden-crowned kinglet, ruby-crowned kinglet, Swainson's thrush, Tennessee warbler, magnolia warbler, Blackburnian warbler, bay-breasted warbler, rose-breasted grosbeak (*Pheucticus ludovicianus*), and evening grosbeak (*Coccothraustes vespertinus*).

In a review of the habitat affiliations of 40 species of boreal breeding birds believed to be declining according to the evidence summarized by Blancher (2003), Manning (2004) noted that the following species have affinities for old forest habitat: Connecticut warbler, (*Oporornis agilis*) mourning warbler, blackpoll warbler (*Dendroica striata*), Canada warbler (*Wilsonia canadensis*), Swainson's thrush, grey-cheeked thrush, western wood pewee (*Contopus sordidulus*), and white-throated sparrow.

Kirk et al. (1996) examined breeding bird communities in the mixed boreal forest of central Saskatchewan. They analyzed species densities in four forest age classes ranging from young (0-9 yrs) to old (80 years) and found that low canopy and bark gleaners were most abundant in old stands. Four species (black-throated green warbler, brown creeper, golden-crowned kinglet, and evening grosbeak) occurred only in old stands, and 19 other species were most abundant there.

A summary of this literature is presented in Table 4.5. From Table 4.5, several important points arise:

- The age at which old forest was determined to commence varied across studies, and across forest types. For example, in Newfoundland, Thompson, Hogan, and Montevecchi (1999) defined old balsam fir forests as commencing at 80 years, and in the aspen-dominated mixedwoods of Alberta, Schieck, Nietfeld, and Stelfox (1995) defined old forest as commencing at 120 years.

- In studies reviewed for this paper, several species were commonly found to be associated with old forest. Species which were identified in at least three studies were bay-breasted warbler, brown creeper, black-throated green warbler, Cape May warbler, golden-crowned kinglet, pine siskin, red-breasted nuthatch, and winter wren. Many of the examples in Table 4.5 were from Saskatchewan and west, reducing the probability that old-growth affiliated species with more easterly distributions, such as the gray-cheeked thrush (*Catharus minimus*), would be noted in the table.
- A further complication is that habitat affinities of species are not always consistent geographically and across forest types. As an example of the variation across communities, Erskine (1977) listed 19 bird species which vary either in habitat preference or density over parts of their range in boreal Canada. This may explain why a species such as yellow warbler, which is frequently associated with young sites and thickets (Godfrey 1966), was identified by Schieck, Nietfeld, and Stelfox (1995) as having an affinity for old-growth.
- In spite of the fact that statistical rigour was used in most of the studies identified in Table 4.5, some early successional forest species may be identified as old-growth species. This may also explain why species such as yellow warbler and mourning warbler appear in the table. Their presence may be due to patches of suitable habitat being located in otherwise old forest, difficulties in forest typing, or simply sampling error.
- All regions of the boreal forest are not equally represented in the studies of Table 4.5. As noted above, studies from Saskatchewan are abundantly represented. However, studies from other parts of boreal Canada are conspicuous by their absence.

Table 4.5 Species Associated with Old Forest in Several Studies

Study	Forest	Old Forest Definition	Species ¹⁰																
			ALFL	AMRE	BBWA	BBWO	BCCH	BLBW	BRCR	BTNW	CAWA	CMWA	CSWA	EVGR	GCKI	GCTH	HAWO	LEFL	MAWA
Welsh 1987 ¹	Ontario boreal mixedwoods	Not provided			X			X	X	X				X					
Schieck, Niefeld, and Steffox 1995 ²	Alberta aspen-dominated mixedwoods	> 120 yrs		X				X	X							X			
Thompson, Hogan, and Montevecchi 1999 ³	Nfld. balsam fir	> 80 yrs				X								X					
Hobson & Bayne 2000 ⁴	Sask. boreal mixedwoods	80–110 yrs			X					X									
Kirk & Hobson 2001 ⁵	Sask. jack pine	> 100 yrs								X									
Kirk & Hobson 2001 ^{6,7}	Sask. jack pine-black spruce mixedwoods	> 110 yrs	X									X							
Cumming & Diamond 2002 ⁸	Sask. boreal mixedwoods	> 100 yrs			X												X		X
Kirk et al. 1996 ⁹	Sask. boreal mixedwoods	> 80 yrs								X	X	X						X	
	Total		1	1	3	1	1	2	5	3	1	3	1	1	3	1	1	1	1

(Continued on next page. See notes at end of table)

Table 4.5 Continued

Study	Forest	Old Forest Definition	Species ¹⁰																
			MOWA	OVEN	PISI	PIWO	RBGR	RBNU	RCKI	REVI	SWTH	TEWA	WETA	WTSP	WIWR	WCWR	YBSA	YRWA	YWAR
Welsh 1987 ¹	Ontario boreal mixedwoods	Not provided	X																
Schieck, Niefeld, and Stelfox 1995 ²	Alberta aspen-dominated mixedwoods	> 120 yrs	X	X								X	X	X			X	X	
Thompson, Hogan, and Montevecchi 1999 ³	Nfld. balsam fir	> 80 yrs							X										
Hobson and Bayne 2000 ⁴	Sask. boreal mixedwoods	80-110 yrs			X										X				
Kirk and Hobson 2001 ⁵	Jack pine	> 100 yrs					X												
Kirk and Hobson 2001 ^{6,7}	Jack pine-black spruce mixedwood	> 110 yrs							X										
Cumming and Diamond 2002 ⁸	Sask. boreal mixedwoods	> 100 yrs																X	
Kirk et al. 1996 ⁹	Sask. boreal mixedwoods	> 80 yrs	X															X	
	Total		1	2	4	1	2	4	2	4	1	2	2	1	3	2	1	1	1

- 1 – Data provided show disproportionate use by BBW, GCKL and OVEN of late successional stands (110-220 yrs), but no statistical analyses are provided. Paper also refers to CMWA, RBNU, BRGR, BTNW, and BLBW as late seral species, but no data are provided, so those species are not indicated in this table.
- 2 – Species shown are those for which there was significantly ($P < 0.01$) greater use of old stands (120 yrs) compared to mature (51-63 yrs) and young (23-26 yrs) stands.
- 3 – Species shown are those which were detected more frequently ($P < 0.05$) in old balsam fir forests than in forests of 40-60 or 60-80 yrs.
- 4 – Species shown are those which were detected more frequently ($P < 0.05$) in old forest compared to young (15-25 yrs) and mature (50-60 yrs) stands.
- 5 – Species shown are those which were detected more frequently ($P < 0.05$) in overmature jack pine stands compared to young (≤ 30 yrs), immature (40-60 yrs), or mature (70-100) stands.
- 6 – Species shown are those which were detected more frequently ($P < 0.05$) in overmature jack pine-black spruce mixedwood stands than in mature (80-100 yrs) stands.
- 7 – The same study also compared species detections in overmature jack-pine-aspen mixedwoods (> 80 yrs) compared to young (< 30 yrs), immature (40-50 yrs), mature (60-70 yrs) and found no species more frequently detected in the overmature stands.
- 8 – Species shown are those which were detected more frequently ($P < 0.05$) in stands beyond rotation age (80-90 yrs) than at or below rotation age.
- 9 – Study compared presence of birds in stands of age classes: very young (0-9 yrs), young (15-20 yrs), mature (40 yrs), and old (80 yrs). Statistical analyses were not conducted on data for all species. Only OVEN was identified with old-forest affinity ($P < 0.05$) based on statistical tests. All other species identified in this table occurred at least 10 times and most often in old forest, but not in all of the other forest age classes, and were not subjected to statistical tests.
- 10 – Species codes are: ALFL – Alder Flycatcher, AMRE - American Redstart, BBWA – Bay-breasted warbler, BBWO – Black-backed woodpecker, BCCH – Black-capped chickadee, BLBW – Blackburnian warbler, BRGR- Brown Creeper, BTNW - Black-throated green warbler, CAWA – Canada warbler, CMWA – Cape May warbler, CSWA – Chestnut sided warbler, EVGR - Evening grosbeak, GCKI – Golden crowned kinglet, GCTH – Gray-cheeked thrush, HAWO – Hairy woodpecker, LEFL – Least flycatcher, MAWA - Magnolia warbler, MOWA – Mourning warbler, OVEN – Ovenbird, PISI – Pine siskin, PIWO – Pileated woodpecker, RBGR – Rose-breasted grosbeak, RBNU – Red-breasted nuthatch, RCKI – Ruby-crowned kinglet, REVI – Red-eyed vireo, SWTH – Swanson’s thrush, TEWA – Tennessee warbler, WETA – Western tanager, WTSP – White throated sparrow, WIWR – Winter wren, WWCR - White-winged crossbill, YBSA – Yellow-bellied sapsucker, YRWA – Yellow-rumped warbler, YWAR – Yellow warbler

Schmiegelow and Mönkkönen (2002) discussed data from a series of studies in the boreal mixedwoods of north-central Alberta. They reported that old-forest specialists account for almost one third of all birds breeding in older forest forests in Alberta. They drew particular attention to resident species, noting that among boreal bird species that specialize on older forests, residents should exhibit the greatest sensitivity to habitat loss due to their lower abundance. They attribute the lower abundance of residents (compared to migrants) to the fact that they are regulated by severe weather and low seasonal food availability. They noted that many boreal residents are reliant on older forests because of nesting (availability of suitable trees for cavities) and foraging (dead or decaying wood) requirements.

Imbeau, Mönkkönen, and Desrochers (2001) attempted to assess the threats to breeding boreal birds caused by forestry practices. One of the threat factors considered was whether the species was an old-growth or fire specialist. They found that six landbird species were at high risk, at least partially because of their affinity for old forests: bay-breasted warbler, brown creeper, black-throated green warbler, Cape May warbler, golden-crowned kinglet, pine siskin, red-breasted nuthatch, and winter wren. In addition, as Thompson, Larson, and Montevecchi (2003) point out, black-backed woodpeckers are probably “semi-obligate old-forest inhabitants” because they require large snags within large forest stands, or large burns where snags remain standing following the fire.

Clearly, from this review of the literature, much remains to be learned about the relationship between birds and habitat provided in the boreal forest region. There is no question that some species find adequate habitat in older forests, and much of this habitat can be legitimately called old-growth. Based on abundance measurements, old-growth is probably superior habitat for several species. However, it is also evident that some species of birds may prefer older habitat in one part of the forest region, and early successional habitat in other parts of the region. Based on this review of the literature, species resident all year in the boreal forest are likely to find old-growth as superior habitat. Resident species have evolved to depend on older trees with cavities and over-wintering insects as a food source, and these habitat characteristics are present in old-growth forests.

Some species that migrate into the boreal in summer have also evolved to use the habitat provided by older forests, although the evidence that they require “old-growth”, as opposed to mature forests, is not as strong. Species suggested in this category include bay-breasted warbler, brown creeper, black-throated green warbler, Cape May warbler, golden-crowned kinglet, pine siskin, and winter wren. However, much more research is needed to confirm that old-growth forests are superior habitat for these birds.

4.4 Amphibians and Reptiles

4.4.1 *General Habitat Concerns*

Habitat loss appears to be a serious threat to herpetofauna on a worldwide basis (Ryan et al. 2002; Gibbons and Stangel 1999; Green 2003), and the impact of landscape alteration on amphibian and reptile communities is a concern. Most salamanders and reptiles seek out microhabitats that meet their needs for moisture and feeding substrate. These microhabitats are often associated with rocky substrates, downed wood, and leaf litter, which are more abundant as time passes following a disturbance. Some authors have concluded that most species of woodland salamanders appear to reach their peak abundance in late seral stage or old-growth forests (Hartwell and Droege 2001; DeGraaf and Yamasaki 1992; Dupuis, Smith, and Bunnell 1995; Ruggiero, Jones, and Aubry 1991). The older forests in these studies are characterized by abundant dead woody material on the ground and an extensive leaf litter that provides cover, food, and moisture. However, these conclusions come from studies in eastern hardwood forests or western coniferous forests.

4.4.2 *Habitat in the Boreal Forest*

Few studies of amphibian or reptile habitat in the boreal forest have been conducted and there has been little or no focus on the abundance of this class of vertebrates compared to successional stages in the boreal. Based on the ecology of amphibians and reptiles, mature and old-growth forests are probably better habitat than young forests, although scientific evidence that old-growth forests provide better habitat than mature forest stands is lacking for the boreal forest region.

One of the few studies of amphibians in the boreal forest, conducted in Alberta, compared anurans' (frogs) abundance on areas disturbed by fires with areas disturbed by timber harvest, and could not detect a difference in populations between those two habitat types (Constible, Gregory, and Anholt 2001). However, the study did not compare old-growth stands with other stands.

Many habitat studies of amphibians have been conducted in the Great Lakes-St. Lawrence type forest (Herrmann et al. 2005; deMaynadier and Hunter 1999). These studies have been able to demonstrate that forest cover near wetlands where amphibians lay their eggs is important; however, no evidence is available from these studies to show that old-growth forests are better than other forest types. Herrmann et al. (2005) concluded that "Amphibian species richness was most strongly influenced by the proportion of surrounding forest within a 1000 m radius of the wetland; however, there were some differences among species in the scale of response." Major findings from deMaynadier and Hunter (1999) are that wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) benefited from efforts to maintain connectivity between upland forest habitats and aquatic breeding sites. Juvenile wood frogs and spotted salamanders appeared to be even more discriminating than adults in their choice of closed overstory forest habitat for upland movements. When offered a choice immediately upon metamorphosis, emigrating wood frogs selected closed canopy forest conditions and areas of dense understory vegetation.

Based on the evidence available, vegetative cover around wetlands and other breeding habitat of amphibians and reptiles is probably the most significant factor in their ecology. Dense cover, including shrubs, young trees, and an abundance of dead and downed woody material on the ground, seems to be the most important factor in the ecology of this group of vertebrates.

4.5 **Insects**

4.5.1 *State of Knowledge*

Previous sections of this report have discussed the habitat affinities of individual species and the relations between the species and old-growth forests. In several, cases there remains considerable effort required to fully understand the habitat relations and the importance of old forests relative to other successional stages. For insects, our relative lack of knowledge is much more striking. In the greater scheme of things, relatively little is known about "non-outbreak species" (Danks and Fottit 1989⁸; Hammond 1997; Paquin and Coderre 1997; Spence et al. 1997). Danks and Fottit (1989) estimated that about 22,000 species of insects occur in Canada's boreal zone forests, but that only about half of the species have been described. By 1997, Spence et al. (1997) evidently believed that little progress had been made in furthering broad understanding as they cited earlier references to note that 45% of insect species inhabiting the boreal region remain unknown to science.

Economically important herbivorous insects have been the subject of most study, but efforts to catalogue and understand the habitat affinities of major groups such as Acarina (mites), Hymenoptera

⁸ Although Danks and Fottit (1989) is now somewhat old by the standards of scientific papers, it remains the standard reference work for boreal insects, as evidenced by the frequency with which it is cited in even the most recent papers.

(ants, wasps and bees), Diptera (flies), Coleoptera (beetles) and Araneida (spiders) are conspicuous by their absence (Danks and Fottit 1989; Hammond 1997; Paquin and Coderre 1997). The lack of understanding of boreal insects, at least to some extent, reflects a lack of understanding of insects in general in Canada. Danks and Fottit (1989) estimated that one-half to two-thirds of Canadian species occur in the boreal and its adjacent transition zones.

4.5.2 *Insect Use of Old-Growth Forests*

Given the broad scarcity of research on Canada's forest arthropods, it is not surprising that there are relatively few investigations specifically or peripherally on the relationship between old forests and insects. The body of recent work on insects and forests which exists most strongly represents the western mixedwoods (Buddle 2001; Hammond 1997; Spence et al. 1997; Hammond, Langor, and Spence 2004; Niemelä and Spence 1994; Niemelä, Spence, and Spence 1992; Work et al. 2004), although work from other forest types and areas does exist (Gandhi et al. 2001; Saint-Germain, Drapeau, and Hébert 2004; Paquin and Coderre 1997; Thompson, Larson, and Montevecchi 2003). Not all of this work, however, is relevant to the topic of old-growth insects.

Spence et al. (1997) examined the abundance and diversity of carabids (ground beetles) and staphylinids (rove beetles) in boreal mixedwood forest of central Alberta. They examined beetles collected from stands of four age classes (8 years since harvest, approximately 40 yrs, approximately 60 yrs, and > 120 yrs). They found that diversity of the 44 species of carabids they collected was highest in the youngest stands (representing what they believed is colonization by open-habitat specialists), and that the carabid fauna of these stands was most dissimilar from the three older age classes. Carabid abundance (i.e., number of individuals trapped) varied significantly with age and was lowest in the young stands. Carabids were somewhat (but not significantly) less abundant in old-growth (> 120 yrs) than in the 40 and 60 year old classes. The patterns for the 86 species of staphylinid beetles they identified were somewhat different from the carabids. For the staphylinid beetles, there was a trend of greater diversity in old-growth forest for one of the two years for which data were collected. Stand age had a significant effect on staphylinids' abundance, with the youngest stands having fewest; however, unlike the patterns for ground beetles, the staphylinids did not appear to be less abundant in old-growth compared with the 40 and 60 year old stands.

To examine the dependence of beetles on old-growth, Spence et al. (1997) developed an index of old-growth dependence assuming rotation ages of 50 and 70 years. A species was designated as old-growth dependent if > 80% of the mean standardized catch of that species occurred within old-growth stands. Eight species of Staphylinidae and one species of Carabidae met the criterion for old-growth dependence, and all except one species did so under both short and long rotation periods. The authors conclude that there is no compelling evidence for old-growth specialists among carabids in the mixedwood forests they studied (but see Niemelä, Langor, and Spence 1993 who conclude otherwise for montane lodgepole pine forests only a few hundred kilometres to the west), but that clear evidence exists for old-growth dependence among staphylinid species at their study sites.

Niemelä, Langor, and Spence (1993) studied the habitat use by carabid beetles in the foothills of central Alberta by examining the communities in 10 stands ranging in age from 1 to 27 years since harvest and 10 other stands ranging in age from 80 to > 100 years. All stands (except for the four 1- and 2-year-old stands) had high (minimum 86%) conifer composition of the overstory. They found that more species were captured in the regenerating stands than in the mature stands (23 vs. 15 on average). In spite of the fact that the old forest communities were dominated by fewer species than were the younger forests, the pattern of similarity of beetle assemblages in the older stands was more complex than in regenerating stands. The authors attributed this to the more diverse habitat structure among old-growth forests than in regenerating sites. The authors provide a case for identifying three groups of species in response to cutting effects: a) forest generalists (2 species) which are not

dramatically affected; b) species of open habitat (27 species) which appeared to increase in abundance in regenerating stands; and c) mature forest species (10 species) which disappear or decrease in abundance following logging. Of the 10 mature forest species, populations of three were strongly depressed in the youngest stands, indicating high sensitivity to habitat change, and populations of the seven other species appeared to decrease more slowly, disappearing entirely in less than nine years.

The high number of species and the more even dominance structure in the regenerating sites produced higher values of the diversity index identified in Niemelä, Langor, and Spence (1993), as calculated by rarefaction and compared to mature stands. These authors cite studies from other countries and forest regions which showed similar reductions in dominance after logging. Lower species diversity in mature natural forests seems to be the general pattern for carabids regions (Russia: Arnoldi and Matveev 1973; southern Appalachia: Lenski 1982; eastern Europe: Szyszko 1983; Acadian Forest: Jennings, Houseweart, and Dunn 1986; and Scandinavia: Niemelä et al. 1992).

The same general pattern of declining species richness was found by Paquin and Coderre (1997) working in the boreal forest of northeastern Quebec; however, their study was oriented more towards successional stages moving from a young (47 yr old) deciduous forest to an old (230 yr old) coniferous forest, than on comparisons of old forests vs. recently harvested sites. In addition to coleopterans, Paquin and Coderre (1997) studied arthropods belonging to Diptera, Diplopoda (millipedes), Hemiptera (bugs), Hymenoptera, Pseudoscorpionida (pseudoscorpions), and Thysanoptera (thrips). Larval diptera and larval and adult coleoptera dominated the communities of the three forest stages studied. Not only did richness decline significantly with successional stage, but abundance of individuals did too. Although some species were found in all three forest types, others were more closely associated with a particular forest type.

Decomposers represented the greatest proportion of organisms in the deciduous forest, but with forest succession, there was a decrease in the importance of this trophic level, while the predator proportion increased. Consistent with the discussion above, as the forest stages proceeded through succession, they constituted a type of habitat less suitable to a larger number of arthropods. The authors attributed these changes to the tendency for pH to decrease with succession in this forest type, and changes in the nature of dead plant matter (e.g., the gradual elimination of deciduous debris and of bacteria and fungi associated with their decomposition). These results are similar to those found by Niemelä et al. (1992), who found a higher diversity of carabids in patches of aspen litter than in a surrounding carpet of needle litter in Finland. Paquin and Coderre (1997) suggest that the coniferous litter does not provide a comparable abundance of feeding substrate as does deciduous litter, explaining the decrease in decomposer species. Furthermore, predacious insects are not restricted to feeding substrates, and are more mobile than are decomposers, contributing to their higher relative abundance.

Although larval Diptera and larval and adult Coleoptera were the most abundant taxa, the relative importance of these groups varied accord to the forest successional stage. Diptera represented the greatest proportion of the deciduous environment community, but were less numerous in the mixed site and were very rare in the coniferous site. Coleoptera followed this tendency in a less pronounced manner.

Somewhat in contrast to the trends in richness found by Paquin and Coderre (1997), Work et al. (2004) found that species richness amongst carabids and spiders did not differ across forest types with a progression in the relative abundance of deciduous and softwood species in northwestern Alberta. However, Work et al. (2004) did not describe the habitats as a continuum of successional stages and did not provide the ages of the forest types included in the study. Their work is best characterized as an examination of arthropod communities in forests of different cover types irrespective of forest age. However, the authors investigated and commented on the importance of coarse woody debris (CWD) as habitat substrate, and note that forest age can be a determinant of the abundance of CWD.

In the “wet boreal” of western Newfoundland, Thompson, Larson, and Montevecchi (2003) identified 21 species of coleoptera that were found only in old-growth balsam fir forests, and 29 species of coleoptera found “only or predominantly in old-growth” (Table 2, page S35 of Thompson, Larson, and Montevecchi 2003).

Niemelä (1996) provided a review of the effects of boreal forest management on invertebrates in Fennoscandia and offered that old-growth specialists tend to disappear from clearcuts although, consistent with other studies, species richness may increase as forest generalists persist and numerous open habitat species appear. They also note that relative proportion of old-growth specialists differs among taxa. From Scandinavia, Punttila et al. (1991) and Niemelä et al. 1992 indicated that groups of species found only in the old-growth forest make up less than 10% of the forest fauna in different forest floor arthropod communities. Approximately 90% of carabids and spiders and 100% of ants collected along a successional gradient from cut-overs to old forest occurred in regenerating stands of age less than 20 years since harvesting. However, the authors note that such high proportions are likely not to occur in some other taxa. For example, they note that Økland (1994) considered that 30% of forest Mycetophilidae (fungus gnats) species to be old-growth specialists, likely related to the high diversity of fungi in old forests. Although the observations of Niemelä (1996) are insightful, they should be extrapolated to Canadian boreal forests with care; although forest types are similar, they are not identical, and although insect species communities are similar, they too are not identical.

Pettersson (1996) studied the effects of forestry on abundance and diversity of arboreal spiders in the boreal forest of northern Sweden. He found that lichen-rich forests had more than three times more spiders on branches than did lichen-poor forests. The author concludes the habitat structure (branch size and epiphytic lichen abundance) could explain the greater number of spiders in old lichen-rich spruce forests. As with the observations of Niemelä (1996), Pettersson’s (1996) interpretations should be extrapolated to Canadian boreal forests with care; although forest types are similar, they are not identical, and although insect species communities are similar, they too are not identical.

Bird and Chatarpaul (1986) examined the effects of whole-tree and conventional forest harvesting on soil arthropods in the Great Lakes-St. Lawrence boreal transition forests near Chalk River, Ontario. Although they found significant effects on abundance of Collembola (springtails) and Acari, and the species composition shifted dramatically in response to harvesting, their study did not examine the use of old-growth forests, nor the relative important of old forests compared to forests of other ages (except for recently cut forests).

4.5.3 *Dead and Decaying Wood*

Several studies have considered the habitat structures associated with arthropods’ affiliation with old forests. The feature most prominently discussed in the literature is coarse woody debris (CWD). Although CWD occurs in all successional stages, it is most prominently associated with old forests (and recently burned forests). The general habitat provided by dead wood is colonized by a complex of arthropods, reflecting individual species’ parsimonious use of habitats. Different species attack wood in various stages of decay and in association with different microhabitats (Danks and Fottit 1989; Niemelä 1996; Buddle 2001). For example, some beetles prefer to attach to the upper side, and

others the under side of fallen logs (Furniss et al. 1997). Many arthropods are associated with the hypae of fruiting bodies of fungi that help decompose wood. Pielou and Verma (1968) reported 258 species of arthropods associated with a birch bracket fungus in the boreal transition forest. Many of the species colonizing dead wood are saproxylic, thereby relying on dead wood, wood inhabiting fungi, or the presence of other saproxylic species (Speight 1989, as reported in Hammond 1997).

Hammond, Langor, and Spence (2004) examined the suite of saproxylic beetles using aspen stands in mixedwoods of central Alberta. Their study encompassed stands which they classified as mature (60-90 years) and old (> 100 years). They analyzed results based on the collection of 9,571 beetles from 257 taxa (most specimens were identifiable to species, but some only to genus). They found that species richness and abundance of beetles were similar across the stand ages they identified. However, many species were collected exclusively or in great majority from old stands and from snags of large diameter. They also found that species richness increased with the level of wood decay, whereas the total catch tended to be higher in early stage of decay. They concluded that variation in stage of wood decay is an important factor affecting beetle diversity. The authors note that “there is some question as to whether this dependence relates primarily to stand age or whether large woody material in younger regenerating stands would have the same benefit.” They also reported, however, that the preservation of old stands is essential to the conservation of beetles.

Hammond, Langor, and Spence (2004) attributed the increased species richness associated with level of CWD decay to increasing microhabitat diversity within the CWD. They noted that saproxylic organisms are responsible for the mechanical breakdown of woody material both directly, by tunneling and feeding in snags and logs, and indirectly through vectoring and facilitating the action of fungi and other microorganisms that humify wood. Other authors have also identified variability in microclimate as an important aspect of dead and decaying wood as it provides variability amongst the generally hospitable environment of CWD. Niemelä, Spence, and Spence. (1992) found that variation in soil moisture was an important determinant of carabid distribution across a number of forest and non-forest communities. Although their study design did not explicitly categorize forest habitats based on age, they commented on the importance of moist habitats in old forest in affecting beetle species richness. Paquin and Coderre (1997) implied that microhabitat features helped explained both quantitative and qualitative changes in arthropod communities associated with a transition through successional stages in the Abitibi region of Quebec.

Hammond, Langor, and Spence (2004) (whose data are a subset of those analyzed in Hammond (1997) found approximately 40 species of “non-saproxylic” beetle species that use CWD for overwintering, and are therefore dependent to CWD to some extent. Work et al. (2004) also comments on the importance of CWD to provide overwintering habitat for a ubiquitous species of carabid. Hammond (1997) identified the trophic role of the 254 species collected in CWD and found that 74 were fungivores, 111 were predators, 31 were scavengers, 24 were wood borers, and 14 had unknown trophic affiliations. They drew a positive relationship between the richness of species and trophic levels, and the habitats provided by CWD.

Buddle (2001) examined spider use of CWD and the surrounding forest floor in a boreal deciduous forest in north central Alberta. He collected over 10,000 spiders from 16 families and 100 species. Sixty-nine species were collected on wood (natural CWD and untreated telephone poles brought into the study to simulate elevated fallen wood), of which 15 were not collected on the forest floor. In contrast, 25 unique species were collected on the forest floor or adjacent to CWD. Although fewer spiders used wood than used the forest floor, most species found on the forest floor were also found directly on wood surfaces. Therefore, spider species found on CWD are largely a subset of the species that regularly use the forest floor. Although only one species was significantly more common on wood surfaces, 10 additional species were collected most frequently on wood and at least two others

could be considered as having adaptations for life on logs. The author concluded that CWD is an important habitat element for spiders.

Kaila, Martikainen, and Punttila (1997), working in southern and eastern Finland, also found strong links between the availability of CWD and the presence of saproxylic coleoptera. They noted the importance of maintaining CWD in clearcuts as a means of providing habitat for species with affinities for sun-exposed environments which may be adapted to natural disturbances (e.g., fire), but are not well suited for old, closed forests.

4.5.4 Do Unique Old-Growth Forest Insect Communities Exist?

The evidence for boreal forests supporting unique communities of old-growth affiliated insects is equivocal. Spence et al. (1997) concluded that their study found no compelling evidence for old-growth specialists among Carabidae in the mixedwood forests of Alberta; however, Niemelä, Langor, and Spence (1993) did find evidence of old-growth reliance among several carabids in the lodgepole pine forests to the west. Spence et al. (1997) did find evidence for old-growth dependence among Staphylinid species. Pettersson (1996) also found evidence of much higher use of old forests by spiders in Sweden. In Newfoundland, Thompson, Larson, and Montevecchi (2003) noted that for forests older than 80 years, some 40 species of beetles were unique to older forests.

We note that the evidence both for and against the distinction of old-growth forests in relation to insect habitat use is based on a lack of information. Most studies of non-outbreak insect habitat use have focused on carabid beetles, and even they are few, and, in Canada, have focused on the aspen-mixedwoods of Alberta. Clearly there is a striking need for much more work to be done in order to understand the importance of old forest habitats for insects.

There is no question that the habitat provided by CWD is important for many species of arthropods; however, this relation is between the habitat element (CWD) and arthropods, rather than to the age of the forest per se. Given that CWD abundance is a diagnostic element of old forests, a case can be made for the dependence of many arthropods on forest age.

4.6 Lichens

4.6.1 Lichens in the Boreal Forest

There is abundant literature on lichens and their morphology, ecology and population characteristics. From this literature it is clear that lichens are a common component of old-growth boreal forest stands. However, it is also true that lichens are present throughout the boreal forest in all types of stands and open areas where no trees grow. Very few studies have focused on lichen abundance or species composition in early successional or mature stands in the boreal forest and compared them to old-growth stands.

4.6.2 Lichens and Old-Growth

In one study in eastern Canada (Quebec), lichen abundance and species composition were recorded on 22 black spruce-feathermoss (*Pluerozium schreberi*) sites and compared to time since the last disturbance. The authors reported that old-growth stands had no more species than younger forests, but the abundance of epiphytic lichens increased with tree age. Species richness was highest when trembling aspen and jack pine were components of the black spruce stands. The within-site tree heterogeneity increased epiphytic species richness by offering a greater variety of substrates to species colonization. The differences observed in epiphytic communities along the mature to old-growth sequence were mainly related to changes in individual species abundance, rather than changes in species richness (Boudreault et al. 2002). No species was found exclusively in old-growth;

however, some species (e.g., *Mycoblastus sanguinarius*, *Bryoria trichodes* and *Usnea* spp.) were more abundant in old-growth than in earlier stages of succession.

Another study in Quebec (Rheault et al. 2003) examined the abundance of lichens as measured by distance from the edge of a disturbance into the interior of the stand. In that study, the abundance of *Usnea* spp. seemed to be a potentially useful tool for forest managers in determining the size of remnant stands that should be left in harvested forest landscapes to ensure sufficient interior habitat for the persistence of epiphytic lichens. The abundance of lichens at the edge was about half of lichen abundance 50 metres into the forest interior. In general, epiphytic lichens were more frequent in older natural forests than in younger managed serial stages. As in the study by (Boudreault et al. 2002), structural diversity (gaps, snags, veteran trees) and stable climatic conditions in older forests are thought to favour development of sensitive lichens. In Quebec, *Usnea* spp is most abundant in forests older than 160 years, and dispersal limitations is an important cause of low abundance of lichens in younger forests (Rheault et al. 2003).

Findings in an eastern boreal, old-growth balsam fir forest in the northeastern Gaspé Peninsula were somewhat different from the findings expressed in the two studies described above (Despouts et al. 2004). The total number of nonvascular plant species (lichens, mosses, liverworts, saprophytic fungi) found in old-growth stands was higher than in mature stands, although the difference was statistically significant only for Terricolous species, as measured by the Shannon-Weiner index. Approximately 22 species were found in old-growth forests but not in the mature stands. Three species of lichen were abundant in old-growth, and absent in the mature stands. Based on this data the authors concluded

“the very high species diversity observed in old-growth [balsam fir] forests appears to be largely attributable to the structural heterogeneity of the stands. This study demonstrated that old-growth forests harbor a large number of rare or uncommon species, most of which are not found in mature second growth. These are mainly specialist species requiring very specific environmental conditions. Small, recurrent disturbances and the accumulation of woody debris constitute key factors that lead to these forests having a distinct biological diversity.”

Proceviat (2003) measured arboreal lichen biomass in black spruce forest stands in the claybelt region of northeastern Ontario. She found that lichen abundance increased with the age of the stand and achieved the highest abundance in stands 150 years old. However, at 30 years post-harvest, lichen abundance was higher than at 70 years post-harvest. She concluded

“in contrast, sites at 30 years and 150 years post-harvest had more open canopies due to younger age and blow-down, respectively, and light penetration to the forest floor may have facilitated lower branch growth and lichen development.”

Although not conducted in the boreal, a study of dispersal limitations of lichens associated with old-growth Douglas fir forests indicated that specific substrate requirements, such as old bark surfaces or standing coarse woody debris, were an important factor in lichen abundance and diversity in forest stands. These characteristics develop slowly from young, even-aged forests to older forests in the absence of disturbances for long periods. However, species often associated with older forests were found in younger stands when the specific substrate was present. A conclusion from this study was “the single most important action promoting the propagation of old-growth associated lichens in managed forests will be the retention of propagule sources in and near all cutting units.”

5.0 CONCLUSIONS

Several species of vertebrate wildlife find superior habitat in both mature and old-growth boreal forest stands and these stands or forests serve as source populations for them. However, the research available has not identified any wildlife species that is totally dependent on old-growth forest stands in the boreal forest region. As forest stands age in this region they become better suited to the needs of some species of wildlife such as American marten and brown creeper. Older stands in the boreal contain dead and downed woody debris on the ground, have a complex physical structure in the arboreal component, and provide the resident wildlife protection from severe weather. Maximum fitness is achieved in these habitats.

Species resident in the boreal forest region all year, and which thrive in older forest stands include woodland caribou, American marten, red-backed vole, red-breasted nuthatch, three-toed woodpecker, black-backed woodpecker, and boreal chickadee. These species may also live in younger habitats under some circumstances, and may be “healthy” in the sense that they are not in danger of being classified as threatened or endangered. However, it seems clear that for some resident species, old-growth and mature boreal forest stands are vital to sustain their populations over long time periods and in the face of environmental variability.

Studies of bird habitat in the boreal forest region reveal that the relationship between birds and old-growth forest stands is complex and varies across the region. A further complication is that habitat affinities of species are not always consistent geographically and across forest types. In a few cases, a species such as yellow warbler, which is frequently associated with young sites and thickets in the eastern part of its range, has been identified as having an affinity for old-growth in the west. This type of variability is expected in the natural world with all the complication inherent in any forest ecosystem, although it does make generalization very difficult, if not impossible.

Birds that are more abundant in old-growth include bay-breasted warbler, brown creeper, black-throated green warbler, Cape May warbler, golden-crowned kinglet, pine siskin, boreal owl, gray-cheeked thrush and winter wren. A major unresolved problem, however, concerns what these species would do if no old-growth were available. The research indicates that these birds are more abundant in old-growth stands, and this may be an indicator of fitness for these species as it relates to old-growth. However, would they also regard mature forests as appropriate habitat? This is a crucial question and should be the subject of more research.

Another major problem in understanding the relationship between species and their survival is the fact that habitat is not the only variable that influences the fitness of a species of wildlife. Woodland caribou, for example, use old forest in the winter, but the use of that habitat may be important because it keeps them separate from the habitat used by moose and wolves, as well as providing food and protection from weather. The role of habitat, as one of several factors that influence populations, needs more clarification.

The Newfoundland marten provides an example of how a species that seems most fit in old-growth forests, can also be influenced by mortality from human agency. This animal is endangered, and old-growth forests are vital to its health; however, concern for the habitat is not enough to ensure the population return to a healthy status. The entire suite of factors in the animals' environment must be considered. If trapping mortality is excessive, superior quality habitat will not be sufficient to maintain the population.

The use of habitat classified as mature, as opposed to old-growth, is a confounding element in understanding the dependency of species on old-growth in the boreal. Mature stands of jack pine produce lichens and protect woodland caribou from extreme weather, but it is not clear if that habitat is as good for these mammals as the old-growth stage of the same forest type. For other mammals and many birds, very little research focuses on the difference between old-growth and mature forest habitat. So far, at least, a threshold between mature and old-growth stands that is meaningful to wildlife has not been identified, and studies have not been able to find the subtle differences that may be detectable by the animals under study. In order to advance our understanding of the value of old-growth to wildlife, more studies are needed that attempt to discriminate, from a wildlife perspective, between mature and old-growth stands in the boreal forest.

6.0 KNOWLEDGE GAPS AND RESEARCH NEEDS

While there is clear evidence that some species of wildlife use both mature and old-growth stands in the boreal forest region, more knowledge is needed that ascertains if some species distinguish between mature forests and old-growth forests. For some birds, it seems clear that they are more abundant in old-growth, but whether they are more fit in old-growth is not yet supported by research. Measures of fitness of wildlife species that use old-growth forests are vital. Are species that use old-growth for some or all of their habitat needs more fit than species that do not use those habitats? Direct measures of fitness are difficult and expensive, yet are the most reliable in understanding the relationships between wildlife and their habitat.

Measurements of the total biomass of arboreal and terrestrial lichens and vascular plants utilized by caribou are important, yet largely unavailable for the boreal forest region. More knowledge of this food source will be helpful in understanding the role of habitat as compared to the role of predation and human disturbance in caribou ecology.

There is a lack of data on the effects of snow conditions limiting caribou access to forage in the boreal ecosystems. Research examining how snow cover influences caribou food habitats and energetics would facilitate assessment of the impact of winter condition on caribou demography.

The idea that old-growth characteristics can be produced in stands younger than the old-growth stage needs more elucidation. Some evidence is available that some small mammals may find the habitat present in thinned stands of pine and spruce as appropriate for their needs. Limited research on other mammals and birds on this topic leaves question unanswered for most vertebrates in the boreal forest region.

Virtually no research is available on the relationship between amphibians and reptiles and old-growth forest stands in the boreal forest region. In fact, little research is available on the general ecology of amphibians and reptiles in this important forest region. Most knowledge about reptiles and amphibians comes from other forest regions, and while the general principles are probably similar, significant research is needed to assist our understanding of the ecology of these vertebrates.

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