



NATIONAL COUNCIL FOR AIR AND STREAM IMPROVEMENT

**WILDLIFE RESPONSES TO STAND-LEVEL
STRUCTURAL RETENTION PRACTICES
IN THE BOREAL FOREST**

**TECHNICAL BULLETIN NO. 964
AUGUST 2009**

by
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PRESIDENT'S NOTE

Retaining structural features post-harvest is common practice in boreal forest management because it is thought it helps minimize the negative effects of harvesting on terrestrial wildlife while at the same time shortening the times required for returning to old-growth characteristics. Some wildlife species are thought to be associated with late seral stage characteristics, and practices have therefore been developed to retain such structures as coarse woody debris, snags, and mature green trees on harvest units. However, it is unclear exactly what benefit for wildlife is derived by retaining these structures on a landscape, and what quantities and configurations of retained structures are best suited to meet the goal of conserving biodiversity.

The purpose of this report is to examine our current state of knowledge of the short- and long-term responses of vertebrate wildlife (birds, mammals, and amphibians) to various stand-level management practices that retain increased quantities of live trees, snags, understorey vegetation, and coarse woody debris post-harvest. The report focuses primarily on practices in the boreal forests of Canada, with some references to Fennoscandia and other forest systems.

The authors suggest that while superficially, there appears to be an abundance of literature on the topic of retained structures, there are significant limitations within the literature, as many studies failed to account for stand-level structure and to consider the appropriate spatial and/or temporal scale. There was also significant variability in the quality of published studies, particularly those that relate to mammals. The majority of studies focused on the relationship between green tree retention and birds, particularly in Canada's western boreal. The mammal and herptile (amphibians and reptiles) literature was more diverse, but often less directly related to the topic.

While the authors suggest that there is significant evidence that green tree retention is effective for benefiting wildlife and hastening the convergence of harvested areas with later seral stages, there is insufficient research into the effects of other retention practices on wildlife. The report outlines various research gaps, including a lack of understanding of the effects of increasing levels of late seral stage characteristics in harvested stands and the identification of thresholds (if they exist), as well as a lack of understanding surrounding the relative value of clumped versus dispersed green tree retention.

This report is an important first step in reviewing the relationships between retaining structures and biodiversity, and will help identify areas which require new research efforts.



Ronald A. Yeske

August 2009

MOT DU PRÉSIDENT

La conservation des aspects structuraux suite à des coupes forestières est une pratique commune de la gestion des forêts boréales puisque elle est perçue comme pouvant minimiser les effets négatifs des coupes sur la faune tout en diminuant le temps requis pour que des caractéristiques de forêt mature réapparaissent. On pense que certaines espèces sauvages sont associées aux caractéristiques des vieilles forêts et en conséquence des pratiques ont été développées afin de maintenir ces caractéristiques dans les secteurs de coupes, comme : les débris ligneux grossiers, les chicots et les arbres matures. Par contre, le bénéfice découlant du maintien de telles caractéristiques d'aménagement n'est pas clairement établi. Aussi, les quantités et configurations des structures les mieux adaptées pour rencontrer les objectifs de conservation de la biodiversité ne sont pas clairement déterminées.

L'objectif de ce rapport est d'examiner l'état actuel des connaissances des effets à court et long termes sur la faune vertébrée (oiseaux, mammifères et amphibiens) occasionnés par les différentes pratiques de gestion de peuplements arboricoles qui conservent des quantités supplémentaires d'arbres vivants, chicots, végétation de sous-bois et de débris ligneux grossiers, suite à une coupe. Ce rapport se concentre principalement sur les pratiques utilisées dans les forêts boréales du Canada, mais inclut quelques références à d'autres types de systèmes forestiers comme la Fennoscandie.

Les auteurs suggèrent que bien que superficiellement il semble y avoir une abondance de littérature sur le sujet de la rétention de structures et qu'il existe des limitations significatives dans la littérature car plusieurs études ne tiennent pas en ligne de compte la rétention de structures au niveau du peuplement tout en négligeant de considérer les échelles spatiales et temporelles appropriées. Il y avait aussi une variabilité significative de la qualité des études publiées, particulièrement en ce qui a trait aux études portant sur des mammifères. La majorité des études se concentraient sur la relation entre la rétention d'arbres vivants et les populations d'oiseaux, particulièrement dans les forêts boréales de l'ouest canadien. La littérature concernant les mammifères et les herptiles (amphibiens et reptiles) était plus diverse, mais fréquemment éloignée du sujet spécifique de ce rapport.

Selon les auteurs, il existe suffisamment d'évidences démontrant que la rétention d'arbres vivants est avantageuse pour la faune et permet d'accélérer la convergence entre les aires récoltées et les zones de forêts matures mais il n'existe pas suffisamment de recherches sur les effets des autres pratiques de rétention sur la faune. Ce rapport décrit les lacunes dans la recherche, incluant le manque de compréhension de l'effet de l'augmentation de la présence de caractéristiques de forêts matures dans les zones de coupes et l'identification de seuils (s'ils existent). De plus, le manque de compréhension au sujet de la valeur relative de la rétention d'arbres vivants selon qu'ils soient groupés ou dispersés est également discutée dans ce rapport.

Ce rapport une première étape importante pour la revue de la corrélation entre les structures de rétention et la biodiversité, tout en permettant d'identifier les sujets requérant de nouvelles recherches.



Ronald A. Yeske

Août 2009

WILDLIFE RESPONSES TO STAND-LEVEL STRUCTURAL RETENTION PRACTICES IN THE BOREAL FOREST

TECHNICAL BULLETIN NO. 964
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ABSTRACT

Old-growth attributes are important in the boreal forest and elsewhere for maintaining various forest values, including several wildlife species. In recognition of the fact that the relative amount of older forest stands may be lost over time due to wildfire, forest harvesting, insect infestation, windthrow and other factors, growing attention is being paid to the potential for stand-level structural retention practices to mitigate impacts of forestry on wildlife. This literature review examines our current state of knowledge of the short- and long-term responses of vertebrate wildlife (birds, mammals, and amphibians) to various stand-level management practices that manipulate the quantity and quality of live trees, snags, understorey vegetation, and coarse woody debris (CWD) available to wildlife post-harvest. While superficially, there appeared to be a broad body of research on which to base such a review, on closer examination, relevant material was limited by a failure of many studies to explicitly account for stand-level structure, or to do so at an appropriate scale, and by the highly variable quality of the research, particularly with regard to mammal responses. Both green tree retention (GTR) and well developed understorey practices appear to enhance both the short- and long-term habitat value of stands for the broadest array of wildlife groups. CWD retention was found to have a significant influence on marten and their prey, possibly in concert with overstorey and understorey retention. No patterns in wildlife responses to snag retention were apparent. There was insufficient information to draw conclusions on optimal quantities or spatial configurations for any of the structural variables reviewed. Key information gaps identified in this review include our lack of knowledge of stand-level thresholds of wildlife response to retained structures, and the lack of comparative studies that have examined responses to dispersed live tree retention. In the absence of this information, forest managers are encouraged to employ a variable range of stand-level structural retention practices in a mix of configurations.

KEYWORDS

biodiversity, coarse woody debris, green tree retention, landscape management, old-growth forests, snags, structural retention, sustainable forestry

RELATED NCASI PUBLICATIONS

Technical Bulletin No. 959. (December 2008). *Fragmentation in the boreal forest and possible effects on terrestrial wildlife.*

Technical Bulletin No. 958. (December 2008). *Biodiversity response to stand structural features in southern pine forests: A literature review.*

Technical Bulletin No. 954. (September 2008). *The biological basis for forest practices rules for retaining coarse woody debris in managed forests of the Pacific Northwest.*

Technical Bulletin No. 924. (October 2006). *Similarities and differences between harvesting- and wildfire-induced disturbances in fire-mediated Canadian landscapes.*

Technical Bulletin No. 909. (December 2005). *Defining old-growth in Canada and identifying wildlife habitat in old-growth boreal forest stands.*

Technical Bulletin No. 892. (December 2004). *Bird-forestry relationships in Canada: Literature review and synthesis of management recommendations.*

Technical Bulletin No. 877 (May 2004). *Dynamics of coarse woody debris in North American forests: A literature review.*

Technical Bulletin No. 728 (January 1996). *Influence of landscape pattern, forest type, and forest structure on use of habitat by marten in Maine.*

Technical Bulletin No. 822 (February 2001). *Accommodating birds in managed forests of North America: A review of bird-forestry relationships.*

Technical Bulletin No. 728 (January 1996). *Influence of landscape pattern, forest type, and forest structure on use of habitat by marten in Maine.*

EFFETS SUR LA FAUNE DES PRATIQUES DE RÉTENTION DES STRUCTURES À L'ÉCHELLE DU PEUPEMENT DANS LA FORÊT BORÉALE

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RÉSUMÉ

Les attributs des forêts anciennes sont importants pour les forêts boréales et ailleurs afin de maintenir les valeurs intrinsèques des forêts parmi lesquels on retrouve plusieurs espèces fauniques. Étant donné qu'après un certain nombre d'années, la quantité relative de forêts anciennes peut diminuer suite à des feux de forêts, des coupes forestières, des infestations d'insectes, des bourrasques de vents et d'autres facteurs, on porte plus d'attention au potentiel des pratiques de rétention à l'échelle du peuplement afin d'atténuer les impacts de la foresterie sur la faune. Cette revue de littérature examine notre niveau de connaissance actuel des effets à court et long termes sur la faune vertébrée (oiseaux, mammifères et amphibiens) occasionnées par les différentes pratiques de gestion à l'échelle des peuplements. Dans ces pratiques, on ajuste la quantité et la qualité d'arbres vivants, chicots, végétation de sous-bois et de débris ligneux grossiers (DLG) disponibles pour la faune, suite à une coupe. Superficiellement, il semble y avoir un vaste éventail de recherches pour effectuer cette revue de littérature. Toutefois, après un examen plus attentif, l'information réellement pertinente s'avère limitée puisque la majorité des études n'incluent pas l'aspect des structures à l'échelle du peuplement (ou ne l'incluaient pas à niveau approprié) et puisque la qualité des recherches était très variable, particulièrement en ce qui a trait aux effets sur les mammifères. Il semble que la rétention d'arbres vivants (RAV) et les pratiques de gestion des sous-bois bien développées aient toutes deux un effet bénéfique sur la valeur habitable à court et long terme des peuplements pour le plus vaste éventail de groupes fauniques. Il a été déterminé que la rétention de DLG avait une influence significative sur les martes et leurs proies et ce probablement de concert avec des pratiques de rétention des sous-bois et des couverts. Aucune tendance apparente de réponses fauniques n'a été établie en lien avec les pratiques de rétention de chicots. Il n'existait pas suffisamment d'informations pour tirer des conclusions quant aux quantités optimales ou quant aux configurations spatiales des variables structurelles passées en revue. Parmi les principales lacunes identifiées dans cette revue, les auteurs notent le manque de connaissance des seuils à l'échelle du peuplement en lien avec la réponse faunique aux structures de rétention et le manque d'études comparatives ayant examinées les effets de la rétention d'arbres vivants dispersés. Puisque cette information n'est pas disponible, on encourage les gestionnaires forestiers à utiliser un éventail variable de pratiques de rétention des structures dans une variété de configurations.

MOTS CLÉS

biodiversité, débris ligneux grossiers, rétention d'arbres vivants, gestion du paysage, forêts anciennes, chicots, rétention des structures, gestion durable des forêts

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique n° 959. (décembre 2008). *Fragmentation in the boreal forest and possible effects on terrestrial wildlife.*

Bulletin technique n° 958. (décembre 2008). *Biodiversity response to stand structural features in southern pine forests: A literature review.*

Bulletin technique n° 954. (septembre 2008). *The biological basis for forest practices rules for retaining coarse woody debris in managed forests of the Pacific Northwest.*

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Bulletin technique n° 892. (décembre 2004). *Bird-forestry relationships in Canada: Literature review and synthesis of management recommendations.*

Bulletin technique n° 877 (mai 2004). *Dynamics of coarse woody debris in North American forests: A literature review.*

Bulletin technique n° 728 (janvier 1996). *Influence of landscape pattern, forest type, and forest structure on use of habitat by marten in Maine.*

Bulletin technique n° 822 (février 2001). *Accommodating birds in managed forests of North America: A review of bird-forestry relationships.*

Bulletin technique n° 728 (janvier 1996). *Influence of landscape pattern, forest type, and forest structure on use of habitat by marten in Maine.*

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WILDLIFE RESPONSES TO STAND-LEVEL STRUCTURAL RETENTION PRACTICES IN THE BOREAL FOREST

1.0 INTRODUCTION

Increasingly, forest managers across the boreal forest are being required by government regulations, certification programs, and/or marketplace demands to develop, implement and monitor cost-effective strategies and practices that retain structural complexity in harvested areas to meet biodiversity conservation objectives, including the provision of wildlife habitat. Young forest stands regenerating after natural disturbance generally have higher levels of structural complexity than clearcut areas in the form of biological legacies from the previous stand such as large live trees, standing snags and coarse woody debris (CWD). Alternative silvicultural systems to clearcutting aim to bridge the gap between old-growth and second-growth forests by providing some degree of structural heterogeneity as a means to maintain ecological and biological processes. Silvicultural practices that maintain or recruit stand-level structure into the regenerating stand can include clearcut with reserve or protection of regeneration, types of variable retention (e.g., dispersed single tree, patch retention), various forms of partial cutting (e.g., group selection, shelterwood, seed-tree), and single tree or small group removal systems. Stand tending activities such as pre-commercial and commercial thinning can maintain structure in regenerating second growth stands.

The prevailing forest management paradigm guiding stand-level structural retention is natural disturbance pattern emulation (NDPE). Guidelines developed to aid implementation of stand-level structural retention practices (e.g., OMNR 2001) have largely been based on comparisons of the patterns and variability of residual structure in naturally disturbed and managed stands, rather than on a broad body of empirical evidence of wildlife response. Hence, the effectiveness of alternative silvicultural systems in providing short-term (i.e., < 10 years) and long-term wildlife habitat remains uncertain.

Evaluating the biological effectiveness of site-level structural retention requires monitoring the responses of indicator/focal species or species groups to anticipated changes in macro- and microhabitat characteristics through a combination of retrospective and manipulative experiments. There has been a growing body of research over the last decade into the response of wildlife to stand-level structural retention in the boreal forest, including useful reviews for various wildlife groups (e.g., Song 2002 – woodpeckers, songbirds and mammals; Fisher and Wilkinson 2005 – mammals; Schieck and Song 2006 – grouse, woodpeckers and songbirds), that could be synthesised to better inform forest managers of the utility of various management techniques in achieving wildlife conservation objectives and to guide forest researchers in designing effectiveness monitoring programs. The purpose of this review was to critically evaluate the available peer-reviewed (e.g., published papers and academic theses) and grey (e.g., unpublished government and consultant reports) scientific literature on the short- and long-term responses of vertebrate wildlife (birds, mammals, and amphibians) to retained structures in the boreal forest. Further, the report was intended to produce a resource that describes the scope of available information, critically reviews current knowledge, identifies key information gaps for further research, and discusses the utility of this information for forest managers aiming to incorporate wildlife conservation objectives into their operations. The review focuses on studies from Canadian boreal forest, but draws on relevant literature from Fennoscandia and Alaska. Literature related to disturbance-prone forest regions other than the Boreal Forest has also been considered where it directly addresses wildlife response to stand-level structural retention or documents novel approaches to structural retention practices that could be applied to boreal forests.

Specific objectives of the review are to

- summarise the scope of available scientific and other literature, with specific reference to geographic focus, forest types, wildlife species or group, wildlife response variables, structural attributes, retention practices, and spatial and temporal scale studied;
- synthesize and critically review current knowledge of short- and long-term responses of vertebrate wildlife to stand-level structural retention;
- identify key data gaps in current knowledge; and
- discuss the management implications of the current state of knowledge of wildlife responses for stand-level structural retention practices.

2.0 METHODS

A search of the *Forest Science Database* (CAB International) and *Agricola* (USDA National Agricultural Library) using the primary and secondary search terms detailed in Appendix A resulted in a report of 439 references. A preliminary review of this report to remove publications unrelated to the topic of interest (e.g., literature relating to vegetative response to logging or pest outbreaks) resulted in an initial list of 134 references. Further review of this subset of references led to a reduced list of 55 studies of direct relevance to the review after exclusion of material related to invertebrate response to forest structure or material that did not explicitly address the influence of forest structure, or did not do so at the appropriate scale. Additional material relating to the review topic was sourced from Domtar (Ontario and Quebec), Louisiana Pacific (Manitoba), NCASI, and a search of the Internet for grey literature, using Google and Google Scholar.

Through this process, 68 articles or reports from the scientific literature were identified for further examination in the review, as well as five reports detailing provincial government or forest company guidelines for stand-level structural retention practices for wildlife. The literature was categorised as either of core, peripheral, or background relevance to the review topic. Core studies were those that directly examined wildlife responses to retention of forest structure at a stand-level during harvest in boreal forests. Peripheral studies were those that directly addressed the topic in a non-boreal setting, or only indirectly examined the responses of wildlife to structural retention practices. Core studies are highlighted in bold text in the references section of this report.

The review is limited to vertebrate wildlife (i.e., birds, mammals, and amphibians); the extensive body of literature examining invertebrate responses to structural retention, particularly from Fennoscandia, has not been included. The review also focuses on literature from the last 10 years, as this largely coincides with the increased research and management interest in alternative harvesting methods to clearcutting, although older literature has been included where recent studies were limited. Similarly, studies from non-boreal regions have been included where few studies were available for boreal forests or where boreal studies were restricted to one forest type or region. Responses of wildlife to riparian buffer retention are touched on in the review, but the extensive body of literature on this topic precluded a more detailed examination; this topic may warrant its own review. As such, the issue of upland versus riparian retention strategies is not addressed.

3.0 RESULTS AND DISCUSSION

3.1 Scope of Available Literature

3.1.1 *Definition of Terms*

For clarity, it is useful to define terms that are used throughout this report.

“Clearcut harvesting” refers to harvesting of areas in which all merchantable timber is removed. Clearcut harvesting is most often used in pine and hardwood forest where full sunlight is desired to maximize regrowth (USDA Forest Service 1989). It is in this context that structural retention practices are used to enhance the value of harvested areas for wildlife. Depending on the forest management paradigm in place (e.g., Natural Disturbance Pattern Emulation, OMNR 2001), the forest and ecosystem types (e.g., boreal, Great Lakes/Saint Lawrence) or the forest management objectives, clearcut harvesting may be the dominant harvesting method, or it may only make up a small portion of the harvesting methods on the landscape.

“Green-tree retention” (GTR) is the practice of leaving behind live merchantable trees that may serve a variety of purposes in the development of the stand after harvest. As live trees decay they may become snags which may be useful for wildlife as nesting, denning or foraging structures, they may act as “legacy trees” providing sources of seeds and seedlings in the regenerating stand, or they may decay and fall over to become a source of coarse woody debris. GTR may be done as single trees, small groups, or larger clumps, or “retention patches”.

“Partial harvesting” or “selective harvesting” refers to an uneven-aged system of harvesting in which a subset of the merchantable timber in a given area is harvested. The relative amount of timber removed and the species of trees selected will depend on the management objectives and the economic needs of the harvesters.

“Pre-commercial thinning (PCT)” is a silvicultural approach used to reduce the density of saplings, as high sapling densities can reduce timber yields (Marzluff et al. 2002). PCT may also be used to increase tree growth rates (Daniel, Helms, and Baker 1979; Homyack et al 2005b), increase the frequency of favoured tree species (Carey and Johnson 1995), decrease fire risk, and decrease time to develop old-growth characteristics (DeBell et al 1997).

“Understory” may be variously defined, but generally refers to the layer formed by young trees and shrubs that are growing beneath the tall mature trees in a stand (USDA Forest Service 1989). For the purposes of quantifying the amount and density of the understory, some authors specify a height at which an understory plant becomes part of the overstory. “Overstory” refers to the canopy layer formed by the mature trees in a stand (USDA Forest Service 1989).

“Old-growth” is a particularly difficult term to define, as the characteristics attributed to later seral stages will differ by forest type, climate, site conditions and disturbance regime (for a review see NCASI 2005). There are primarily two ways to qualify a forest stand as “old-growth”. The first is based on the age of a forest stand, with “old” being determined relative to the age of forest stands on the surrounding landscape. The second method is process-based, whereby a stand is determined to represent “old-growth” when physical characteristics or ecological processes within the stand reach a certain point (NCASI 2005).

“Forest structure” refers to the woody plant and leaf matter within the 3 spatial dimensions of the stand. On the forest floor, structure is made up of fine and coarse woody debris. Moving vertically, forest structure includes the understory, the number and density of the forest canopy layers, and the number and density of snags (standing dead wood). Complex forest structure is generally associated with later seral stages, and in some cases increases in biodiversity. There is evidence that vertebrates

select habitat based upon structural “clues” to the resources that confer survival value, which suggests that habitat selection may be heritable, that is, it has a genetic basis (e.g., Hilden 1965; Wecker 1964).

3.1.2 *Types of Literature*

Of the 68 scientific articles identified as having most relevance to the review, 62 were research papers, four were review articles, and two were research syntheses of multiple studies. Most of the articles were from peer-reviewed scientific journals (Table 3.1), with additional material from a book chapter, published reports, post-graduate theses, and an unpublished report.

Table 3.1 Publication Details of Scientific Articles That Were Used in the Review

Publication type	Peer Review		Total
	No	Yes	
Book chapter		1	1
Journal		57	57
Published report	4	1	5
Thesis		4	4
Unpublished report	1		1
Total	5	63	68

A steady supply of articles was published each year during 1998-2008 (Table 3.2) including several review and synthesis articles that have been published since 2002.

Table 3.2 Years of Publication of Scientific Articles Used in the Review

Year	Reference Type			Total
	Research	Review	Synthesis	
1998	5			5
1999	4			4
2000	5			5
2001	5			5
2002	7		1	8
2003	5			5
2004	5			5
2005	9	1	1	11
2006	5	1		6
2007	7	1		8
2008	1			1
Total	62	4	2	68

3.1.3 Forest Type

Most papers have arisen from studies that have been conducted in coniferous and/or mixedwood boreal forest (Figure 3.1). Relatively fewer studies have been conducted in boreal deciduous forests. The majority of articles are from boreal forests. However, additional material came from non-boreal regions such as from sub-boreal forests of British Columbia, Acadian forests from eastern North America in transitional forests between temperate deciduous forests and boreal mixedwood forests, and temperate coniferous forests in of the U.S. Pacific Northwest.

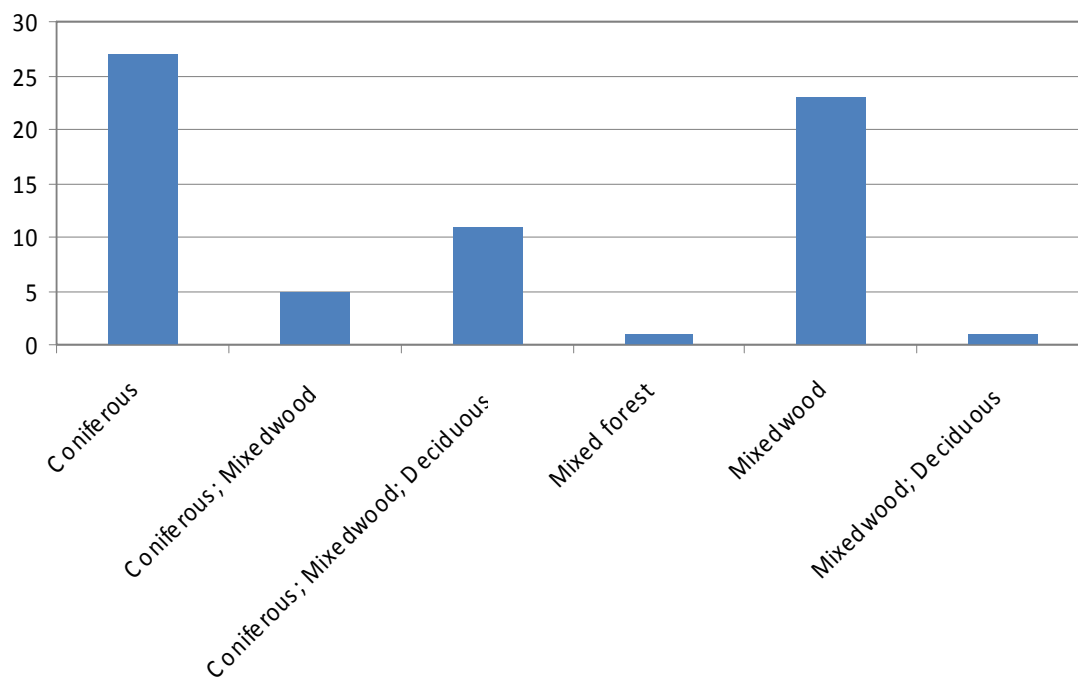


Figure 3.1 Broad Boreal Forest Types Studied in Scientific Articles Used in the Review

3.1.4 *Geographic Focus*

Although this review is focused on studies from Canadian boreal forest (Figure 3.2), the literature search was conducted without a geographic bias toward particular regions of the boreal (Appendix A). Within Canada, there are distinct biases toward western and central regions in the literature, with the majority of studies from boreal forest in Alberta and Quebec (Figure 3.3). There are obvious gaps in the literature from parts of western, eastern and northern Canada.

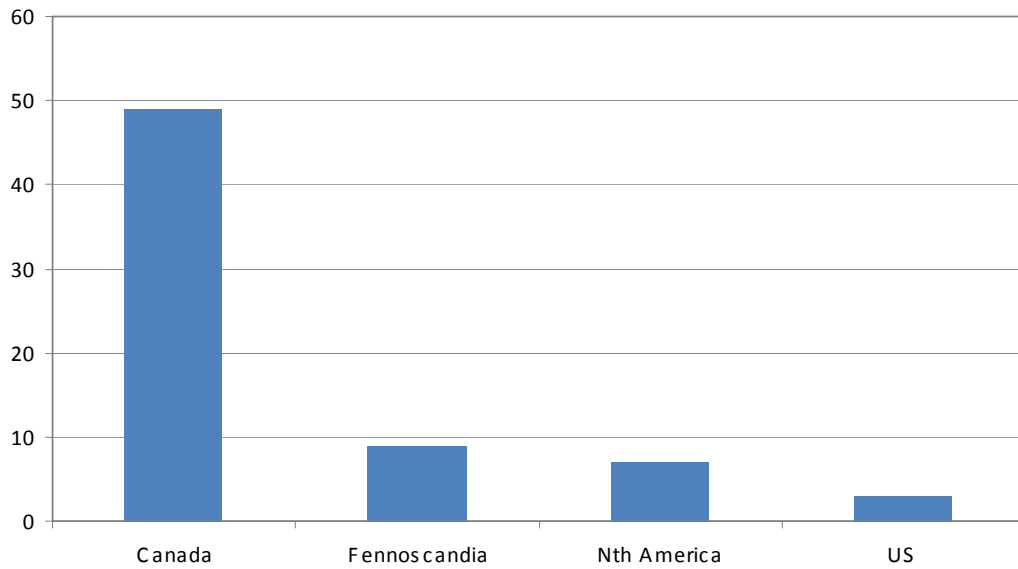


Figure 3.2 Global Distribution of Scientific Articles from the Boreal Forest Used in the Review

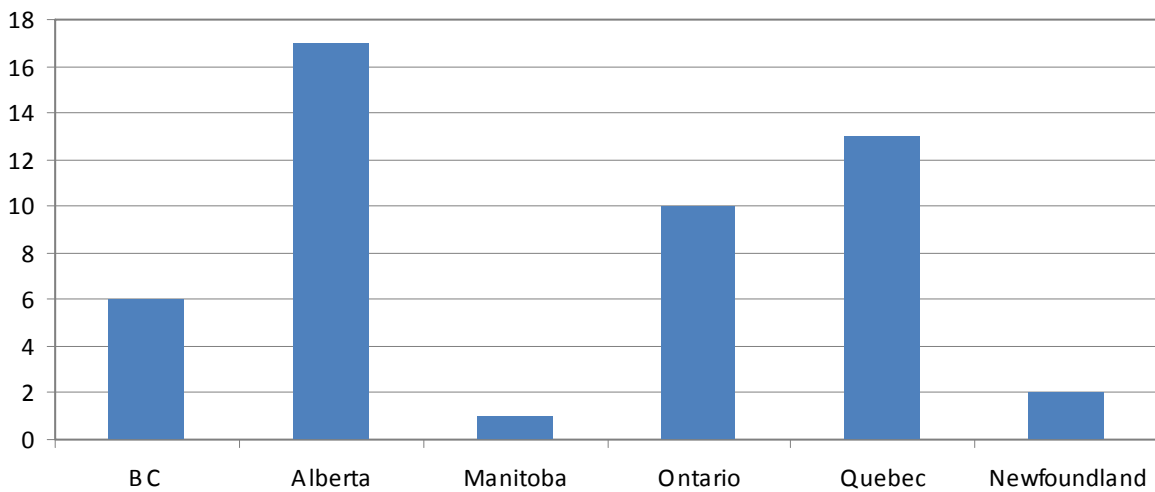


Figure 3.3 Geographic Distribution of Scientific Articles from the Canadian Boreal and Non-Boreal Forest That Were Used in the Review

3.1.5 Structural Retention Types

Most studies have focused on three broad types of stand-level structural retention: dispersed, patch or group, and green-tree (a generic name for combinations of dispersed and patch/group retention) retention (Figure 3.4). Some studies examined multiple retention types.

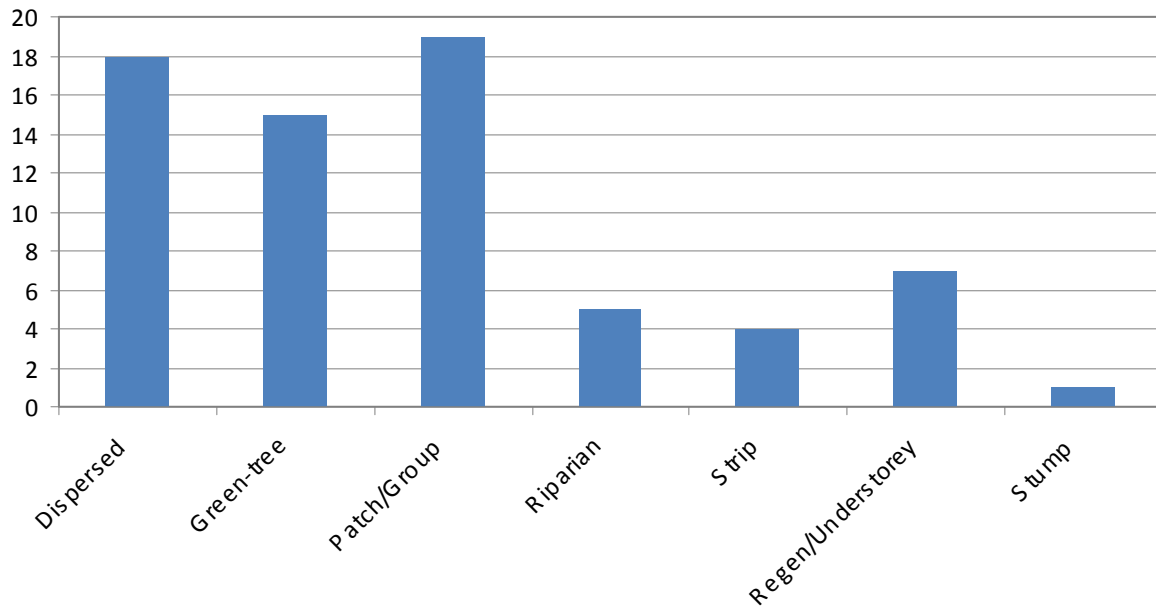


Figure 3.4 Types of Stand-Level Structural Retention Studied in Relation to Wildlife Responses

3.1.6 Harvest Methods

Many studies involved comparisons between multiple harvest methods, and generally included clearcutting as one of the treatments (Fig. 3.5). In addition, variable retention, partial or selective logging, clearcut with retention and commercial thinning were the most studied retention harvest methods. In general, there was a lack of consistency in the terminology used for various harvesting methods, and some interpretation was required to allocate studies to one of these categories.

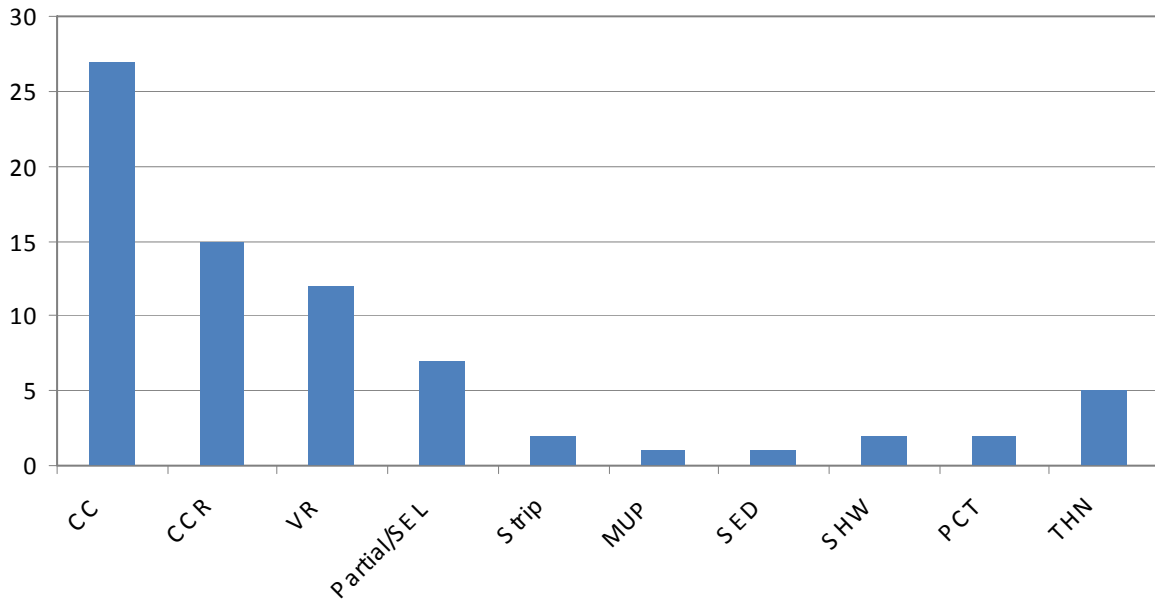


Figure 3.5 Harvest Methods Studied in Relation to Wildlife Responses to Stand-Level Structural Retention [CC = Clearcut; CCR = Clearcut with retention; VR = Variable retention; SEL = Selective logging; Partial/SEL = Partial or Selective logging; Strip = Strip logging; MUP = Mixedwood understorey protection; SED = Seed-tree retention; SHW = Shelterwood retention; PCT = Pre-commercial thinning; THN = Commercial thinning]

3.1.7 Wildlife Responses

Studies of wildlife response to stand-level structural retention are dominated by birds and mammals, particularly boreal songbird communities, small mammals, and in terms of focal species/groups, woodpeckers, grouse and ungulates (Figure 3.6). A number of studies examined the responses of multiple wildlife groups. Herptiles and carnivores have received very little attention.

The majority of studies have focused on patterns of species occurrence, abundance, movement and habitat use in response to stand-level structural retention practices (Figure 3.7). Five studies examined habitat response variables rather than the biological responses of the associated taxa. Very few studies have examined reproductive success.

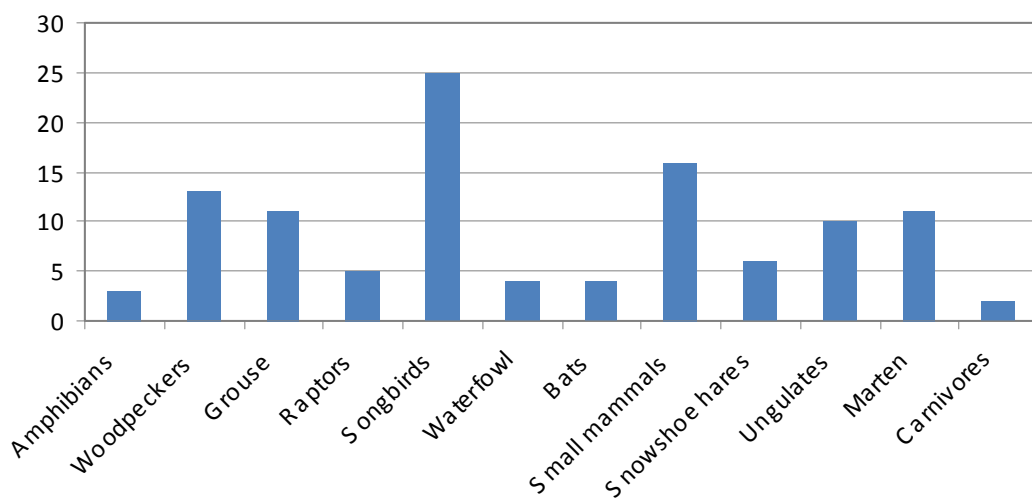


Figure 3.6 Wildlife Groups Studied for Their Response to Stand-Level Structural Retention Harvest Practices

3.1.8 *Spatial and Temporal Scale*

Not surprisingly, two-thirds of the papers reviewed focused at the level of the forest stand. However, 23 papers examined the relative influence of stand-level versus landscape-level variables to wildlife response to forest structure in harvested landscapes.

Studies of short-term effects of harvesting on wildlife dominate the literature, with 63% of articles examining the response of wildlife in the first ten years after harvesting. The remaining studies used space as a surrogate for time by retrospectively examining chronosequences of stands through succession. No study has been found that monitored treatment effects for 10 years or more post-harvest.

3.1.9 *Structural Attributes*

The most common retained structural attributes examined in relation to wildlife response were live trees, understory vegetation, coarse woody debris (i.e., logs), and snags (Figure 3.1-8). Most studies considered multiple stand-level attributes in assessing patterns of wildlife response.

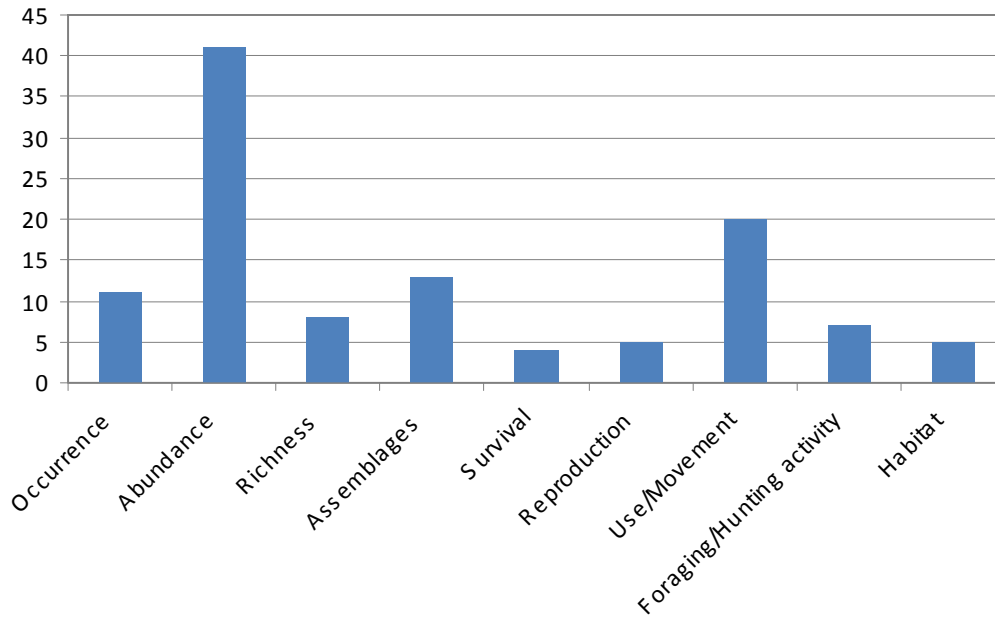


Figure 3.7 Wildlife Response Variables Examined in Scientific Articles That Were Used in the Review

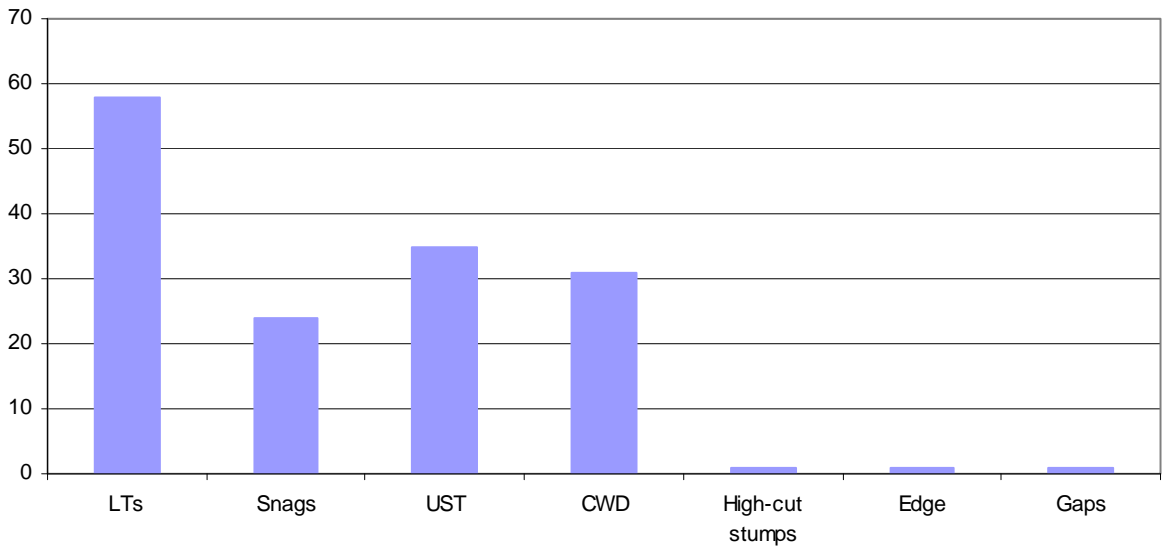


Figure 3.8 Structural Attributes Examined in Scientific Articles That Were Used in the Review (LTs = Live trees; UST = Understorey; CWD = Coarse woody debris)

3.1.10 Study Designs

A range of study types were represented in the literature, but most studies focused on the post-logging period, with no pre-logging data (Table 3.3). Nine studies examined a retrospective chronosequence of stands following harvesting or natural disturbance or both. Nine pre-/post- studies did not incorporate a control post-harvest.

Table 3.3 Types of Studies Represented in the Literature

Study Type	Total
Before-After-Control-Impact (BACI)	1
Chronosequence	9
Meta-analysis	2
Modeling	2
Post-	43
Pre-, Post-	9
Total	66

The majority of studies simply compared harvested areas with unharvested, usually mature or old-growth, control stands (Table 3.4).

Table 3.4 General Study Designs Represented in the Literature
(ND = Natural disturbance)

Study Design	Total
Cut	3
Cut succession	2
Cut succession; ND succession	1
Cut; ND	1
Cut; Uncut	48
Cut; Uncut; ND	4
Descriptive	1
Partial block design (EMEND)	5
Predictive	2
Validation	1
Grand Total	68

3.1.11 Summary of the Scope of the Literature

In summary, this preliminary review of the scope of available literature revealed some pronounced information gaps on wildlife responses to stand-level structural practices in boreal forests. With the exception of Alberta, there was a lack of studies from western Canada, few from eastern Canada and none from northern Canada. Few studies have examined responses of herptiles, raptors or carnivorous mammals to structural retention practices. Reproductive responses of all wildlife groups have rarely been examined. No long-term (i.e., > 10 years) monitoring studies were found.

3.2 Wildlife Responses to Stand-Level Structural Retention Practices

This section forms the core of the review. While most reviews are primarily organised by taxonomic group (i.e., birds, small mammals, arboreal mammals, furbearers, etc.), this review is primarily organised by the structural attributes that can be manipulated by harvesting, followed by a consideration of the short- and long-term responses of each taxonomic group (largely birds and mammals).

In a recent review of the effects of green-tree retention (GTR) on forest biodiversity, Rosenvald and Lohmus (2008) defined three main objectives for GTR: (1) life-boating species and processes over the regeneration phase; (2) enriching regenerated forest stands with structural features; and (3) enhancing landscape connectivity. Life-boating suggests continuous occupancy of a stand, structural enrichment means the creation of suitable conditions for occupancy at some point after the re-establishment of the stand, and landscape connectivity refers to the successful movement of individuals through GTR areas. While developed in the specific context of live tree retention, these objectives can be reasonably applied to retention at harvest of all stand-level structures, including snags, CWD and understorey vegetation. In this review, the concept of life-boating has been modified to distinguish short-term life-boating (i.e., continued occupancy from pre-disturbance forest through the initiation and early-seral stages of forest regeneration) from long-term life-boating (i.e., the continuous occupancy of a stand). Similar to Rosenvald and Lohmus (2008), this review has found that most studies have been of short duration, and hence, have focused on the short-term life-boating effects of structural retention on wildlife. For bird communities however, there have been some useful retrospective chronosequence studies that have examined long-term life-boating effects as well as patterns in wildlife response to structural enrichment. Very few studies examining landscape connectivity as a consequence of stand-level structural retention could be found.

3.2.1 Live Trees

There is a suite of harvesting practices and/or silvicultural systems that can result in retention of live trees, commonly referred to as green-tree retention (GTR). These practices range from single-tree selection, through partial harvesting and shelterwood systems, to clearcut areas. Wedeles and Van Damme (1995) make a point of distinguishing between “commercial” clearcut areas, where non-commercial trees are left standing after harvest, often resulting in residual green-trees after harvest, and “silvicultural” clearcut areas where every tree is felled to free up all the growing space for new trees. In this review, the term “clearcut with retention” is used instead of “commercial clearcut” and “clearcut” refers to a silvicultural clearcut. Any harvesting practice that results in retention of live trees is considered, even if the intent is not to retain the residuals for the full rotation (e.g., two-pass harvesting systems such as shelterwood logging). The only criterion is that the residuals be present at the time wildlife responses are measured.

3.2.1.1 *Birds*

Boreal forests are known for their rich bird faunas, with approximately 222 breeding landbird species recorded (Blancher 2003). The composition of bird communities is strongly linked to the structural attributes of their habitat (Hannon 2005), so it is not surprising that bird community response to green-tree retention (GTR) has received considerable attention in the literature. In addition to providing habitat for resident birds, boreal forests are particularly important as breeding grounds for species from all over the western hemisphere. So the responses of bird communities to boreal forest management practices have implications for bird habitats elsewhere.

Due to their association with fire-dominated landscapes, boreal bird communities are expected to display a relatively high level of resilience to forest disturbance, and therefore respond positively to forest management practices that aim to emulate natural disturbance. However there are such fundamental differences in early successional forest habitats created by the two disturbance types, particularly the quantity of live and dead residual trees, that using natural disturbance as a reference point to evaluate the short-term (< 10 years) performance of GTR is relatively uninformative. It is well established that post-fire and post-harvest bird communities exhibit their greatest differences during this period (e.g., Hobson and Schieck 1999; Schieck and Hobson 2000; Song 2002; Schieck and Song 2006; but see Stuart-Smith, Hayes, and Schieck 2006). Because much of the impetus for using GTR practices has arisen from a concern that recent clearcut areas cater to only a limited number of wildlife species, we considered clearcut areas to also provide an informative reference for the performance of GTR, at least in the short term.

Intuitively, retention of live trees at harvest is expected to provide immediate benefits to canopy-nesting and foraging bird species relative to clearcutting. Key issues for consideration are the proportion of old forest bird communities that may benefit from GTR, whether there are deleterious effects on some species or groups of species, to what extent reproductive success is affected by GTR, and whether the amount and/or spatial arrangement of trees retained at harvest influences bird community responses.

The short-term responses of bird communities to GTR can be highly variable, depending on forest type, tree species composition, landscape context, and the amount or type of understorey present, for any given retention level (Schieck and Song 2006). However, all studies have found that the retention of residual trees at harvest resulted in increased use of cutblocks by old-forest associated bird species relative to clearcut areas.

Key findings on the short- and long-term responses of birds to GTR are summarised in Table 3.6 at the end of this section.

Short-term community-level responses

Most studies have found that species richness and abundance of bird communities in GTR blocks lie at intermediate levels between clearcut areas and old-growth forest (e.g., Norton and Hannon 1997; Schieck, Stuart-Smith, and Norton 2000; Harrison, Schmiegelow, and Naidoo 2005; Schieck and Song 2006), although Lance and Phinney (2001) observed an increase in total bird diversity in GTR blocks relative to clearcut areas and old forest. They found that GTR blocks two years after harvest contained species from old forest, from clearcut areas and from neither site type in the sub-boreal conifer forest they studied. Norton and Hannon (1997) and Harrison, Schmiegelow, and Naidoo (2005) found a strong linear relationship between bird species richness, abundance, and species similarity to old forests, and the proportion of forest cover retained in boreal mixedwood forests of northern Alberta for deciduous, mixed, and conifer sites (but not deciduous-understorey sites; Figure 3.9). Schieck, Stuart-Smith, and Norton (2000) found a similar relationship between the density of large live deciduous trees retained in boreal mixedwoods at harvest and the degree of similarity

between bird communities in harvest and old-growth sites one to two years after harvest. Although the study was conducted in a forest type subject to very different natural disturbance regimes (with canopy gap dynamics the primary disturbance regime, with infrequent fires), Preston and Harestad (2007) found similar patterns of bird community responses to GTR in coastal western hemlock forests on Vancouver Island. Species richness was significantly lower in clearcut areas, with control and group retention blocks being similar. In addition, bird community composition in GTR blocks was intermediate between controls and clearcut areas. So, relative to clearcut areas, GTR generally results in an increase in bird species richness and abundance, largely through the provision of habitats for some old forest bird species, and the higher the retention level, the greater the effect.

Studies that have examined changes in bird species' guilds after harvesting have generally found that nesting and foraging guilds associated with shrub or tree cover are the most negatively impacted by GTR in the short term, but again, this varies depending on the level of GTR and forest type. At relatively low retention levels, cutblocks and post-fire stands are dominated early on by ground-nesting and foraging species (Harrison, Schmiegelow, and Naidoo 2005; Stuart-Smith, Hayes, and Schieck 2006), with shrub-associated species becoming more common as the understorey regenerates. Similarly, Schieck, Stuart-Smith, and Norton (2000) found that bird species more commonly associated with parkland and open-country habitats had high densities in harvest areas that contained abundant shrubs and few residual trees or snags. Foliage gleaners and cavity-nesters (Norton and Hannon 1997; Virkkala 2004; Harrison, Schmiegelow, and Naidoo 2005) are generally absent or occur at very low abundance. As retention levels increase, foliage-gleaners, shrub-associated species and secondary cavity-nesters become more common, while ground-nesting and foraging species become less so.

Short-term species-level responses

Short-term species-level responses to GTR are much more variable than long-term community-level responses. Norton and Hannon (1997), in a study of the responses of songbird communities to two levels of partial cutting (30.1% and 40.3% canopy cover retention, although measured by spherical densitometer, see Cook et al. 1995) relative to clearcut areas with retention (8.5%) and unharvested old boreal mixedwood stands, found that 41% of species decreased in abundance on clearcut areas, 31% in partial cuts, but only 3% in unharvested controls one year post-harvest. Seven of eight species that were absent from clearcut areas (red-breasted nuthatch, winter wren, Swainson's thrush, black-throated warbler, Canada warbler, American redstart, and rose-breasted grosbeak) did occur in partial cuts, but at significantly lower abundances than in unharvested old forest. The western tanager was only observed in unharvested old-growth stands. All of these, except winter wren, require trees and shrubs for nesting or foraging. They found that Lincoln's sparrow and house wren, species associated with open habitats, were most abundant in clearcut areas, while chipping sparrow was most abundant in partial cuts. White-throated sparrow was the most abundant species in all treatments before and after logging and appeared to be a true habitat generalist.

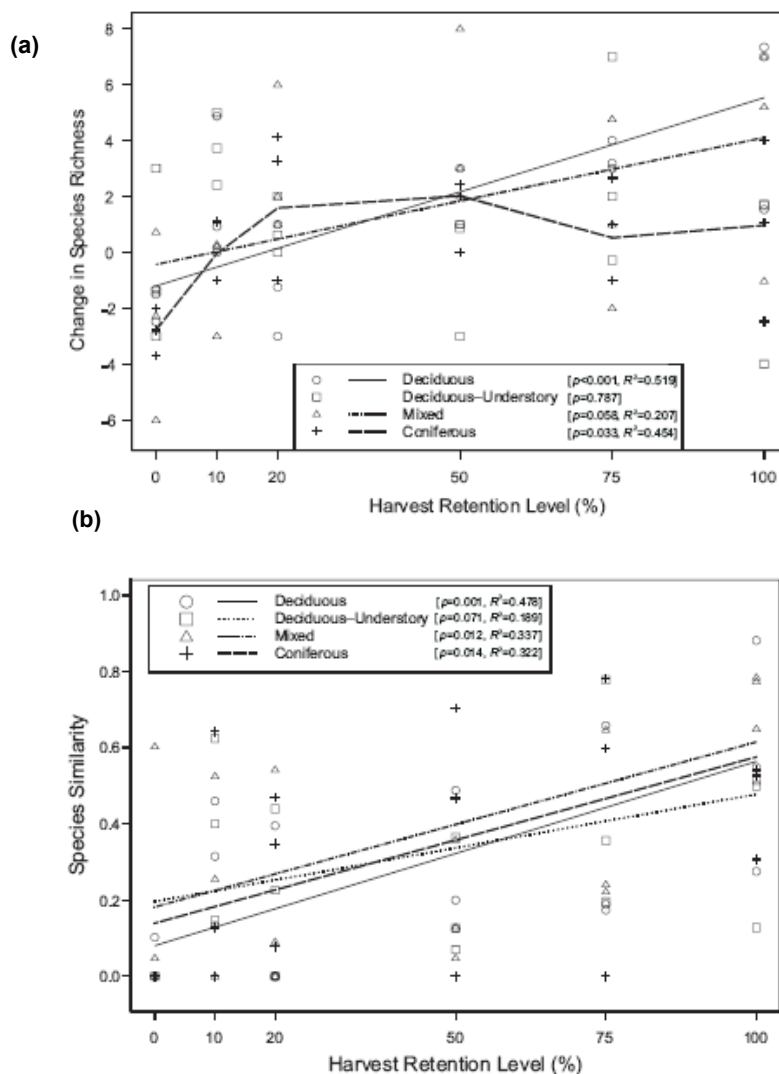


Figure 3.9 Mean Changes in Bird (a) Species Richness and (b) Species Similarity between 1998 and 2000, in Relation to Harvest Retention Levels of Different Forest Cover Types at EMEND, Alberta, Canada [reproduced from Harrison et al. (2005), p. 1558]

In a meta-analysis of three studies that examined the responses of bird communities one-two years after harvest to the amount and dispersion of residual trees retained at harvest, Schieck, Stuart-Smith, and Norton (2000) found that 34 of 54 bird species studied had higher densities in old growth (> 100 years old) than in harvested stands (1 - 2 years post-harvest). These species had their predicted highest densities in harvested stands with many large residual trees and snags, and included species such as brown creeper, black-throated green warbler, hairy woodpecker, warbling vireo, and western tanager. Twelve species were not detected in old-growth stands and had their predicted maximum densities in stands with few large trees and snags and abundant high shrubs, including common nighthawk, alder flycatcher, common yellowthroat, LeConte's sparrow, clay-coloured sparrow, and Lincoln's sparrow. The final eight species were detected in both harvest and old-growth stands, but their predicted maximum densities were at intermediate levels of live tree and snag retention. None of the bird species detected only in harvested stands, or that had higher densities in harvested stands than old growth, nested in the canopy and only four of the twenty were cavity-nesters.

Harrison, Schmiegelow, and Naidoo (2005) were among the few investigators to attempt to measure the reproductive response of bird communities, albeit indirectly, by weighting bird abundance by the reproductive status or behaviour of birds observed in point counts. They examined the responses of breeding forest songbirds to a series of harvesting treatments established as part of the EMEND (Ecosystem Management by Emulating Natural Disturbance) project. This is a multi-disciplinary experiment to compare clearcut areas and partial-retention cuts in four upland forest-cover types with uncut forest and experimentally burned stands in the boreal mixedwoods of northwestern Alberta. They found that most species' declines relative to unharvested controls occurred in the clearcut areas and in the lower residual treatments (10-20% tree retention), by species typically associated with shrubs and trees, such as golden-crowned kinglet, red-eyed vireo, Swainson's thrush, and yellow-rumped warbler. The ovenbird, a ground-nester and forager, also declined in lower residual treatments, but it is considered to require the presence of canopy trees. At higher levels of retention (up to 80% tree retention), species declines in abundance (i.e., golden-crowned kinglet, ovenbird, and Swainson's thrush) were not statistically significant. Most increases in species' abundance relative to controls also occurred in the clearcut areas and lower residual treatments. These were primarily ground-nesting and foraging species such as dark-eyed junco, Lincoln's sparrow, and white-throated sparrow.

Similar findings have been made in studies of bird community responses to GTR in sub-boreal and temperate forests of western Canada. In their study of bird community responses to retention harvesting in the sub-boreal coniferous forests of central interior British Columbia, Lance and Phinney (2001) found that species composition differed more than species numbers across the clearcut areas, retention stands and unharvested controls studied. Over three years of bird census they found that 16 of the 64 bird species were only observed at the retention sites, five only at the control sites, and only two were restricted to the clearcut areas. Twenty-nine species occurred at both retention and control sites, and 20 at both retention sites and clearcut areas, and eight species were shared between the controls and clearcut areas. The distributions of individuals reinforced these patterns, with 39% of species that occupied at least two of the three treatment types, showing significantly greater abundance at retention sites, versus 22% for control sites, and only 7% for clearcut areas. At clearcut and control sites, relatively few species accounted for most of the bird numbers. In clearcut areas, habitat generalists such as the dark-eyed junco, robin, and Lincoln's sparrow, and habitat specialists such as the song sparrow and pine siskin dominated. Control sites were dominated by forest-dependent birds such as the golden-crowned kinglet, Swainson's thrush, and magnolia warbler. Some strongly forest-dependent species such as the kinglets, winter wren, yellow-rumped and magnolia warblers were less common in retention sites, and the boreal chickadee was absent altogether. However, others such as MacGillivray's warbler, red-breasted sapsucker, Cassin's vireo, American redstart and pine siskin were more numerous on the retention sites than in the mature uncut control sites.

In the temperate coniferous forests of coastal British Columbia, Preston and Harestad (2007) examined the community- and species-level responses of songbirds to group retention practices (also referred to as Variable Retention or VR) within the first five years after harvest. Retention levels on the VR blocks ranged from 7.0-41.3%). With some exceptions, they found that species that occurred in controls also occurred in the retention blocks (exceptions included northern pygmy-owl, merlin, and pileated woodpecker). Six species were observed in controls and retention blocks, but not clearcut areas (sooty grouse, black-throated gray warbler, band-tailed pigeon, gray jay, northern flicker and ruffed grouse). Nine species were only found in retention blocks and included: brown-headed cowbird, Cassin's vireo, chipping sparrow, European starling, golden-crowned sparrow, olive-sided flycatcher, violet-green swallow, warbling vireo, and willow flycatcher. Of the 29 species found to occur in control blocks, 13 species (comprising 92.2% of the total abundance of birds in the community) had home ranges or territories small enough (i.e., ≤ 8 ha) to be contained within the

study blocks, and occurred often enough in all treatments that they were considered likely to be major components of the songbird community rather than vagrants. Twelve of these species were selected for analysis of their responses to retention (one was excluded due to low detection probabilities). They found significant differences in mean abundance among treatments for 10 of the 12 species. Of five species of forest-dwelling birds that were consistently more abundant in control blocks, their abundance was also significantly greater in retention blocks compared to clearcut blocks. These species included chest-nut backed chickadee, golden-crowned kinglet, Pacific-slope flycatcher, varied thrush and brown creeper; all considered strongly forest-dependent. In GTR blocks, Hammond's flycatcher and hairy woodpecker were significantly more abundant than in clearcut areas, and American robin was significantly more abundant than in controls. Winter wren and rufous hummingbird abundances were similar across treatments.

Edge effects and nest predation

One of the concerns raised in response to the increased use of retention harvesting practices is the potential for elevated levels of nest predation that may be associated with an increase in forest edge habitat. This is considered to be a particular concern in the early seral stages following harvesting when the contrast between cut and adjacent uncut forest is greatest. Tittler and Hannon (2000) examined this question in stands with high (86-133 trees/ha), intermediate (48-55 trees/ha) and low (10-36 trees/ha) levels of GTR and in forested controls (246-414 trees/ha) three years after harvest. They placed artificial ground and shrub nests in and adjacent to the treatment sites, as well as within residual clumps of trees. No relationship between nest predation and the level of GTR or the size of clumps was found. Hannon (2005) reported similar findings in her synthesis of research studies carried out as part of the Landscape Structure and Biodiversity Project (LBSP). No major effects of proximity to edge on reproductive success were observed nor did predator communities appear to change after logging. However, Bourque and Villard (2001) did attribute a decrease in reproductive success for the ovenbird to edge effects in first-entry selection harvests in New Brunswick relative to uncut control forest. Conversely, another species considered an old forest specialist, the black-throated blue warbler, exhibited a higher density and reproductive success in response to the selection cuts. Predictions of elevated levels of nest predation following GTR do not seem to be borne out.

Short-term responses to the amount of residual trees

Few studies could be found that explicitly examined the responses of boreal bird communities to the amount of residual retention after harvest. Schieck and Song (2006) conducted a meta-analysis of 15 studies that had examined the influence of GTR on birds within the first 10 years after harvest. Due to a lack of details in some studies and the broad range of retention levels reported in others, they grouped studies into three levels of retention: < 1% retention (two studies); 1-10% (five studies); and, > 10% (eight studies). No clear effect on bird communities of retaining different levels of green-trees was apparent. Cutblocks with < 1% of their area covered by live residual trees had bird communities that did not differ significantly with cutblocks with 1-10% retention. Similarly, bird communities in cutblocks with < 10% retention did not differ significantly from those with > 10% (Figure 3.10). These results contradict those of many of the individual studies examined, which found that as levels of retention increase bird communities become more similar to those in old forest (e.g., Norton and Hannon 1997; Schieck, Stuart-Smith, and Norton 2000; Harrison, Schmiegelow, and Naidoo 2005).

However, patterns are inconsistent among individual studies. Norton and Hannon (1997) found no significant difference between cutblocks with low (25%) and high (36.7%) retention in terms of species richness, abundance or guild structure, although high retention blocks were significantly different from clearcut areas. Harrison, Schmiegelow, and Naidoo (2005) found that the benefits to short-term bird-diversity in partial cuts with 10-20% retention were relatively small, and concurrent behaviour monitoring in these stands at EMEND showed the presence of mature forest species was not reflected in reproductive activity (Harrison 2002 in Harrison, Schmiegelow, and Naidoo 2005),

indicating the apparent short-term benefits may be illusory. Schieck, Stuart-Smith, and Norton (2000) found positive short-term responses of some old forest species to relatively low levels of GTR (2-6%); however, they noted that even at levels of 40% retention, many bird species had higher densities in old-growth forest than in retention blocks.

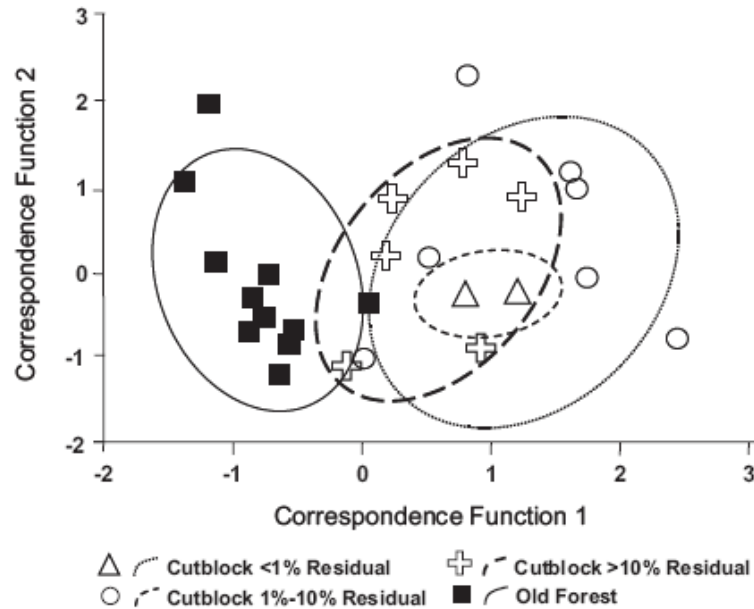


Figure 3.10 Correspondence Analysis of Bird Communities Found 0-10 Years after Harvest of Aspen-White Spruce in the Boreal Forest of Western North America [Each symbol represents a separate study site. Cutblocks were categorized by residual live trees after harvest. Bird communities in continuous old forest were included for reference (reproduced from Schieck and Song (2006), p. 1315)].

In non-boreal forests, Preston and Harestad (2007) found the amount of forest retained at the stand-level was a significant factor for predicting the probability of occurrence (i.e., presence/absence) for 10 of 12 songbird species examined. All species displayed a sigmoidal response, although thresholds of response were generally poorly defined. An exception was the chestnut-backed chickadee, which showed a strong response threshold at relatively low retention levels. At 20% retention there was a 64% probability of occurrence. Not all species responded positively to increasing levels of GTR. The dark-eyed junco, a species preferring open habitats, had a strong, negative response to increasing retention (Figure 3.11).

Conversely, Tittler, Hannon, and Norton (2001) found that boreal songbird responses were related more to the size of live trees retained rather than the number. When residual live tree basal area was examined rather than density, they found that more species were both positively and negatively affected by GTR. In the first year after logging (with residual tree densities of 10-133 trees/ha, or 0.50-10.65 m²/ha), abundances of American redstart, mourning warbler, Swainson’s thrush, yellow warbler, total songbird abundance, and total abundance of generalist species increased with increasing basal area on cutblocks. In the third year after logging, abundance of yellow-rumped warbler, least flycatcher, winter wren, and ovenbird, and the total abundance of generalist species also increased with increasing basal area. However, Lincoln’s sparrow, Connecticut warbler, common yellowthroat, LeConte’s sparrow, and total abundance of “cutblock” species (i.e., species found to be positively affected by clearcutting with no residuals) decreased in abundance with increasing basal area.

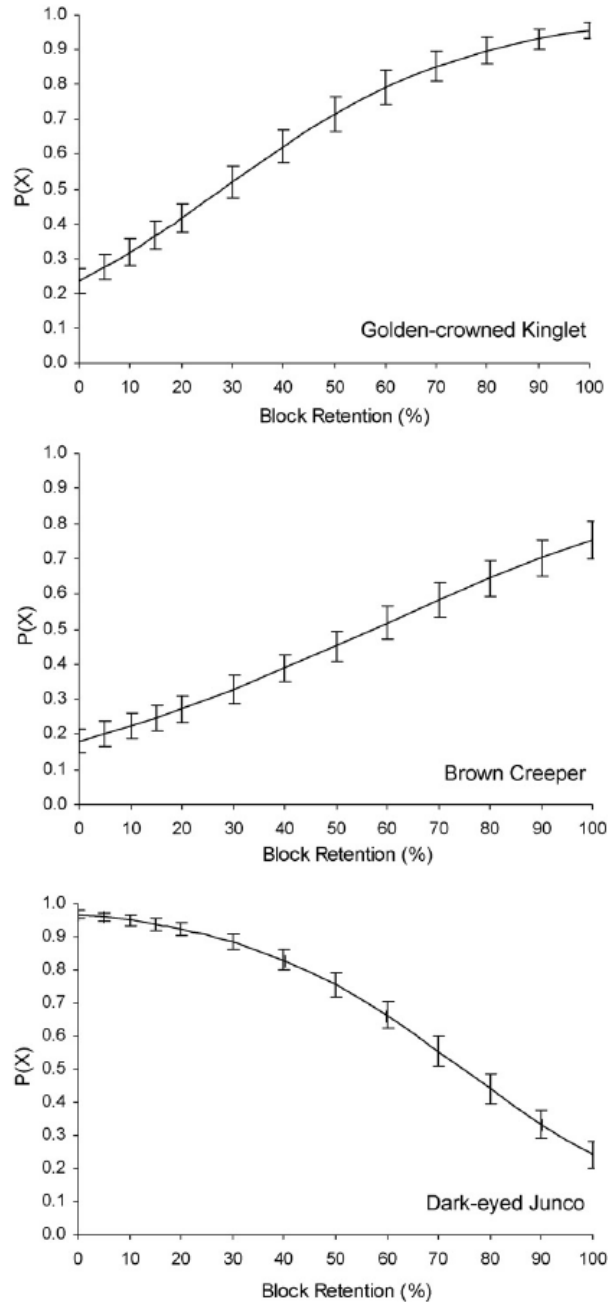


Figure 3.11 Predicted Probability of Occurrence $P(X)$ from Binomial Logistic Regression in Relation to Percentage Block-Level Retention for Golden-Crowned Kinglet, Brown Creeper, and Dark-Eyed Junco [Reproduced from Preston and Harestad (2007), p. 163. Retention levels in the harvested areas ranged from 0-41.3%.]

Short-term responses to the amount and configuration of residual trees

Only one study could be found that examined the influence of the spatial arrangement of retained live trees on boreal bird response. Schieck, Stuart-Smith, and Norton (2000) used a combination of aerial photographs and ground surveys to examine the relative influence of dispersed residual trees and residual tree clumps (defined as groups of ≥ 5 large trees within 5 m of one another) on bird community composition and abundance as part of their meta-analysis. They found that bird species with relatively high densities in old-growth stands (>100 years old) appeared to have higher densities in harvested stands (1–2 years post-harvest), not only when many residual trees and snags were retained, but when they were retained in clumps. Specifically, they found that bird communities in harvest areas were more similar to those in old-growth forest when $> 80\%$ of large residual trees was retained in clumps. Although the statistical strength of this relationship was relatively low, it was consistent across all three studies, and was apparent even when few residual trees were retained in harvest areas.

Bird community response to patch size has also received relatively little attention in the literature. Schieck and Hobson (2000) surveyed birds in a range of patch sizes (1 – $> 3,000$ live trees) produced by fire or harvest in boreal mixedwood forest. Immediately post-disturbance, bird communities from large patches (> 100 residual trees) were more similar to those from old forest than were communities from small patches (≤ 10 trees). Bird communities from small residual patches were dominated by sparrows and warblers that nest and forage in open, parkland, or riparian habitats, although shrub-associated and generalist species were also common. Some bird species typically associated with continuous old forest were found in large, but not small, patches, including red-breasted nuthatch, and yellow-rumped warbler. However, a number of bird species that were common in continuous old forest were either absent from large patches or occurred at very low densities, including golden-crowned kinglet, Swainson's thrush, yellow warbler, black-throated green warbler, American redstart, and pine siskin. Notably, bird communities immediately post-fire were very different from those post-harvest regardless of patch size. All sizes of patches post-fire were dominated by cavity-nesting species such as downy woodpeckers, hairy woodpeckers, three-toed woodpeckers, black-backed woodpeckers and northern flickers. These species were much less common in continuous old forest and in large residual patches immediately post-harvest, and extremely rare in small patches of the same age. In a preliminary analysis of songbird species responses (probability of presence/absence) to the amount of forest retained at harvest, using only data from the group retention treatments, Preston and Harestad (2007) found a significant ($p = 0.032$, $r^2 = 0.077$) relationship between species' responses and the amount of residual retention, although the amount of variation explained was minor. They concluded that retention performance cannot be solely attributed to retention amount and that the size of retention patches, which ranged from 0.25 to 2.0 ha, may be more important in modifying songbird responses to harvest.

Landscape connectivity

The potential for stand-level structural retention practices to enhance landscape connectivity for boreal bird communities has been studied in the context of riparian buffer retention. Robichaud, Villard, and Machtans (2002) examined whether a 100-m-wide riparian buffer strip was used as a movement corridor by forest songbirds in the first four years post-harvest. They found that the buffer strip facilitated movement of adults and juveniles mainly in the first two years post-harvest, with the effect rapidly declining as the forest regenerated on the adjacent cutblock. Nevertheless, some species such as Philadelphia and red-eyed vireos, the red-breasted nut-hatch and ovenbird continued to use the buffer strip as a movement corridor four years post-harvest. Further, Lambert and Hannon (2000) found that male ovenbirds continued to hold breeding territories and attract mates in riparian buffer strips of at least the same width immediately post-harvest, but were absent from 20-m-wide buffers. So there is some evidence that stand-level riparian retention practices may not only facilitate the movement of individuals but also have positive implications for reproductive success.

Long-term community-level responses

In the long-term (i.e., ≥ 10 years post-disturbance), post-fire and post-harvest bird communities of boreal mixedwood forests tend to converge, irrespective of the presence of residual trees (Schieck and Song 2006; Stuart-Smith, Hayes, and Schieck 2006). Hobson and Schieck (1999) observed that the large initial differences in bird communities post-fire and post-harvest begin to diminish as early as 14 years post-disturbance, with fewer open-habitat species in post-harvest stands, fewer snag-associated species in post-fire stands, and increased shrub-associated species in both stand types. This convergence continued during the period between 14 and 28 years after disturbance and was attributed to convergence of forest structure over this period, with a rapid decrease in snags due to windthrow. Bird communities in post-harvest stands changed little over this period. However, significant differences in bird communities were still apparent at this age. Species associated with parkland habitats or old forests were less common during this period than in post-fire periods of the same age. Beyond 30 years post-disturbance, only Schieck and Hobson (2000) have examined the relative trends in bird communities post-harvest in this forest type. They found a reasonably strong similarity between bird communities at 60 years post-harvest when no residual trees were retained and post-fire bird communities of the same age. However, this was based on very few sites: three post-fire and two post-harvest (Table 2 in Schieck and Hobson 2000, p. 1290).

In a retrospective chronosequence study of songbird community responses to wildfire and harvest, with varying levels of residual trees in each disturbance-type, Stuart-Smith, Hayes, and Schieck (2006) found similar trends in bird community response, although they differed between the two temperate coniferous forest types studied. They studied a chronosequence of stands ranging in age from 7 to 45 years post-disturbance, with residual tree densities from 0-320 conifer overstorey, 0-832 conifer understorey, and 0-68 broadleaf trees/ha. Unlike previous studies (see above) they did not find significant differences in bird communities in the early age-class in one of the forest types examined (Montane Spruce (MS) dry cool biogeoclimatic (BEC) zone). They attributed this to the fact that no post-fire stands < 7 years old were available for study and that considerable convergence in post-fire and post-harvest bird communities had already occurred. Their results in the other forest-type studied (Engelmann Spruce-Subalpine Fir (ESSF) dry cool BEC zone) were consistent with previous studies, and they found that disturbance type explained relatively little ($\leq 15\%$) of the variation in bird communities. As stands aged, bird communities in burned and logged stands became more similar in the ESSF, but not the MS forest type. The latter result was attributed to the higher levels of overstorey residual trees in the older harvested age classes which were high-graded, relative to the more recent harvests in the MS which were generally variable retention cuts with a high density of understorey residuals. In general, their results indicated that long-term differences in bird

communities were mainly in abundance rather than community composition, with considerable overlap between bird communities in burned and logged stands.

When residual live trees have been retained at harvest, bird communities in harvested stands have become more similar to those in old forest throughout early- and mid-seral stages (Schieck and Hobson 2000; Schieck and Song 2006). The general patterns of bird community responses to GTR relative to clearcut areas and natural disturbance in mixedwood forests are summarised in Table 3.5. While all species common to clearcut areas were still common in GTR stands between 11 and 30 years post-harvest, many cavity-nesting species, old-forest species, and species associated with parkland areas and old shrubby forest had higher abundances during this period when large live residual trees were retained at harvest. Basically, bird communities in GTR stands of this age reflected the broader range of habitat types available to birds, relative to regenerating clearcut areas. Although in mid-seral stages post-harvest bird communities become somewhat similar regardless of whether residual live trees are retained, densities of many old forest species were much higher when large live trees were retained at harvest. No cutblocks older than 60 years with residuals retained at harvest have been studied. The closest analogue examined by Schieck and Hobson (2000) was 80-year-old post-fire sites. They found increased convergence with old forest bird communities in forests of this age post-fire, but not complete convergence. Based on the similarities between bird communities 60 years post-harvest and 80 years post-fire, Schieck and Song (2006), in their seminal review of the long-term responses of bird communities to residual retention in western Canadian boreal mixedwood forests, predicted complete convergence of bird communities would occur by the time forests of both disturbance types reached an old-growth stage, albeit mediated by the successional trajectory of the stand towards old coniferous, old deciduous or old mixedwood forest (Schieck and Hobson 2000). Although based on a small sample size, the lack of complete convergence between 80-year-old post-fire and old forest bird communities has implications for harvest rotation age.

Table 3.5 Summary of Changes in Boreal Bird Communities through Forest Succession, Following Harvest with and without Residual Live Trees, Relative to Natural Disturbance in Boreal Mixedwood Forests of Western Canada [from Schieck and Song (2006)]

Serai stage	Bird community response			Key similarities/differences to natural disturbance (i.e., fire)
	Without residual live trees (clearcut areas)	With residual live trees		
0-10 yrs post-harvest	Many sparrows and other bird species that forage in aquatic, open-meadow or shrubby habitats initially common after aspen or mixedwood harvest. As aspen regenerated & shrubs regrew, open-meadow species become less common and shrub-associated species more common.	Some bird species that live in parkland, burned or old forest, old forest with abundant shrubs, or all forests were common. Diversity may be higher. At higher levels of retention, old-forest birds were more common & open-meadow birds less common. Even with 30-45% retention of large trees, not all old-forest bird species were present & others had lower abundance.		Bird communities post-fire & post-harvest differ greatly with or without residuals due to greater abundance of snags post-fire. Fire often results in larger (> 5 ha) residual patches than harvest that may provide interior forest conditions for old-forest birds.
11-30 yrs	Dominated by species associated with shrubby habitats, young forests and all forest types. Cavity-nesting species uncommon.	All species common in clearcut areas are still common. Many cavity-nesting birds and birds that live in old forest, parkland areas, or shrubby old forests had higher abundances in this period when large, live residuals retained.		Cavity-nesting species common throughout this period post-fire. Post-fire and post-harvest bird communities begin to converge during this period as snags fall and new cohort of trees grow, but composition of communities still significantly different.
31-75 yrs	Bird communities dominated by a small number of species that live in a wide variety of forest types. Cavity-nesting species and a few old-forest bird species uncommon until trees > 15 m tall and reach high abundances 50-75 years post-disturbance.	As for younger cutblocks, many species living in parkland areas, old forests, or shrubby old forests had higher abundances when large live trees retained at harvest.		Regenerating clearcut areas of this age had very similar bird communities to those in forests 31-75 years post-fire even without residual retention (but only one study), largely due to scarcity of large snags in post-fire forests of this age, as fewer residual live trees available post-fire for snag recruitment in mid-seral stages..
76-125 yrs & > 125 yrs	No studies.	No studies.		Birds common in 31-75 year-old forest still common. Cavity-nesters become more common. Species associated with old forests with & without shrubby understoreys also common. Species assemblages largely determined by proportion of aspen and white spruce trees in canopy. Expected that differences between disturbance types disappear in old forest as there were few differences apparent between post-fire and post-harvest communities in the preceding period.

Essentially, GTR appears to accelerate the rate of convergence toward old forest bird communities through the provision of habitat structures, such as large live trees and snags, in early- and mid-seral stages that would otherwise not be present in clearcut areas or in fire-disturbed forests with no or few live residuals (Figure 3.12).

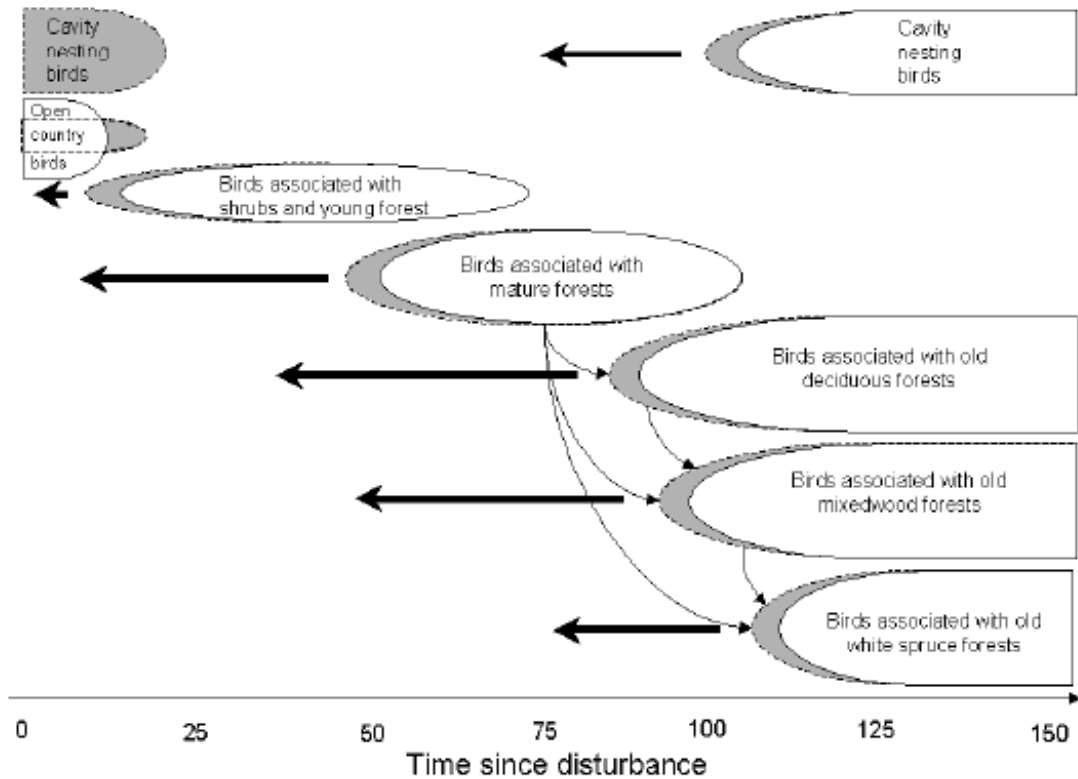


Figure 3.12 Simplified Schematic Describing Major Changes in Bird Communities over Time Following Fire (in shadow), Harvest (in white) in the Boreal Mixedwoods of Western Canada, with Large Arrows Illustrating the Effects of Retaining Live Residual Trees [Bird species were categorised by breeding habitat. Narrow arrows indicate the possible trajectories through varying mixedwood and conifer states (reproduced from Schieck and Song (2002), p. 9-38 in Song 2002).]

Long-term responses to the amount & configuration of residual trees

The rate and/or timing of convergence with old forest bird communities over the long-term may be influenced by the amount and configuration of residual trees. Although Schieck and Hobson (2000) found that larger patches (> 100 residual trees) performed much better than small patches (≤ 10 trees) in capturing old forest bird species in the short-term, partial convergence of the bird communities between small and large patches occurred over time, largely due to bird communities in small patches becoming more similar to those from old forests (Fig. 3.13). By 60 years post-harvest, bird communities from small patches shared some of the species common in continuous old forest and most of the species present in small residual patches in post-fire forests of the same age. Importantly, birds associated with old-forest were present in all patch sizes 15, 30 and 60 years post-disturbance,

although larger patches had higher densities of these species throughout succession. In neither case, however, was bird communities associated with residual patches identical to those in continuous old forest, even 60 years post-harvest.

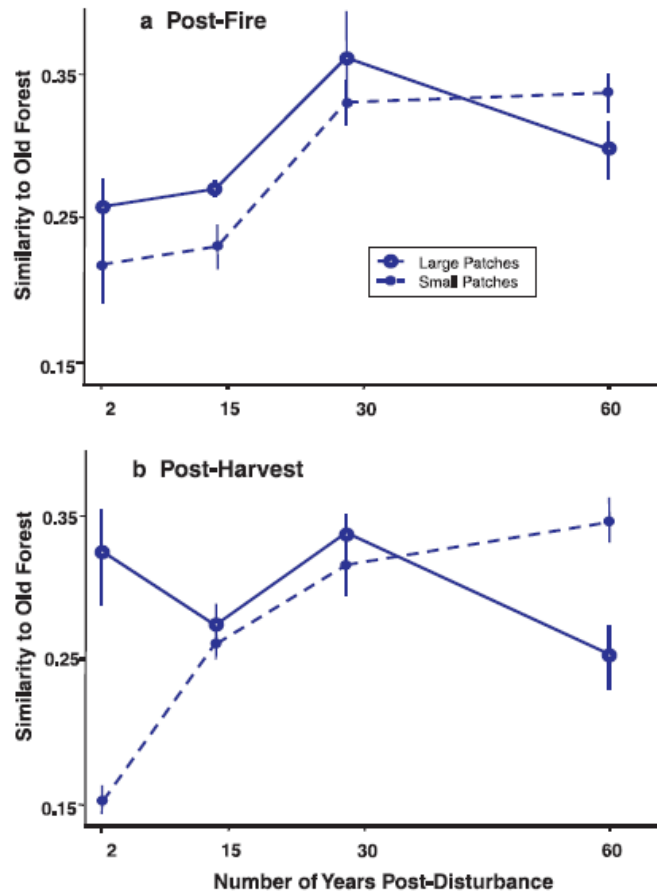


Figure 3.13 Degree of Similarity (mean \pm SE) between Bird Communities from Residual Tree Patches at 2, 15, 30, and 60 Years Post-Disturbance and Bird Communities in Continuous Old Mixedwood Forests in Alberta [Patches were categorized as large (> 100 residual trees) or small (≤ 10 trees) (reproduced from Schieck and Hobson (2000), p. 1289).]

Disturbance severity, as reflected by the amount of residuals post-disturbance, rather than disturbance type, explained much of the variation in bird communities in Stuart-Smith, Hayes, and Schieck's (2006) study of the long-term responses of songbird communities to wildfire and logging. In the MS forest type, community- and species-level analyses indicated that variation in bird communities was most closely related to variation in residual conifer overstorey trees. Density of residual understorey trees was also significant. Associations with residual conifer overstorey trees were positive for some species, including those known to nest or forage in mature conifers (e.g., Townsend's warbler and golden-crowned kinglet) and negative for others associated with open and early seral stands (e.g., dusky flycatcher, orange-crowned warbler, and American robin). Only dark-eyed junco and olive-

sided flycatcher were positively associated with the amount of residual understorey conifers. Associations with broadleaf trees were positive for all species except yellow-rumped warbler. The density of broadleaf trees was also the only residual tree variable to significantly influence total bird abundance. Conversely, in the ESSF, understorey conifer density was the most influential structural variable. Density of residual overstorey trees was not significant in this forest type. They concluded that differences in the quantity of residual trees strongly influenced bird community responses to both disturbance types in each of the forest types studied. The density of conifer overstorey trees was higher in the MS than the ESSF for both disturbance types and age classes, reflecting both natural differences in forest composition and variations in harvesting practices. Nevertheless, the general trends they found were consistent with studies from the boreal. Logged and burned stands had relatively similar bird communities 7-45 years after disturbance and the degree of similarity was influenced by the density and type of residual trees.

3.2.1.2 Mammals

The responses of mammal species to wildfire and timber harvesting in the North American boreal forest have been well reviewed by Fisher and Wilkinson (2005). They grouped studies into four successional stages of forest development for each disturbance type to determine patterns in the diversity and abundance of 25 mammal species. In general, they found that small mammals and ungulates were most abundant immediately post-disturbance and decreased as stands aged. Lynxes and hares were rare in young and old forest, but common through mid-successional periods. Bats, arboreal sciurids and mustelids increased in abundance with stand age, and were most abundant in old growth (>76 years old). However, the degree to which retention of live residual trees may modify these responses was unclear. Due to a lack of explicit treatment of within-stand forest structure in most of the literature reviewed, Fisher and Wilkinson (2005) generally had to speculate on the likely responses of mammal species or species groups based on known or assumed relationships with structural attributes. As a result, this review focuses on the few studies that have explicitly examined mammal responses to GTR.

3.2.1.2.1 Small Mammals

Small mammals (i.e., mice, voles and shrews) have been advanced as a potential bioindicator group for sustainable forest management due to the strong associations of some species with structural habitat variables and their relatively predictable response to forest management at a stand level, largely based on studies of clearcut areas (Pearce and Venier 2005). In the short term, clearcutting and fire both tend to result in a shift in the dominance of small mammal communities, from red-backed voles (which are most abundant in old-growth forests) to deer mice, with meadow voles becoming more abundant 5-10 years post-disturbance. These patterns are correlated with changes in the structural attributes of the stand; however it can be difficult to determine whether small mammals are responding to the vegetation characteristics of the stand, CWD or both.

Table 3.6 Summary of Key Findings of Studies of Short- and Long-Term Bird Responses to Green-Tree Retention Harvesting Practices (Non-boreal studies are highlighted in italics.)

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Alberta; British Columbia (BC)	Aspen white-spruce mixedwoods; Sub-boreal spruce; Coastal western hemlock.	Short-term (ST) & Long-term (LT)	Relative to clearcut areas, GTR generally results in an increase in species richness and abundance.	Norton & Hannon (1997); Schieck et al. (2000); <i>Lance & Pinney (2001)</i> ; Harrison et al. (2005); Schieck & Song (2006); <i>Stuart-Smith et al. (2006)</i> ; <i>Preston & Harestad (2007)</i> .
Alberta; BC; Fennoscandia	Aspen white-spruce mixedwoods; Scots pine; Douglas-fir - white spruce & Engelmann spruce – sub-alpine fir.	ST	As retention levels increase, foliage-gleaners, shrub-associated species & secondary cavity-nesters become more common, while ground-nesting & foraging species less so.	Norton & Hannon (1997); Schieck et al. (2000); Virkkala (2004); Harrison et al. (2005); <i>Stuart-Smith et al. (2006)</i> .
Alberta; BC	Aspen white-spruce mixedwoods; Sub-boreal spruce; Coastal western hemlock.	ST & LT	Species-level responses are much more variable.	Norton & Hannon (1997); Schieck et al. (2000); <i>Lance & Pinney (2001)</i> ; Harrison et al. (2005); <i>Stuart-Smith et al. (2006)</i> ; <i>Preston & Harestad (2007)</i> .
Alberta	Aspen white-spruce mixedwoods.	ST	Predictions of elevated levels of nest predation do not seem to be borne out.	Tittler & Hannon (2000); Hannon (2005).
Alberta; BC	Aspen white-spruce mixedwoods; Coastal western hemlock.	ST & LT	Individual studies indicate that as levels of retention increase bird communities become more similar to those in old forest, but patterns are inconsistent among studies.	Norton & Hannon (1997); Schieck et al. (2000); Harrison et al. (2005); Schieck & Song (2006); <i>Preston & Harestad (2007)</i> .
Alberta	Aspen white-spruce mixedwoods.	ST	Even at levels of $\geq 40\%$ many bird species had higher densities in old forest.	Norton & Hannon (1997); Schieck et al. (2000); Harrison et al. (2005).
Alberta	Aspen white-spruce mixedwoods.	ST	Size of trees retained may be as important as the number.	Schieck et al. (2000); Tittler et al. (2001).
Alberta	Aspen white-spruce mixedwoods.	ST	Bird communities in harvest areas were more similar to those in old growth (>100 years old) when trees retained in clumps (or patches).	Schieck et al. (2000).
Alberta; BC	Aspen white-spruce mixedwoods; Coastal western hemlock.	ST & LT	Large patches contained bird communities more similar to old forest than small patches.	Schieck & Hobson (2000); <i>Preston & Harestad (2007)</i> .

Table 3.6 Continued

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Alberta	Aspen white-spruce mixedwoods.	ST	Stand-level retention of riparian buffer strips of at least 100 m wide may facilitate landscape connectivity for individuals and/or propagules.	Lambert & Hannon (2000); Robichaud et al. (2002).
Alberta, BC	Aspen white-spruce mixedwoods; Douglas-fir - white spruce & Engelmann spruce – sub-alpine fir.	Long-term (LT)	Post-fire and post-harvest bird communities converge irrespective of the presence of residual live trees, with differences mainly in abundance rather than in community composition.	Hobson & Schieck (1999); Schieck & Hobson (2000); Schieck & Song (2006); <i>Stuart-Smith et al. (2006)</i> .
Alberta	Aspen white-spruce mixedwoods.	LT	Lack of complete convergence between 80 year-old post-fire and old forest bird communities.	Schieck & Hobson (2000).
Alberta	Aspen white-spruce mixedwoods.	LT	GTR accelerates the rate of convergence toward old forest bird communities.	Schieck & Song (2006).
Alberta	Aspen white-spruce mixedwoods.	LT	Similarity between bird communities in small patches and old forest increases over time, but still lags behind large patches.	Schieck & Hobson (2000).
Alberta	Aspen white-spruce mixedwoods.	LT	Neither large nor small patches contain bird communities identical to those in old forest, even 60 years post-harvest.	Schieck & Hobson (2000).

Short term responses

In one of the few studies to examine the responses of small mammal communities to partial harvesting, Von Trebra, Lavender, and Sullivan (1998) found that red-backed vole abundance and recruitment was 50% higher in shelterwood than unharvested controls in the sub-boreal spruce stands studied, although the effect was short-lived. Deer mice, on the other hand, appeared relatively unaffected, and both species, which were the most common small mammals prior to harvest, continued to be dominant in the first two years post-harvest. No differences in average survival were detected for either species. The authors speculated that shelterwood harvesting may have increased short-term availability of forage (i.e., insects, seeds and hypogeous fungi), as well as thermal and security cover through production of CWD.

In a more detailed examination of small mammal responses to residual retention, Moses and Boutin (2001) experimentally manipulated levels of standing trees and CWD in boreal mixedwood forest stands. They compared abundance, survival and reproductive activity of red-backed vole, deer mouse, and meadow vole populations to four retention treatments: “zero residual” – zero live trees + zero CWD; “low residual” – zero live trees + CWD; “moderate residual” – 10% basal area live tree retention + CWD; and, “uncut” – 100% live trees + CWD. They found that patterns of small mammal abundance were similar on uncut and moderate residual treatments, with red-backed voles and deer mice dominant. But red-backed voles were virtually absent from the zero and low residual treatments during the breeding season immediately after logging, although they recovered to low numbers in the following two years. Deer mice were common on low and zero residual treatments in all years. No effects of the treatments on rates of survival or reproductive activity were observed for either species. Meadow voles displayed an opposite pattern to red-backed voles and were uncommon in uncut and moderate residual treatments, but abundant in low residual stands. In short, the effect of clearcut logging was not modified by presence of CWD alone, but by presence of residual tree patches with CWD.

Similarly, Fuller, Harrison, and Lachowski (2004) found that partial harvesting (41-48% live tree basal area retention) did not reduce habitat quality for red-backed voles, deer mice and short-tailed shrews relative to mature mixed-forest types of north-central Maine. Darveau et al. (2001) found no effect of thinning (1/3 of all trees) on red-backed vole abundance in 20-m-wide riparian buffer strips retained at harvest in balsam fir forests of Quebec. In uncut forest, however, this species was generally less abundant in the 20 m closest to streams relative to upland areas. Conversely, St-Laurent et al. (2007) found little association between red-backed vole abundance and live tree retention. They used the patterns of relative abundance of this species in residual stands in two differently configured harvested landscapes to develop a habitat use model that incorporated landscape- and stand-level variables. Of the nine variables included in the red-backed vole model, six related to stand-level structural characteristics. However, with the exception of alder basal area, variables relating to overstorey trees were predicted to have a negative influence on abundance.

Long-term responses

In the longer term, deer mice tend to dominate mid-successional stages, but all voles and mice generally occur at lower abundances in mid-successional forests than in other stages (Fisher and Wilkinson 2005). Red-backed voles gradually regain dominance as stands age, reaching their highest levels in mature (>50 years of age) forest (Pearce and Venier 2005). Deer mice are generally less abundant, but overall small mammal species richness is higher at older seral stages (Fisher and Wilkinson 2005).

Despite the lack of empirical studies explicitly dealing with in-stand forest structure, Fisher and Wilkinson (2005) concluded that presence of CWD, live residual trees and snags post-disturbance would facilitate convergence of small mammal communities over the long term to a pre-disturbance state. However, where structural attributes such as these have not been retained at harvest, mid-successional thinning of even-aged stands may achieve a similar result. For example, Homyack et al. (2005a) found that pre-commercial thinning (PCT) of mid-successional stands appeared to accelerate development of habitat characteristics for small mammals more typical of mature forest. They examined responses of mice, voles and shrews to pre-commercial thinning (PCT) across a chronosequence of 16 years, where PCT had been applied to stands 15-20 years after clearcutting. They found that PCT resulted in increased abundances of red-backed voles and masked shrews. No effect on deer mice or short-tailed shrews was observed, although abundance of deer mice generally increased with time since thinning. There was limited evidence of higher lactation rates of adult female deer mice in unthinned stands, but insufficient information on survival and/or reproductive success was obtained to confirm this. No relationship between these patterns and CWD quantity was found. Instead, larger stem diameters, a partially open canopy, and more structurally diverse understoreys, resulting from PCT were considered important. Larger stem diameters may result in enhanced infusion of larger CWD later in succession relative to unthinned stands. Fisher and Wilkinson (2005) similarly speculated that residual retention at harvest would facilitate the maintenance of small mammal populations through the long-term infusion of CWD into the cut block.

3.2.1.2.2 *Bats*

Forest habitat use by foraging bats is influenced by harvesting via effects on flight and indirectly through effects on prey and roost abundance (Patriquin and Barclay 2003). Vegetation density influences physical clutter, reducing flight efficiency and acoustical clutter for echolocation. The mobility of bats may allow them to avoid local disturbances by exploiting suitable habitat patches at a larger spatial scale. However, bats may face a trade-off between food-poor patches with minimal clutter versus richer but more cluttered habitats. Different bat species resolve this differently, depending on their size and manoeuvrability (e.g., large species with long narrow wings must fly more quickly and are therefore less manoeuvrable and therefore are generally limited to more open habitats). Erickson and West (2003 in Fisher and Wilkinson 2005) suggested that, based on structural studies of stands in western Oregon and Washington, bats should be able to use stands of any seral stage, provided the appropriate roosting structure—trees and snags—were present.

Comparative habitat use

Few studies of comparative habitat use by forest-dwelling bats have been done specifically within the boreal forest. Even fewer have examined the effects of logging treatments on forest bat activity, and most of these based their interpretations of bat response to logging on structural attribute associations established in comparative habitat use studies. Only two boreal studies that specifically examined the short-term response of bats to green tree retention were found (Hogberg, Patriquin, and Barclay 2002; Patriquin and Barclay 2003). There have been no long-term studies of bat response to structural retention.

When examined at the level of species groups, differential patterns of bat habitat use emerge. Jung et al. (1999) compared bat use of several forest types in Central Ontario, of which one was a boreal-type mixedwood. Their data supported predictions that old-growth forests are important for bat species and that logging in conifer-dominated forests reduced use by most bat species. In uncut forest, bat detection rates were correlated with canopy and subcanopy structure. However, silver-haired bats were recorded more often in uncut canopy gaps and subcanopy, and more often in logged stands than in the mature mixedwood type, while small bats (i.e., *Myotis* spp.) were recorded more often in unharvested forests (including the mixedwood) than logged forest, and more frequently in the canopy and above it.

Short-term responses - foraging and commuting activity

Patriquin and Barclay (2003) studied bat foraging and commuting activity immediately post-harvest in treated areas of clearcut, thinned (20% and 50% removal), and uncut forest within deciduous, coniferous and mixedwood forest in the EMEND (Ecosystem Management by Emulating Natural Disturbance) study area in the boreal mixedwood forest of northwestern Alberta. Use was evaluated at the scale of the treated “patch”, with mean patch size equal to 10 hectares and no direct study of structural attributes within forest types or treatments within forest types was conducted. By studying the response of individual species, they again found that foraging habitat selection was a function of body size and wing morphology. Smaller bats (i.e., *Myotis* spp.), such as little brown bats and northern long-eared bats, were more active in conifer-leading stands, perhaps due to the availability of resources such as roosts, but were not, overall, influenced by forest type, patch type or location (edge or centre of patch). Larger bats were more active in clearcut areas than any other treatment, including thinned patches, likely due to the absence of clutter. Habitat use for the two *Myotis* species differed, with little brown bats more active along the edges of deciduous clearcut areas. In contrast, clearcut areas reduced the activity of northern long-eared bats which were more likely to be found in intact uncut patches, presumably due to their ability to glean off foliage. The findings by Patriquin and Barclay (2003) indicated that thinning treatments had no short-term effect on bat foraging activity as compared to clearcut or uncut stands. However, the study did not address tree requirements for roosting habitat. They suggest there may be long-term implications of thinning treatments related to recruitment of large live and dead tree roost site opportunities which could be explored through longer-term studies.

The creation of forest-edge habitat associated with GTR practices may positively affect bats as many insectivorous bats prefer to commute and/or forage along edge habitats (Hogberg, Patriquin, and Barclay 2002). Insect abundance and diversity may be greater along edges; however, where insect abundance is greater in forest interior, bats still stay along the edge, suggesting other factors besides food availability. Manoeuvrability is likely key. However, interior forest may also offer shelter in the form of roost trees. Hogberg, Patriquin, and Barclay (2002) examined bat activity immediately post-harvest (1.5 years) at edges of cutblocks, the outside edges of residual tree patches (0.2-0.46 ha), and in the centres of the clearcut portions of cutblocks, again at the EMEND study area in northern Alberta. Their objective was to explicitly assess the effectiveness of patches of residual trees in cutblocks as bat commuting and foraging habitat. They too predicted that small manoeuvrable bats would use the edges of cutblocks and tree patches equally, while big bats would show no preference. As anticipated, *Myotis* species were equally active along edges, regardless of edge type, and least active in the centre of clearcut areas. Larger bat species (i.e., big brown bats, hoary bats and silver-haired bats) displayed no preference. They concluded that cutblocks that incorporate remnant patches do provide additional habitat for bats compared to clearcut areas; small bats were at the edges in higher numbers than in clearcut. They suggested that remnant patches increase in value if they offer both foraging (edge) and roosting habitats.

3.2.1.2.3 *Arboreal Squirrels*

Arboreal sciurids (i.e., squirrels) are a species group most likely to be heavily impacted by removal of live trees from a stand; they also may derive the most benefit from retention of live trees (see review in Fisher and Wilkinson 2005). In the boreal forest, the red squirrel is a conifer seed specialist, while the northern flying squirrel specializes in mycorrhizal hypogeous (summer) and epigeous (winter) fungi and lichen food sources (Wheatley 2007). Both species prey to a small degree upon insects and other protein sources (e.g., bird nests). Large live and dead trees are important attributes for dens and food sources.

Arboreal sciurids require a supply of live and dead trees in a stand for the short-term, as well as CWD for food source (e.g., hypogeous fungi and insects) and shrub cover for protection during foraging. Live residual trees provide for long-term recruitment of CWD into a stand which in turn provides cover, travel paths, burrow sites and a substrate for arboreal sciurid food such as fungi and lichen (see review in Fisher and Wilkinson 2005). Retention of live residual trees may facilitate maintenance of lichen within a stand, and/or foster lichen recolonisation of disturbed areas. Mature residual conifer trees provide seed, an important overwintering food source for red squirrels, which preferentially nest in large diameter trees. Based on understanding of habitat relationships, flying squirrels are expected to be largely absent from cutblocks without large residuals because of a lack of large old trees of food, den sites and cover. Red squirrels are also anticipated to be more abundant in old/mature stands because of cone crop dependency as well as fungi and other food sources.

In studies of old boreal mixedwoods, arboreal squirrels have been positively correlated with canopy heterogeneity, sapling density and large trees; northern flying squirrels were more specifically associated with white spruce, shrub and sapling densities, as well as intermediate decay stages of CWD, which support fungi and lichen (Roy, Stelfox, and Nolan 1995 and McDonald 1995, in Fisher and Wilkinson 2005). In addition, canopy gaps in old forests provided protective shrub cover for flying squirrels foraging on the ground.

Key findings on the short- and long-term responses of arboreal squirrels to GTR are summarised in Table 3.7 at the end of this subsection.

Short-term responses

Though response to clearcutting is variable in many studies, most find a general reduction of arboreal squirrel use in recently harvested sites (see review in Fisher and Wilkinson 2005). Thompson et al. (1989) is frequently cited as an example of reduced red squirrel abundance in young clearcut areas as compared to older cuts and uncut stands, as deduced from winter track counts.

Arboreal squirrels are often used as an indicator of forest structural complexity. As such, studies have been done throughout North America to examine their habitat use patterns and responses to site- and stand-level effects of alternatives to clearcutting. Carey (2003), for example, explored squirrel responses to variable density thinning to create canopy mosaic in second growth stands in the Pacific Northwest (PNW) five years after treatment. He found that thinning of “legacy” stands (historically clearcut but with live and dead trees and CWD maintained from preceding old growth) resulted in an immediate reduction in squirrel use, but use recovered within five years.

Holloway (2006) examined the impacts of partial harvesting on squirrel habitat use in white pine and hardwood forests in central Ontario, using live-trapping data to develop habitat models at stand and landscape scales. Northern flying squirrel and red squirrel densities were significantly lower in recently harvested (3-10 years since harvest) shelterwood pine stands than unmanaged stands. Harvested stands had undergone one or two cuts (seeding and first removal cuts) in a series of 3-4 cuts planned at approximately 20-year intervals to remove at least half of the overstorey. The reduction in use of shelterwood stands appeared to be a consequence of significantly lower densities of large (≥ 25 cm dbh) snags (mean 4.7 stems/ha) in recent (3-10 year old) shelterwood cuts versus old (100 years) forest (11.1 stems/ha), fewer large hardwood trees (mean 12.4 stems/ha in cut versus 27.4 stems/ha in uncut), and lower understorey stem densities on shelterwood cuts. While not significant, large spruce trees were less abundant after shelterwood harvest (3.2 and 8.1 stems/ha for shelterwood and old forest respectively). The densities of northern flying squirrels and red squirrels were strongly related to densities of large spruce, large hardwood trees, and snags in conifer sites (Holloway 2006). Large hardwood snags were a key nesting substrate (derived from radio-telemetry data), and spruce was the primary host tree of mycorrhizal hypogeous fungi. Shelterwood harvesting as practiced in central Ontario appeared to decrease density of large spruces and hardwoods below critical thresholds for

northern flying squirrels and red squirrels. In white pine dominated forests (Holloway 2006), models predicted that forest managers need to retain at least 8 spruce trees/ha ≥ 25 cm dbh, and 27 hardwood trees/ha ≥ 25 cm dbh to maintain northern flying squirrel densities in shelterwood stands at 80% of their mean level in old forest areas.

Pre- and post-harvest experimental manipulations are rare, particularly for boreal forest. In the boreal forest of northern Alberta, Fisher and Bradbury (2006) report on the response of red squirrels to mixedwood understorey protection (MUP) harvesting, where mature deciduous canopy trees are selectively removed (70-85% of deciduous overstorey removed) leaving some mature and immature trees in the overstorey and understorey (>55%), and promoting release of understorey conifers. Squirrel abundance, body mass and reproductive status were examined two years before and two years after harvest. Red squirrel abundance and masses were not statistically different pre- and post harvest. Across all stand types (conifer, deciduous, mixedwood reserve, MUP) red squirrel abundance was predicted by abundance of spruce trees and fungi. The authors concluded that MUP harvesting retains forest structure required by red squirrels and accelerates the ability of regenerating stands to maintain populations of mature-forest red squirrels. The persistence of red squirrels with MUP is sharply contrasted with clearcutting which renders the stand unsuitable for red squirrels (Thompson et al. 1989). The authors recommend longer-term monitoring because abundance can be misleading as a response variable. Poor habitats can be occupied by dispersing juveniles or non-reproductive individuals in poor condition, but that was not the case here. Squirrel mass and reproductive potential did not differ statistically between the MUP stands and uncut mixedwood benchmark reserves.

Responses to patch size

In a northern Alberta boreal study of red squirrel cone predation on seed trees left to achieve uniform dispersal of seed throughout cutover areas, Peters, Boutin, and Macdonald (2003) found that if spruce retention is high enough to allow squirrels to maintain territories in and adjacent to cutblocks (red squirrels utilize multiple stands within a territory), then local populations of red squirrels are maintained and seed trees are vulnerable to cone predation in the first 2-3 years post harvest. Seed trees represented 4.9-54.2% retention of pre-harvest spruce volume, retained as both single trees and in patches ranging from two to 50 + trees. Seed trees in large patches (>20 trees) had significantly more cone loss (i.e., higher squirrel use) than single trees.

In boreal Quebec, Potvin, Courtois, and Belanger (1999) undertook a pre- and post-harvest study of the effects of clearcut with understorey retention on various response groups. Though not specifically surveying for squirrels, a small number of red and flying squirrel captures as by-catch in Sherman live traps set for small mammals indicated that flying squirrels were only found in uncut controls, while there were low numbers of red squirrels in both uncut controls and clearcut areas. They concluded that squirrels need uncut forest habitat and can subsist in buffer strips as their home ranges are small enough to fit into linear fragments.

Bayne and Hobson (2000) found that red squirrel abundance increased slightly with forest fragment size in a fragmented agricultural landscape in the southern boreal mixedwood forest of Saskatchewan. Fragments ranged in size from 0.2 to 82 ha. They also compared squirrel abundance in forest fragments with that in contiguous forest and found that red squirrels were significantly more abundant in forest fragments than in contiguous forest and suggested that forest fragmentation might not be detrimental to habitat generalists like the red squirrel. They speculated that changes in dispersal patterns in fragmented forest habitats, higher squirrel survival in forest fragments, and differences in diet between contiguous and fragmented forest habitats contributed to this pattern.

Landscape effects

Both Peters, Boutin, and Macdonald (2003) and Potvin, Courtois, and Belanger (1999) noted the larger scales at which arboreal squirrels operate (i.e., territories and home ranges larger than the individual site or stand). Holloway (2006) obtained evidence that harvest of the surrounding landscape had additive effects for squirrels beyond the local site level; interspersed large harvested and unharvested blocks (15-45 ha) on the landscape may be important to ensure the persistence of red squirrels, and may also be important for northern flying squirrels. Fisher, Boutin and Hannon (2005) reported that red squirrels occasionally forage in young clearcut areas on seasonally available berries and fungi in the boreal forest, and that the juxtaposition of coniferous and deciduous stands and cutblocks is a positive predictor of summer presence of red squirrels.

Long-term responses

No studies of the long-term response of arboreal sciurids to stand-level structural retention practices in boreal forest were found. In fact, there are very few long-term studies of such responses anywhere. Carey (2003) reported that flying squirrels were twice as abundant in legacy stands with structural complexity, compared to simplified timber stands. In the former, stands harvested in 1937 maintained live and dead trees and CWD from preceding old growth. Simplified timber stands, however, were clearcut in 1927 and then conventionally thinned twice prior to the study, removing most of any legacy structure. Carey (2003) reported that flying squirrels remained rare (some of lowest densities ever recorded in PNW) in the simplified timber stands, perhaps due to dense homogeneous understorey that promoted excessively high and uniform chipmunk abundance, resulting in the competitive exclusion of arboreal sciurids through interspecific competition for the same food resources. Bayne and Hobson (2000) also note the potential for interspecific competition effects in relation to arboreal sciurid responses to enhanced structural retention. They caution that a positive arboreal sciurid response to enhanced retention, such as found in their study, may result in negative effects on other species, such as forest songbirds.

Table 3.7 Summary of Key Findings of Studies of Short- and Long-Term Arboreal Squirrel Responses to Green-Tree Retention Harvesting Practices (Non-boreal studies are highlighted in italics.)

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Ontario	White pine – deciduous mixed forest.	ST	Shelterwood harvesting appeared to decrease the density of large spruces and hardwoods below critical thresholds for northern flying squirrels & red squirrels.	Holloway (2006).
Alberta	Aspen – white spruce mixedwood.	ST	Mixedwood understorey protection harvesting retained forest structure required by red squirrels and accelerated the ability of regenerating stands to maintain populations of mature-forest red squirrels.	Fisher & Bradbury (2006).
Pacific North-west (PNW) United States	Douglas-fir – western hemlock temperate coniferous forest.	ST	Variable density thinning of second-growth stands resulted in an immediate reduction in squirrel use, but use recovered within 5 years.	Carey (2003).
Alberta	Aspen – white spruce mixedwood.	ST	Large patches (> 20 trees) had significantly more cone loss (i.e., squirrel use) than single trees.	Peters et al. (2003)
Quebec	Mixedwood & Black spruce-leading forest.	ST	Squirrels can subsist in uncut buffer strips (100 m wide) as their home ranges are small enough to fit into linear fragments.	Potvin et al. (1999).
Saskatchewan	Aspen – white spruce mixedwood.	ST	Red squirrels were more abundant in forest fragments (ranging from 0.2-82 ha in size) than in contiguous forest.	Bayne & Hobson (2000).
Ontario	White pine – deciduous mixed forest.	ST	Harvest of the surrounding landscape had additive effects for squirrels beyond the stand-level.	Holloway (2006).
PNW US; Saskatchewan; Ontario	Douglas-fir – western hemlock temperate coniferous forest; Aspen – white spruce mixedwood; White pine – deciduous mixed forest.	ST & LT	There is potential for interspecific competition effects in relation to arboreal squirrel responses to enhanced structural retention.	Bayne & Hobson (2000); Carey (2003); Holloway (2006).

3.2.1.2.4 *Marten and Fisher*

The American marten and fisher are large predatory mustelids typically associated with live tree canopy closure and abundant woody cover not generally found in young successional forest stages (see authors in Fisher and Wilkinson 2005). While young cutblocks contain a small mammal prey base exploitable by predatory mustelids, most data suggest that clearcut areas are avoided, or are sub-optimal habitat for the larger mustelids. Various authors (see Fisher and Wilkinson 2005) note that fishers tend to avoid cutblocks and young seral stages and prefer mature forests with high canopy cover and large CWD. Martens also avoid young cutblocks, regardless of available prey biomass. Although martens prefer mature forests with closed canopy cover, they will enter open areas like clearcut areas to forage.

Fisher habitat requirements

In Ontario, both of these species are highly susceptible to trapping, and both inhabit relatively mature, conifer-dominated forests. Fishers, however, will inhabit stands with fewer conifers and may occasionally thrive in hardwoods (Racey and Hessey 1989). Fishers avoid recently logged areas, probably due to lack of food, cover and/or den sites. Potential den sites include large, standing hollow deciduous trees (> 50 cm dbh) and openings in rock ledges (Racey and Hessey 1989). Mature-to-climax successional stages of conifer-dominated mixed forests provide an abundance of den sites for fisher and porcupines, an important prey item. Early successional mixedwood stands produce an abundance of small mammal prey items such as snowshoe hare, mice and voles, as well as small birds. A high degree of interspersion of early successional stages, to promote prey availability, and later successional stages to provide cover and den opportunities, is considered optimal.

Little research has been done on response of fisher to harvesting in boreal forest, and none on responses to stand-level structural retention practices. Recent work in south-central British Columbia has improved a general understanding of fisher habitat requirements and response to logging, including use of stands with a deciduous component, presumably due to higher structural complexity; avoidance of areas that are too complex, with > 80% closure of the low shrub layer (impedes hunting success of prey species such as hares); use of large pieces of CWD during extended periods of severe cold (< -20° Celsius); and avoidance of areas with < 50% canopy cover (fishers will inhabit second growth forest with sufficient cover) (Weir and Harestad 2003).

Marten habitat requirements

Martens are well distributed across North American coniferous forests, ranging from Alaska to Newfoundland, and from tree-line to the southern extent of coniferous forest (Watt et al. 1996). Their broad distribution and apparent dependence on old forest have resulted in their common use as a boreal management indicator species (e.g., in Ontario, marten ecological requirements must be met before any forest harvesting project can be approved) (Fryxell et al. 2004). Habitat structure required for healthy marten populations generally takes decades to develop and individual home range requirements are typically very large for such a small carnivore (Buskirk and MacDonald 1989 in Sturtevant, Bisonette, and Long 1996).

Marten population growth is limited by their low rate of productivity and by predation from other mammals and birds. Similar to fishers, martens also prefer mature or old coniferous or mixed forest with at least 50% crown closure (Allen 1982 in Racey and Hessey 1989). Snow depths beneath coniferous canopies are lower than either open areas or deciduous stands, and temperature regimes are also moderated by the overhead canopy (Watt et al. 1996). Intermediate levels of canopy closure between 40 and 70% seem to be preferred, while canopy closure less than 30% is avoided (see Watt et al. 1996). Cover is important for both travel and hunting although open areas can be used for both, particularly in the summer. As with fishers, martens also require standing or fallen hollow trees for

maternal dens and winter dens and resting sites. In winter, marten in Ontario use resting sites and dens that are well insulated below the snow (see Watt et al. 1996). Marten are opportunistic feeders, with voles, such as the red-backed vole and the meadow vole, dominating the diet, and larger prey items, such as snowshoe hares, gaining importance during winter (see Watt et al. 1996).

Marten likely choose older forests for thermoregulation and predator avoidance; dense canopy provides cover from goshawks and owls (see Sturtevant, Bisonette, and Long 1996; NSAMRT 2006). Their main mammalian predators—fisher, fox and lynx—are less abundant in older forests compared to successional stands, and tall trees provide elevated escape cover from coyotes. Several authors in Sturtevant, Bisonette, and Long (1996) reported that while canopy closure is often considered critical, the presence of vertical stem structure and CWD appear to provide adequate security, even when overhead cover is absent; the vertical stem structure of trees is reported to provide marten with escape cover from larger terrestrial predators (Drew and Bissonette 1996 in Sturtevant, Bisonette, and Long 1996). Older forests also offer more abundant and varied CWD, critical to facilitating prey availability as well as winter resting sites and dens, and maternal den sites. CWD relationships are discussed in more detail later in this review. However, NCASI (1999 in NSAMRT 2006) noted that despite the provision of CWD, marten will not use regenerating clearcut areas until a threshold of overstorey development is reached (between 14 and 18 m³/ha).

In northern Maine, Fuller and Harrison (2005) quantified marten habitat selection and their use and avoidance of partially harvested stands. Their results, based on extensive marten radiotelemetry, suggest that marten use of partial harvested areas varies by season. Marten incorporated greater amounts of partial harvested areas during the leaf-on season, when leaf cover was greater than 30%. However, marten incorporated less partial harvested areas during leaf-off season, and those marten with significant amounts of partial harvested areas in their home range tended to have larger home ranges, all else being equal. The authors suggested this was a result of a prominent prey item, snowshoe hare, being least abundant in these habitats.

Recent literature presents anecdotal and experimental evidence that martens require structure associated with later-successional stages, but not necessarily old forest itself (Sturtevant, Bisonette, and Long 1996), and may be able to sustain themselves in regenerating forests with sufficient suitable structure (see authors in Fryxell et al. 2004). Despite 50 years of intense timber harvesting in Ontario, resulting in reduced availability of mature forest habitat, there has been no demonstrable decline in numbers of marten harvested by trappers (Novak et al. 1987 in Fryxell et al. 2004). Although it appears that marten are not as restricted to late successional forest as once thought (e.g., Payer and Harrison 2003, 2005), it is clear that they require forests characterized by complex physical structure which tends to accumulate with age; they generally avoid most successional stands younger than 30 years (see NSAMRT 2006). Several authors (in Sturtevant, Bisonette, and Long 1996) note that subsequent second-growth forest from boreal clearcutting can have lower habitat quality due to absence of structural complexity. However, because of the dynamic nature of boreal forested systems, habitat reserves in clearcut matrices cannot be sustained in perpetuity unless they are large enough to ameliorate the impacts of natural disturbance over the long term (Liliehalm, Kessler, and Merrill 1993 in Sturtevant, Bisonette, and Long 1996). Therefore, second-growth forests may have to provide marten with a temporal window of habitat, supplying key structural attributes linked to cover and prey (Bissonette, Fredrickson, and Tucker 1989 in Sturtevant, Bisonette, and Long 1996). Immediately after clearcutting, there is a pulse of CWD and a strong herbaceous growth response providing abundant cover for voles and hares.

Marten use of logged forest

Marten tracks were most abundant in uncut forest (150-200 years) in Ontario than in any other age class of harvested stand (0-30 years) (Thompson et al. 1989). Martens were rarely found in harvested 40- to 60-year-old second-growth stands of balsam fir in Newfoundland, preferring older stands (Thompson and Curran 1995 in Fisher and Wilkinson 2005). Sturtevant, Bisonette, and Long (1996) reviewed and modeled marten habitat requirements and suggested that vital elements of marten habitat are found within over-mature stands. Potvin, Belanger, and Lowell (2000) found that martens avoided open regenerating cutblocks < 20 years old. Potvin and Breton (1997) found that martens exhibited higher natural mortality and dispersal rates in 1-20-year-old harvested landscapes. In Ontario, Thompson (1994) in Fisher and Wilkinson (2005) found that marten densities were 90% higher in uncut forests than in logged forests 0-30 years old. Martens in uncut areas were older than those in logged areas; mortality rates were higher in logged areas than in unlogged areas. Martens rarely stayed in deciduous stands longer than one year post-harvest; those that did, were often younger, experienced higher mortality, and had lower hunting activity and success rates (Thomas and Colgan 1994 in Sturtevant, Bisonette, and Long 1996). Results suggest that young clearcut areas might be population sinks for martens. Snyder and Bissonette (1987) in Sturtevant, Bisonette, and Long (1996) noted that, in Newfoundland, martens generally avoided clearcut areas < 15 years of age without residuals, instead preferring residual stands. However, some martens in their study area were trapped in this clearcut age class; these were resident adults, not juveniles or transients. This indicates that clearcut areas may be usable by martens, but at low densities. Several authors suggest there is a threshold response by marten to forest harvesting, and that the population response is abrupt and nonlinear when the threshold is exceeded (NSAMRT 2006). Clearcutting also alters the species composition of prey, and may restrict hunting opportunities, particularly in winter when marten rely heavily upon snowshoe hare in parts of Ontario (see Racey and Hessey 1989).

The landscape pattern of cuts also influences marten distribution; martens were nearly absent from landscapes where > 25% of the land base had been recently harvested (Hargis and Bissonette 1997; Hargis, Bissonette, and Turner 1999 in Fisher and Wilkinson 2005). In Quebec, Potvin, Courtois, and Belanger (1999) reported the mean size of an annual marten home range to be 9 km² and to encompass more than a single clearcut patch (100-250 ha). They therefore concluded that marten responses are a landscape-level issue. According to several authors (see Racey and Hessey 1989), clearcutting stands in Ontario results in increased home range sizes and reduces marten density. Sturtevant, Bisonette, and Long (1996) noted that marten home ranges in Newfoundland were typically an order of magnitude larger than the average defoliated patch, (ranging in size from 1-100 ha) caused by spruce budworm and hemlock looper (i.e., the primary form of natural stand-replacing disturbance in the wet boreal). They noted that these defoliated patches can act as reservoirs for voles in the landscape, offering temporal windows of foraging habitat for marten.

Available research

A robust body of work exists for marten responses to clearcut logging in the boreal forest, but the bulk of it focuses on habitat selection at the landscape scale. Until recently, very little work has been done to examine marten response to stand-level structure resulting from logging. Most studies are simple comparative habitat use studies in retrospective settings, relying on stand inventory data layers to provide information on age and species composition, both of which are used as surrogates for structural composition and complexity. Experimental frameworks involving manipulative experiments with pre- and post-treatment data were rarely found in this review. There were no studies available specifically looking at marten response to stand-level structural retention practices. As noted, most studies were tracking or telemetry studies conducted in retrospective landscapes with either recent or older clearcut mosaics. Some were conducted in summer; many in winter; a few in both seasons. Some studies were of commercially trapped populations, which significantly affects

density response. Fur trapping interacts with natural demographic processes in most forests in Ontario in determining marten population trajectories (Fryxell et al. 2004).

To date, research has focused on marten habitat use patterns in response to logging as a landscape-level forest management issue. Live tree retention has been given limited consideration, in its capacity as patches of residual forest and unharvested corridors left within the clearcut matrix. Recent research has begun to explore relationships between the apparent requirement for old forest relative to the structural attributes (e.g., CWD, stem density) and complexity offered by such older forest. If sufficient old forest is not left on a landscape, then how can a manager best enhance the clearcut matrix at the time of, and subsequent to, harvest through residual forest patches, structural retention, and stand management practices to a) offer bridge habitat during stand regeneration and b) hasten the rate of recovery with regards to structural and functional complexity?

This review reports on only those boreal studies that clearly address marten response to stand structure. Where informative from a stand-level perspective, marten responses to live tree residual forest patch and corridor retention in clearcut landscapes is also considered.

Key findings on the short- and long-term responses of marten to live-tree structure are summarised in Table 3.12.

Regional trends

Confounding the systematic synthesis of information on marten responses to structural retention practices and logging in general is the broad distribution of the species across the northern and southern reaches of the boreal forest. As noted by Payer and Harrison (2005), studies conducted in different regions of the boreal have yielded inconsistent results. Martens selected late successional, conifer-dominated forests in boreal regions of central Canada; deciduous forests and mid-successional second-growth forests were generally avoided in these regions (Thompson and Curran 1995 in Payer and Harrison 2005). However, martens in boreal forests of Quebec (Potvin, Belanger, and Lowell 2000) and the transitional forests of Maine did not select against deciduous stands (see Payer and Harrison 2005); stands with extensive spruce budworm-caused mortality in Maine had the highest selection index of all stand types (Chapin, Harrison, and Katnik 1997 in Payer and Harrison 2005).

Because of regional differences in stand-scale habitat associations Payer and Harrison (2005) suggested that stand age and tree species composition are poor surrogates for within-stand habitat components required by martens. Habitat requirements are best described in relation to the complex physical structure provided by CWD, shrubs, low-hanging branches, and multi-storied overhead cover (Buskirk and Powell 1994 in Payer and Harrison 2005). Bowman and Robitaille (1997) in Payer and Harrison (2003) found that 100 m² quadrats used by martens in second-growth boreal forest in Ontario had more downed logs and snags, taller trees, and greater canopy closure than unused quadrats (Bowman and Robitaille 1997 in Payer and Harrison 2003).

However, prey availability and forest compositions vary widely across the area of boreal marten distribution. For example, marten require a range of available prey and exploit prey of different size and species seasonally; however, Newfoundland supports a depauperate small mammal fauna, distinct from other populations across the boreal (Sturtevant, Bisonette, and Long 1996). Meadow vole is the only microtine (i.e., no red-backed voles), plus masked shrews and snowshoe hares. Red squirrels, deer mice and eastern chipmunks are recent additions that may be locally abundant. Because relationships between mammals and their habitat vary from one region to another, studies should be conducted to identify regionally-specific associations (Ray 2000 in Hodson et al. 2004).

Habitat selection studies and the role of live tree residual patches in short-term responses to logging within landscapes

Fisher and marten tend to prefer some woody canopy cover (see cited authors in Fisher and Wilkinson 2005) so the presence of residual forest patches should facilitate occupation of a cutblock. Fisher and Wilkinson (2005) cite extensive studies on marten which they suggest corroborate the importance of post-fire live tree skips and residuals to survival and reproduction. To what degree these skips and residuals play a role in the persistence of marten populations in harvested landscapes is under debate. Potvin and Bertrand (2004) reported marten tracks in 33-40% of surveyed forest strips within black spruce-dominated clearcut (clearcut with protection of regeneration or CPR) landscapes in southwestern Quebec. CPR (also referred to as CPRS or clearcut with protection of regeneration and soils) involves harvesting all commercial stems using a network of logging trails spaced 10-15 m, while protecting small diameter trees (<10 cm dbh), shrubs and ground cover between the trails (Ferron, Potvin and Dussault 1998). Potvin and Bertrand (2004) considered their results misleading, however, possibly due to a bias in track count methodology. Although forest strips were used by marten in their studies, Chapin, Harrison, and Katnick (1998) and Potvin, Belanger, and Lowell (2000) both report that landscapes where clearcut areas covered > 60% of the area were not considered suitable habitat for marten.

In an experimental pre- and post-harvest treatment versus control study examining short term responses of various wildlife species to CPR harvesting in western Quebec, Potvin, Courtois, and Belanger (1999) found that species such as marten, with home ranges $\geq 5 \text{ km}^2$, remained in some residual forest patches scattered throughout clearcut areas and in the adjacent uncut forest. Marten was studied at the whole-block scale, with trapping success used as an index of density, and telemetry relocations collected over four years to measure the effects of clearcutting (CPR) on space use, movements, survival, and habitat selection.

Martens frequenting cutovers had larger home ranges than those living only in adjacent uncut forest ($P < 0.10$) (Potvin and Breton 1997). Within home ranges, martens avoided clearcut patches except when patches had a dense shrub layer and coniferous regeneration (Ferron, Potvin, and Dussault 1998). After logging, marten used the same home ranges or were found only in the adjacent uncut forest if the proportion of clearcut exceeded 40-60%. No marten home ranges were composed solely of clearcut areas or buffer strips. Martens living in a clearcut landscape were dependent on uncut forest patches $> 1 \text{ km}^2$. Potvin, Courtois, and Belanger (1999) concluded that buffer strip management in a clearcut matrix did not work for marten. It takes a buffer strip 1.7 km long x 60 m wide to provide 10 ha of forest and such a narrow fragment has many risks associated with edge and lack of interior for security.

Potvin, Belanger, and Lowell. (2000) analysed winter home ranges to measure marten habitat selection in 1992 and 1993, immediately post-logging, in a black spruce-dominated clearcut boreal landscape (123 km²) in western Quebec. The landscape consisted of a centre cutover matrix (74 km² or 60%) surrounded by contiguous uncut forest. Forty-four percent of the landscape was regenerating stands, much of which dated from 1992 when 28% of the block was clearcut with CPR. The residual forest within the landscape was fragmented and composed of narrow corridors 40-100 m wide along streams and permanent brooks or between individual clearcut areas, and small patches of uncut forest reserves, non-commercial young stands and non-productive areas. Telemetry data were analyzed at the landscape scale (i.e., home range composition measured against random mosaics) and the stand scale (i.e., use vs. availability within home ranges) using relocations with individual animals as the sample units. Within-stand habitat surveys were used to characterize CWD, coniferous saplings and trees, and lateral cover (i.e., visual obstruction).

Table 3.8 Summary of Key Findings of Studies of Short- and Long-Term Marten Responses to Residual Live-Tree Structure (Non-boreal studies are highlighted in italics.)

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Newfoundland; Fennoscandia; Maine.	Balsam fir-dominated wet boreal forest; Scots pine & Norway spruce coniferous forest; Acadian forest.	Short-term (ST) & Long-term (LT)	Marten require structure associated with later-successional stages, but not necessarily old forest itself	Sturtevant <i>et al.</i> (1996); Brainerd & Rolstad (2002); <i>Payer & Harrison (2003)</i> .
Maine; Ontario.	Acadian forest; Coniferous & mixedwood forests.	ST & LT	Regional differences in stand-scale habitat associations indicate that stand age and tree species composition are poor surrogates for within-stand habitat components required by martens; but other authors have found these surrogates were successful in characterising stand structure used by marten.	<i>Payer & Harrison (2005)</i> ; Bowman & Robitaille (2005); Hodson <i>et al.</i> (2004).
Ontario; Maine.	Coniferous & mixedwood forests; Acadian forest.	ST & LT	Structure may be a stringer stand-level determinant of habitat suitability than species composition; but others have failed to identify structural variables that reliably differentiated area of low & high use.	Bowman & Robitaille (2005); <i>Payer & Harrison (2003 & 2005)</i> .
Ontario.	Coniferous & mixedwood forests.	ST & LT	Marten make decisions at larger scales about where to locate home ranges, and that finer scale decisions will be constrained by these larger scale patterns.	Bowman & Robitaille (2005).
Maine; Newfoundland.	Acadian forest; Balsam fir-dominated wet boreal forest.	ST & LT	Defoliated stands provided suitable marten habitat, with vertical structure provided by large snags and surviving live trees, off-setting the reduced live-tree basal area of the defoliated stands; Marten perceive stem structure as decreasing predation risk, but selected areas with both overhead cover and woody stem structure, as opposed to areas with one or the other.	<i>Payer & Harrison (2003)</i> ; Drew (1995).
Ontario.	Jack pine & Black spruce-dominated coniferous & mixedwood forests.	LT	Fluctuation in prey abundance is an important source of environmentally-driven variation in marten density; Subnivenean access points provided by regenerating trees did not translate into improved hunting success in logged stands with reduced CWD abundance.	Fryxell <i>et al.</i> (2004); Andruskiw (2003); Andruskiw <i>et al.</i> (2008).

Table 3.8 Continued

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Quebec	Black spruce-dominated coniferous forest, deciduous forest, and mixedwoods.	ST	Large clearcut areas in boreal forest, even with CPR, have a negative effect on marten; could not tolerate > 30-35% cut-over within home ranges.	Potvin <i>et al.</i> (2000).
Quebec; Fennoscandia.	Black spruce-dominated coniferous forest, deciduous forest, and mixedwoods; Scots pine & Norway spruce coniferous forest.	ST & LT	American marten (AM) selected against open habitats and did not select conifer stands, regardless of age; AM preferred deciduous & mixed stands with well-distributed tree stems and dense coniferous shrub cover; Eurasian marten (EM) were reluctant to use clearcut areas when resting and avoided open habitats all the time; EM preferred tall spruce all the time.	Potvin <i>et al.</i> (2000); Brainerd & Rolstad (2002).
Quebec	Black spruce-dominated coniferous forest, deciduous forest, and mixedwoods.	ST	Buffer strip management (40-60 m wide residual strips between CPR clearcut areas) in a clearcut matrix did not work for marten.	Potvin <i>et al.</i> (1999).
Newfoundland	Balsam fir-dominated wet boreal forest.	LT	Thinning second-growth stands before trees enter the stem-exclusion zone may promote understorey vegetation & CWD, enhancing small mammal prey-base in mid-successional stands.	Sturtevant <i>et al.</i> (1996).
Maine	Acadian forest.	ST & LT	Minimum structural thresholds for marten have been conservatively estimated at basal area $\geq 18 \text{ m}^2/\text{ha}$ for trees $\geq 7.6 \text{ cm dbh}$; $\geq 75\%$ overhead canopy.	Payer & Harrison (2003).

Marten clearly selected against open habitats, avoiding open regenerating stands composed mostly of recent clearcut areas with sparse regeneration. Contrary to findings of other studies, marten did not select conifer stands, regardless of age. Rather, stands with coniferous regeneration were used in proportion to their availability. However, there was a significant ($p < 0.05$) preference for deciduous and mixed stands, a large proportion of which had a dense coniferous shrub layer as result of a spruce budworm (*Choristoneura fumiferana*) epidemic 15-20 years prior. Though the number of coniferous stems (0-1.3 m tall) was similar in deciduous and black spruce stands, deciduous stands had denser lateral cover (83 vs. 71-72%). Generally, mature or overmature coniferous forests are thought to provide marten with predator avoidance, prey abundance and needed structural elements (see Potvin, Belanger, and Lowell 2000). However, to minimize predation, marten appear to need well-distributed tree stems and dense coniferous shrub cover, not necessarily a mature or overmature stand. As noted by Potvin, Belanger, and Lowell (2000), prey are not necessarily associated with old forest; red backed voles can be present in all successional stages of black spruce and balsam fir stands and snowshoe hare, generally found in young forest, is often marten's major prey in winter.

Winter home ranges were different from random mosaics, with a larger proportion of uncut forest (> 30 years), larger core area of forest habitat, and less edge between open regenerating stands and uncut forest. Home ranges had < 30-35% open or closed regenerating stands and > 40-50% uncut forest. Potvin, Belanger, and Lowell (2000) concluded that large clearcut areas in boreal forest, even with CPR harvesting, have a negative effect on martens; they could not tolerate more than 30-35% cutover within their home range. Consistent with other authors (e.g., Bissonette, Fredrickson, and Tucker 1989; Thompson and Harestad 1994, in Potvin, Belanger, and Lowell 2000), Potvin, Courtois, and Belanger (1999) and Potvin, Belanger, and Lowell (2000) recommended a landscape management approach to protect or improve habitat. Recommendations to maintain marten habitat at the local scale in the black spruce forests of western Quebec included preserving $\geq 50\%$ uncut forest inside 10 km² units, and clearcutting < 30% of the area over a 30 year period; uncut forest patches should be large (> 100 ha) to maximize core area and edge with open cutovers should be minimized. Clearcut areas need not be small because large cutovers would create large older forest blocks within 30 years.

Note that Potvin, Belanger, and Lowell (2000) commented that they did not examine source-sink dynamics, so they did not know if large uncut blocks are needed to maintain viable populations. The Nova Scotia American Marten Recovery Team (2006) comment that an important deficiency in most recent marten studies is the lack of consideration that habitat may be optimal or suboptimal or that a range of habitat conditions occur. They express the concern that marten may "make do" with available habitats, but have lower net annual productivity and shorter life spans. They suggest that research is needed to assess whether or not this is the case for Nova Scotia marten, and what effect if any this may have on the population's viability.

Modeling Structural Requirements for Stand-level Retention

Sturtevant, Bissonette, and Long (1996) constructed a conceptual model of stand-level dynamics from an empirical study of forests in western Newfoundland and related this to the habitat associations of resident marten. The model suggested that the critical elements of marten foraging habitat are currently found within a senescent forest stand structure. In order to promote these within managed forests, intensive silviculture is necessary, with a density management regime designed to provide a marten habitat window within a reasonable pulpwood rotation period. Sturtevant, Bissonette, and Long (1996) recommended preventing stands from entering the stem exclusion phase using thinning techniques to promote understorey vegetation and providing a potential small mammal resource. In addition, supplying logs at ground level would further increase habitat potential for voles and allow marten to access this prey resource in winter. The authors suggest that this type of stand-level

management should be incorporated into an overall landscape-level management strategy such as that suggested by Bissonette, Fredrickson, and Tucker (1989).

Using snow tracking data and an empirical habitat model from northeastern Ontario, Bowman and Robitaille (2005) set out to validate three expert-based, non-spatial habitat models, including Allen's original 1982 U.S. Fish and Wildlife Service Habitat Suitability Index (HIS) model. All models used existing forest inventories; CWD is not available in these inventories. They found that the expert models were able to characterize stand structure used by marten despite using inputs from stand inventories because stand structural elements such as CWD and high canopy closure were integrated into the models indirectly through relationships with stand age and species composition; i.e., empirical and expert models considered suitable forest stands to be those stands with tall trees (proxy for age) dominated by spruce and balsam fir with large amounts of CWD and high canopy closure. This finding is contrary to the suggestion of Payer and Harrison (2005), who suggested that regional inconsistencies in stand-scale habitat associations indicated that stand age and tree species composition were ineffective surrogates for capturing within-stand habitat components required by martens.

The Ontario Wildlife Habitat Analysis Model (Naylor et al. 1999) and the Habitat Suitability Matrix (HSM; D'Eon and Watt 1994) tried to indirectly integrate CWD through inclusion of development stage (proxied by tree height in some cases) and species composition inputs. Older stands tend to have more CWD as do stands consisting of boreal softwoods. Empirical model scores suggested these expert models did a reasonably good job of capturing components of stand structure important to marten.

Non-spatial, stand-level habitat models do not adequately reflect marten fitness since marten range over territories much larger than a typical stand. Thus, the composition and configuration of forest landscapes (i.e., multiple stands) may contribute significantly to marten fitness (Dunning et al. 1992 in Bowman and Robitaille 2005). Bowman and Robitaille (2005) recognized that marten make decisions at larger scales about where to locate home ranges and so forth, and that finer scale decisions will be constrained by these larger scale patterns. Stand-level, aspatial models should be used in conjunction with larger scale spatial models for habitat management.

Habitat selection studies and the role of live tree residual patches in long-term responses to logging within landscapes

Brainerd and Rolstad (2002) reported on within-home range habitat selection by Eurasian pine martens in managed forests in two study areas in Norway and Sweden, near the southern limit of the boreal forest zone. The study areas represented contiguous regenerating stands of several hundred hectares, now about 80 years old, under intensive timber utilization since the mid-1600s, and subject to continuous clearcutting (5-50 ha openings) and replanting since 1950. In these forests, martens preferred spruce-dominated stands with large (≥ 20 m tall) trees and avoided recent clearcut areas and open habitats. Stand height and age were highly correlated, yet many stands < 70 years had attained heights of > 20 m due to high site productivity. Although marten exhibited selection and avoidance of certain habitat types, they were able to exploit a wide range of successional stages. Brainerd et al. (1994 in Brainerd and Rolstad 2002) found pine martens displayed a generalised use of forest habitat types relative to age, again concluding that forest structure, rather than age *per se*, was influential. Habitats that increase fitness by increasing the chances of survival and reproduction should be preferred to those that do not, regardless of management history (Brainerd and Rolstad 2002). The authors hypothesized that mature spruce forests harbour a great variety of prey species and afford escape cover from the marten's primary predator, the red fox. Most of the forest stands were even-aged and lacked a developed understorey. Rocky glacial till provided abundant underground access points for foraging and resting.

Activity modes on telemetry collars in both seasons allowed authors to examine selectivity during active (movement, hunting, dispersal) and inactive (resting) periods. Within home ranges in the summer, marten avoided open habitats all the time and clearcut areas only when they were active. They used clearcut areas in proportion to availability, presumably for hunting. They were reluctant to use clearcut areas and open areas when they were resting, and avoided open habitats, presumably due to predation risk, though prey availability may have influenced their response. Similar to the way in which American martens often rested in red squirrel middens in Alaska (Buskirk 1984 in Brainerd and Rolstad 2002), Eurasian pine martens relied heavily on nests of Eurasian red squirrels in spruce trees as resting sites; these features were unavailable in clearcut and open habitats. Marten preferred tall spruce all the time, regardless of season. In the winter, there was no selection difference between active and inactive modes.

In 2003, Hodson et al. (2004) set baited track plates in forests logged from 1960 to 2000, as well as in primary forests stratified into mature conifer (80+), mature deciduous (60+) and old growth (121+). Their objective was to address the aforementioned issue of regional habitat use patterns raised by researchers such as Payer and Harrison (2005) and Ray (2000 in Hodson et al. 2004), specifically in the context of the regional applicability of the Ontario Ministry of Natural Resources guidelines for provision of marten habitat to the Temagami-Algonquin region of central Ontario.

Preliminary results indicated a greater proportion of track plates in deciduous mixedwood and deciduous forest types had marten detections relative to those placed in coniferous and conifer mixedwood, but sample size was too low to evaluate statistical significance. Preliminary results were consistent with those from western Quebec and Maine, but inconsistent with boreal Ontario and Algonquin Park where marten preferred conifer dominated forests. The mature hardwood site, which had greatest number of detections, lacked the CWD observed in younger deciduous stands (within a 1970s logged site). However the mature deciduous site did have a substantial conifer understorey density which may offset the limited overhead cover which results under a deciduous canopy in leaf-off conditions. The authors suggested that these preliminary results were consistent with recent findings that structure may be a stronger stand-level determinant of habitat suitability than species composition. They suggested that a valid habitat suitability model might incorporate more accurate measures of forest structure (e.g., CWD). This is not supported by the findings of Bowman and Robitaille (2005) reported above.

Payer and Harrison (2003, 2005) conducted an examination of marten habitat use in relation to forest structure in an industrial forest (2003) and in an adjacent unharvested reserve (2005) in the transitional forests of Maine, on the boundary between the boreal and northern hardwood forests. Forests in this transitional zone appear to be more structurally complex than most boreal forests. Higher structural complexity may explain more generalized habitat use observed at the scale of a forest stand in the transitional forests of Maine and Quebec (Payer and Harrison 2005). The reserve was a second-growth, 55-km² wilderness area with no recent harvesting or trapping, comprised of 70- to 100-year-old deciduous, coniferous and mixed stands dotted with regenerating stands from a spruce budworm epidemic. These affected stands had abundant CWD, < 50% canopy closure, and a dense understorey layer. All habitats were used by resident, adult marten. Structural differences between high marten use and low marten use areas were small and the authors could not identify structural variables that reliably differentiated areas of low versus high use. They concluded that forest structure occurred at or above minimum thresholds required by marten throughout the study area, which had high marten densities and was dominated by mature, well-stocked forest.

In the industrial forest, used and unused areas were distinguished by characteristics related to stand maturity. Unused areas were generally young, regenerating stands clearcut between 1974 and 1982. Used areas had higher basal areas and densities of live trees, taller trees, greater snag volume, and denser overhead canopy. Spruce budworm defoliated stands had greater volumes of snags, downed

logs and root masses, and included taller trees and higher basal areas of live trees than regenerating clearcut areas (Payer and Harrison 2000 in Payer and Harrison 2003). Defoliated stands provided suitable marten habitat; vertical structure was provided by large snags and surviving live trees in combination with plentiful CWD and understorey vegetation. These characteristics offset the reduced live-tree basal area of these defoliated stands as compared to intact mature stands.

Overall estimates for forest structural characteristics in areas occupied by martens in an intensively managed industrial forest (Payer and Harrison 2003) were used as conservative estimates of minimum structural thresholds for martens (these were uniformly exceeded across the wilderness forest). In the industrial study area, suitable marten habitat had approximately 100 m³/ha CWD (interquartile range: 52-170), including 900 sound to moderately rotten downed logs/ha with a minimum diameter of 7.6 cm; root masses (63/ha), standing dead trees (160/ha) and stumps (290/ha) also contributed to available CWD; basal area ≥ 18 m²/ha for trees ≥ 7.6 cm dbh; $\geq 75\%$ overhead canopy; and dense understorey vegetation (approx 15000 woody stems/ha).

Structurally-mediated responses

Fryxell et al. (2004) reported on a cohesive research program in northwest Ontario aimed at exploring causal relationships behind observed patterns of marten habitat use. Researchers are attempting to understand the role of mature forest patches as potential source habitats, and the potential ability of martens to sustain themselves in most forest landscapes, regardless of habitat composition. An unlogged control landscape (1000 km², natural origin, 40-100 years old) was paired with two non-contiguous logged landscapes (200 and 800 km²) of 20- to 50-year-old regenerating stands; all stands were jack pine and black spruce leading. One key difference between logged and unlogged forests was the abundance of CWD on the forest floor, with logged forests being relative depauperate.

As reported by Fryxell et al. (2004), early data showed a positive association between vole abundance and deciduous composition. This suggests that conifer stands, which are often preferred marten habitat, do not necessarily supply higher abundance of prey in this region of Ontario. Variation in marten density over time and space was “plausibly related” to variation in prey density across time and landscape treatment (note: small sample size). This suggests that fluctuation in prey abundance is an important source of environmentally-driven variation in marten density in northern boreal forests.

As part of this larger initiative, Andruskiw (2003) conducted an investigation into habitat-mediated variation in predation risk of marten prey species (Andruskiw et al. 2008). Red-backed voles were abundant in both logged and unlogged forests; voles were likely at a peak in their cycle during the study period. Prey choice was simple for marten in the unlogged study forests; red-backed voles were the most abundant and used prey type due to the near absence of any larger prey. Prey choice was more complex in logged forests, where a substantial number of snowshoe hares were present (Andruskiw 2003). No attacks on hares were observed, however, and snowshoe hares were postulated to have higher pursuit and handling costs relative to the abundant voles.

Marten investigate breaks in the snow surface around CWD structural elements and smell or listen for prey at the upper openings of subnivean access points (i.e., any hole in the snow large enough and deep enough for a marten to enter to the forest floor [diameter ≥ 10 cm]). These points are generally located around CWD, tree trunks and low hanging branches of young trees. Despite having lower levels of CWD, the availability of subnivean access in regenerating forests was not reduced relative to uncut stands ($P = 0.948$) (Andruskiw 2003). Additional access was created in these regenerating stands by low-reaching branches of young conifer trees. However, marten hunted with less success in regenerating forest as compared to uncut forest. Encounters with small mammals per access point in regenerating forest were 41% less frequent than in uncut forest ($P < 0.001$). Marten home ranges in regenerating forest had 30% less CWD from all decay classes (1-5) combined than those in uncut forest, and 55% less when they considered only CWD in decay classes 1-3 ($P < 0.001$). Differences in

predation efficiency were linked to higher abundance of CWD, which seems to offer sensory cues to martens, thereby increasing the odds of hunting success. In this system, search efficiency was most affected by habitat complexity, rather than probability of successful capture once prey was encountered. Structural habitat complexity enhanced the efficiency of predatory search.

The association of marten with late-seral forest habitats has been linked to requirements for access to subnivean prey and thermally advantageous resting sites. However, Drew (1995) posited that the risk of predation could account for association with these habitats. The author tested for a response to predation risk in western Newfoundland and Yellowstone National Park in Wyoming by using bait boxes offered at various distances from the edge of three habitat types; he provided a spectrum of habitat cues while holding food resources constant. He found no difference in the use of bait boxes in old growth (80- to 100-years-old; Drew, *pers. comm.*) versus defoliated habitats, indicating foliar cover may not have a strong influence on predation risk in winter. Marten used bait boxes to greater extent in old growth than those in open habitats lacking both foliation and stem structure ($P < 0.001$) suggesting marten perceive stem structure as decreasing predation risk. However, in captive experiments, marten selected areas with *both* overhead cover and woody stem structure, as opposed to areas with just one or the other; both structural attributes were apparently required to reduce the perception of predation risk (Drew 1995).

3.2.1.2.5 *Ungulates*

Availability and quality of forage, thermal protection and security (or escape) cover are critical habitat elements for ungulates during winter (Stelfox, Roy, and Nolan 1995). Harvesting and wildfire can influence availability of these at multiple spatial scales (e.g., Mansson et al. 2007). However, given the large home ranges of ungulates, much of the focus of research into disturbance-induced changes in habitat availability has been at the landscape scale. At the stand level, there have been relatively few studies of ungulate responses to structural retention. No studies of caribou or white-tailed deer responses to stand-level structural retention could be found in this review (but see Fisher and Wilkinson 2005 for a summary of the responses of these species to wildfire and clearcutting). As such, this review is largely limited to studies of moose responses. White-tailed deer are likely to respond in fairly similar ways to habitat disturbance, but are generally considered more sensitive to the availability of thermal and security cover (Stelfox, Roy, and Nolan 1995; Fisher and Wilkinson 2005).

Comparative habitat use studies have shown that moose make extensive use of young forest post-disturbance in winter (up to 30 years old) relative to older forest-age classes (Fisher and Wilkinson 2005; Mansson 2007), although Stelfox, Roy, and Nolan (1995) found moose made significant use of old (120+ years) mixedwood stands, exploiting early seral vegetation in canopy gaps. No trends in habitat use in summer are apparent (e.g., Stelfox, Roy, and Nolan 1995; Fisher and Wilkinson 2005). The preference for young seral stages is attributed to the increased availability of forage in the form of grasses, shrubs and regenerating trees.

Historically, fire has been a key disturbance factor maintaining young seral stages in boreal forest, but in the presence of fire suppression, forest harvesting has become a significant disturbance agent maintaining moose forage (Fisher and Wilkinson 2005). Moose make extensive use of recent clearcut areas, selecting them over other habitat types (Crête et al. 1995, in Fisher and Wilkinson 2005; Edenius et al. 2002; Mansson et al. 2007). Moose numbers are known to significantly increase with the amount of harvesting in the landscape (Forbes and Théberge 1993 in Fisher and Wilkinson 2005) to the extent that they can significantly retard forest regeneration (Edenius et al. 2002; Mansson et al. 2007). Thompson and Curran (1993) in Fisher and Wilkinson (2005) studied moose browsing activity in cutblocks of different ages and sizes, and found that cuts aged 7-10 years provided the most winter forage. Within this age range, cutblocks 4-50 ha in size were utilised most by moose. So, abundance

of forage is not the sole predictor of moose usage of young cutblocks; distance from edge and available cover also influence moose presence.

Green-tree retention has the potential to modify moose responses to clearcutting via influences on all the critical habitat elements identified above. However, studies have focused on short-term GTR influences on forage availability and security/escape cover.

Short-term GTR effects on forage availability

Bilberry (*Vaccinium myrtillus*) is one of the dominant understorey plants in Swedish boreal coniferous forests, and is a significant natural forage species for moose. Atlegrim and Sjöberg (1996) examined the effects of selective harvesting and clearcutting on the abundance, growth, survival, and reproductive investment and success of bilberry up to four years after harvest. They found that relative to uncut control stands, bilberry ground cover was significantly reduced by both harvesting methods. Neither treatment affected reproductive success. However, significantly lower shoot survival and growth of bilberry was observed in clearcut areas relative to selective cuts and uncut controls. They predicted that the combination of poor vegetative performance and reduced cover of bilberry in recent clearcut areas would result in a much slower recovery of this forage species, whereas recovery following selective cutting would be considerably quicker. The implications of this for herbivore response were not studied.

Conversely, Collins and Schwartz (1998) contend that selective harvest of overstorey trees in Alaska's boreal forest can significantly reduce forage availability for moose if conducted in a manner that does not emulate natural disturbance. They surveyed 96 harvest sites in south-central Alaska over a five-year period to examine the possible influence of overstorey retention, ground disturbance, and size of clearings, on moose habitat value, measured as hardwood regeneration success. Harvest areas ranged from 2 to 20 ha, averaging roughly 10 ha. They found that the best establishment of early successional hardwoods was consistently associated with complete or nearly complete overstorey removal and soil scarification. Selective harvesting resulted in poor regeneration of hardwoods and a shift in the understorey community to bluejoint reedgrass, a widespread grass species that can readily outcompete hardwood seedlings, and can completely colonise new openings in as little as one year after overstorey removal. Even where it occurs at low densities in mature forest, bluejoint can rapidly capitalise on any disturbance which reduces competition from overstorey species. Without significant disturbance to the organic layer of the forest floor through scarification or fire, a dis-climax herbaceous community dominated by bluejoint can result, potentially persisting for 25-100 years. Collins and Schwartz (1998) attributed poor performance of overstorey retention in creating browse for ungulates to the limited light and heat penetration essential for hardwood seedling development under the retained canopy, and to limited opportunities to scarify after harvest as retained trees interfered with machinery. They recommended that selective cutting not be conducted if enhancing moose habitat is one aim of forest management. No consideration of alternative silvicultural treatments such as post-harvest burning was made. Although observational in nature, this study illustrates the potential for deleterious effects of GTR on moose browse, if it is conducted in a way that is incompatible with the natural disturbance dynamics of the forest. It also illustrates the potential for conflict and trade-offs in maintaining multiple wildlife or biodiversity values at the stand scale if, for example, green trees were required for bird communities in these same forests.

Short-term responses to enhanced security/escape cover

The presence of live residual trees after fire or harvest enhances the probability of use of cutblocks by ungulates (Fisher and Wilkinson 2005). They report on a study from Ontario that showed moose preferred to stay near (within ~45 m) hardwood residuals adjacent to young cutblocks (Mastenbrook and Cumming (1989) in Fisher and Wilkinson (2005)). Browse surveys indicated that food availability was not limiting, so this pattern of foraging behaviour was considered more likely due to presence of security (or escape) cover, thermal cover and lower snow depth in the residuals.

The perception of predation risk by ungulates will vary according to the size and shape of cut-over areas, as well as the spatial pattern of residual patches (Rothley 2002 in Schmitz 2005, but see Edenius et al. 2002 for Fennoscandian boreal forest). In large recent clearcut areas, lack of security cover within the harvest area tends to concentrate foraging at the edges (Andren and Angelstam 1993 in Schmitz 2005), despite the high nutritional value of browse in the open. In forest types such as boreal mixedwoods, this can lead to differing stand development pathways within the regenerating stand, with increased white spruce recruitment around the edge and increased deciduous recruitment through the centre. Retention of residual patches within the block rather than just around the edges could be one way to mitigate the risk of predation perceived by ungulates, drawing them out to the centre of harvested areas and perhaps mediating aspen-white spruce interactions more evenly across the regenerating block.

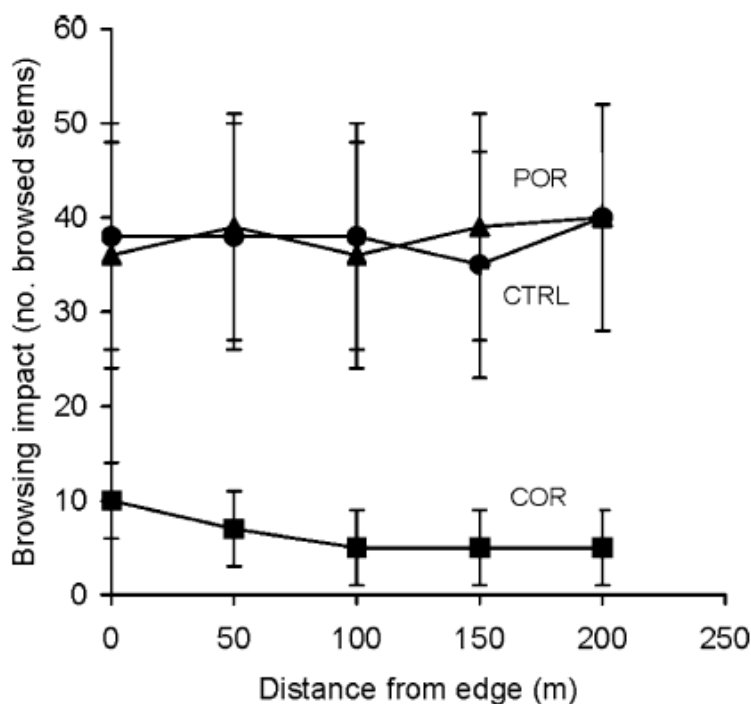


Figure 3.14 Effects of Different Harvesting Methods on Ungulate Use, Measured as Browsing Impacts, along a Gradient from Forest Edge to the Centre of the Treatment Area [Treatments: Clearcut or complete overstorey removal (COR); patch retention or partial overstorey removal (POR); and, unharvested control (CTRL). Values: mean and 95% CI (reproduced from Schmitz 2005, p. 232)]

Schmitz (2005) examined the influence of within-stand retention of residual patches on browsing activity by moose and white-tailed deer in the boreal mixedwoods of northwestern Saskatchewan. He compared herbivore foraging impacts under two harvesting treatments, clearcut and partial overstorey removal, relative to an uncut control in three harvesting areas. Harvested areas ranged from 55-90 ha. The partial overstorey removal resulted in 10-20 patches (averaging ~ 1 ha) of uncut timber left throughout the middle of the harvested area. Within a 250 X 250 m sampling grid, the number of stems browsed along five 250 m² belt transects spaced at 50 m intervals was measured as the index of ungulate use and impacts. He found that browsing activity in retained patches was similar to that in unharvested controls (Figure 3.14) and browsing activity was relatively uniform from the edge to the centre of the blocks. In the clearcut areas, browsing activity rapidly declined a short distance from the edge of the harvest area and remained low towards the centre (Fig. 3.14). By manipulating proximity of food and escape cover, patch retention resulted in a more even use of the harvest area by ungulates, potentially enhancing recruitment of white spruce across the stand.

3.2.1.3 *Amphibians*

Relatively few studies have been conducted on amphibian responses to structural retention practices in the boreal forest or elsewhere, and no long-term studies of amphibian response could be found. Amphibians use both freshwater and forest components of riparian habitats, and in some cases upland habitats. Management strategies that focus exclusively on buffer zones of uncut forest around breeding ponds or along streams may be unsuccessful for many species unless equal consideration is given to amphibian use of terrestrial habitats (Chan-McLeod and Moy 2007). Studies examining effects of forestry on amphibians in North America have produced mixed results (Hannon et al. 2002). Species considered most vulnerable to harvesting are those dependent on terrestrial microclimates and structures associated with older forest such as CWD, closed understorey and canopy layers, and deep leaf litter.

Short-term responses

Hannon et al. (2002) examined response of amphibians to various width buffer strips created around lakes in boreal mixedwood forests of north-central Alberta subject to clearcutting. They were particularly interested in amphibian responses to natural (i.e., lakeshore) and created (i.e., harvested) edge effects that may increase as buffer widths narrowed. Twelve lakes were selected for study with four treatments (20-, 100-, 200-, and 800-m-wide uncut buffers). Amphibians were sampled using pitfall traps one year pre-logging and two years post-logging of adjacent forest, with cutblock sizes ranging from 2 to 49 ha. Vegetation data were recorded at each study site, including: tree density, canopy cover, shrub density and CWD (% ground cover). They predicted that composition of amphibian communities would not change with buffer width, but abundance would decline as buffers narrowed. All four amphibian species known to occur in the region were captured: wood frogs, western toads, Canadian toads, and striped chorus frog. The latter species was excluded from analyses as it was found to readily climb out of the pitfall traps used. Contrary to expectations, they found no significant changes in either amphibian abundance or community composition across the different buffer widths. Similarly, no structural differences in the vegetation within the buffer strips were found. They concluded that the amphibian species in their study region appear to be resilient habitat generalists, found in a variety of vegetation types. This was supported by observations of all four species in the clearcut areas during the course of the study, including observations of breeding in temporary ponds created by harvesting.

Similar results for boreal amphibians were reported by Constible, Gregory, and Anholt (2001). They examined the response of surface-active amphibians to residual lake-edge forest adjacent to clearcut-with-retention (CCR) blocks, and burned areas in mixedwood and black spruce-leading boreal forest in Alberta. They studied 12 lakes in total (six in each of the harvested and burned areas). Within each

area, residual forest ranged from 60 m from lake-edge (CCR blocks), 375 m (CCR controls), 3-100 m (burned areas), and 200 m (unburnt controls). Using time-constrained visual searches to survey the distribution and abundance of wood frog and striped chorus frog, they found the highest numbers of both species at lakes associated with CCR blocks, with no consistent differences observed between logged and burned areas. However, their study was confounded by a number of factors, a major one being marked pre-treatment differences in habitat quality between the logged (mixedwood) and burned (black spruce) areas. Aspen-white spruce mixedwoods are generally considered high quality breeding habitat for wood frogs, whereas peat bogs in black spruce wetland complexes offer poor quality breeding habitat and may in fact be toxic due to low pH and high humic acid levels. Breeding habitat quality adjacent to each of the survey sites was assessed.

In temperate western hemlock forests of coastal British Columbia, Chan-McLeod and Moy (2007) studied responses of red-legged frogs to dispersed and patch retention harvesting practices. Radiotelemetry was used to measure the movement responses of the frogs in relation to retention type, patch size, inter-patch distance and proximity to streams and roads. They conducted a series of release trials of radio-tagged frogs in multiple two-year-old variable retention cutblocks, with retention levels between 10-20%. Residual patch sizes within the blocks ranged from 0.07 to 2.7 ha). They found that residual patches, but not individual trees, were potential short-term refugia for red-legged frogs, but their value was size-dependent and was modified by presence of streams within or adjacent to the patch. Frogs were less likely to leave large patches if a stream ran through the patch or if nearby (i.e., within 100 m) stream densities were high. Other trials indicated that frogs encountered residual patches at random and had to be within 5-20 m of a patch before moving to it in greater proportion than expected by chance. Within this distance, they preferentially selected large patches (0.8 ha) over small ones (0.3 ha). In general, they found that there was a trade-off between patch size and inter-patch distance. Larger patches tended to be further apart and further away from surrounding forest than smaller patches. As such, larger patches are likely to be encountered less often, but they are more attractive habitat. On the other hand, smaller patches will be encountered more frequently but are less attractive. Chan-McLeod and Moy (2007) recommended an optimal patch size for this study area of 0.8-1.5 ha to balance this trade-off.

3.2.1.4 Summary of Wildlife Responses to Green-Tree Retention

Overall, there has been considerably more research into boreal songbird responses to stand-level structural retention practices than any other vertebrate wildlife group. In general, green-tree retention practices produce a short- and long-term life-boating effect for many, but not all, old forest bird species, and this is reflected in increased levels of species richness and abundance relative to clearcut areas. As retention levels increase, bird communities in harvested areas are immediately more similar to those in old forests, and become increasingly so over time. Foliage-gleaners, shrub-associated species and secondary cavity-nesters appear to particularly benefit, but at the expense of ground-nesting and foraging species, which tend to decrease in abundance. However, even at relatively high levels of retention (i.e., $\geq 40\%$) many bird species have higher densities in old forest and some species (e.g., ovenbird, western tanager, and boreal chickadee) remain absent.

Studies have indicated that size of residual trees may be just as important as quantity, with retention of large live trees identified in two studies as significantly influencing bird community composition and abundances. Only one study could be found that explicitly compared responses of boreal birds to dispersed and patch retention practices, so the short- and long-term benefits of retaining dispersed individual trees remains largely unknown. Where residuals have been retained in clumps or patches, indications are that larger (i.e., ≥ 1 ha) patches result in a stronger short-term life-boating effect than smaller ones. However, patch-sizes studied have a limited range, and by definition retained patches are not large enough (≥ 5 ha) to maintain interior forest conditions. Studies to date have failed to find evidence of short-term increases in nest predation that were predicted to be associated with increased

edge creation often resulting from partial harvesting practices, although this is an area requiring further study. There has been insufficient study of the potential for GTR to enhance landscape connectivity for boreal songbirds to draw any firm conclusions, but two studies support this theory.

Longer-term studies of boreal songbird responses to structural retention have been hampered by a lack of older cutblocks with and without residuals available for study. However, the few retrospective chronosequence studies that have been conducted indicate that post-fire and post-harvest bird communities converge over 30-60 years post-disturbance, irrespective of the presence of live residual trees. Outstanding differences in bird communities appear to manifest themselves in patterns of abundance rather than in community composition. The key influence of GTR over the longer-term appears to be an acceleration of the rate of convergence of post-harvest bird communities towards that representative of old forest. There was limited evidence that even small patches of < 10 residual live trees can benefit songbird communities in the longer-term through structural enrichment of mid-successional stands, but again, more studies examining a broader range of patch sizes are required.

While most boreal bird studies have been limited to mixedwood forests of northern Alberta, comparisons with studies from non-boreal areas examining the same research questions indicate that these responses are not restricted to one forest type or region. However, there are a number of limitations to these studies that need to be considered before applying these findings to forest management strategies. Very few studies examined reproductive responses of the species examined, so it is not known how relative changes in occurrence or abundance may be reflected in reproductive success. The landscape context of stands selected for study was rarely measured, but descriptions of study areas in the literature generally indicate that relatively little commercial logging had taken place within the area. So, whether these patterns of boreal songbird responses will hold in more intensively managed landscapes such as in central and eastern Canadian boreal forests is unclear. It is also unclear whether responses of other bird groups such as raptors, or even relatively rare species of songbirds will follow similar patterns as their frequency of occurrence in these studies was too low to allow statistical analyses.

Studies of small mammal responses to green-tree retention have generally found that communities were maintained, or abundances of “old forest” species such as red-backed voles were enhanced in the first few years following harvest. However, it is not clear from these short-term studies, whether the small mammal community was responding to presence of live trees or other factors associated with harvesting. Retention of live trees in patches generally results in retention of other structural attributes such as understorey structure and CWD within patches, both of which are known to be important influences on small mammal habitat use. Most studies were carried out immediately after logging, so it is possible that the species were responding to enhanced availability of food resources resulting from ground disturbance instead of, or in concert with, the influence of retained trees. In addition, all studies were of short duration, so were possibly confounded by the relatively unpredictable inter-annual fluctuations in population size for which small mammals are known (Pearce and Venier 2005). The only longer-term study found (Homyack et al. 2005a) indicated that pre-commercial thinning of stands 15-20 years after clearcutting may benefit small mammal communities up to 16 years after thinning through production of larger stem diameters, which may result in enhanced infusion of larger CWD later in succession.

There has been insufficient study of bat responses to structural retention practices in the boreal forest and no long-term studies to determine patterns of response to GTR. Two studies at the EMEND study area found that GTR had no short-term effects on bat foraging activity relative to clearcut and uncut stands. Studies of the effects on roosting habitat are also needed.

Arboreal squirrels displayed mixed responses to GTR. Shelterwood harvesting in Ontario had significant short-term negative impacts on northern flying squirrels and red squirrels, whereas mixedwood understorey protection harvesting in Alberta maintained pre-harvest populations of red squirrels and appeared to accelerate the ability of regenerating stands to maintain populations of mature-forest red squirrels. Variable-density thinning in PNW U.S. resulted in an immediate reduction in squirrel habitat use, but populations recovered within five years. It is unclear whether these disparate results are a consequence of regional or forest-type differences in arboreal squirrel response, differences in harvesting methods, or the short duration of post-harvest sampling, as indicated by the latter study. Other studies have indicated that arboreal squirrels respond positively to retention of large patches of residual trees, although large is variously defined as > 20 trees in a patch, a 100-m-wide strip, and forest fragments up to 82 ha in size. Two key findings for arboreal squirrel responses were that harvesting in the surrounding landscape can have additive effects for squirrels beyond the stand-level, and that GTR can result in interspecific competition effects that may negate the benefits of retaining residual trees.

The bulk of research into marten habitat selection has been focused at the landscape scale. Very little work has been done until recently to examine marten responses to stand-level structure resulting from logging. There were no studies available specifically looking at marten responses to stand-level structural retention practices in boreal forests. Nevertheless, live-tree retention has been given limited consideration, in the form of patches of residual forest and unharvested corridors within a clearcut matrix. In general, studies across different regions of the boreal have produced inconsistent results. Prey availability and forest composition vary widely across the area of boreal marten distribution. Studies from North America and Fennoscandia have shown that martens clearly select against open habitats, presumably in response to a lack of cover from predators, although prey availability may also be an issue. Contrary to previous findings from other regions, martens did not select conifer stands, regardless of age, but exhibited a significant preference for deciduous and mixed stands in western Quebec. To minimize predation, martens appear to need well-distributed tree stems and dense coniferous shrub cover, not necessarily a mature or over-mature stand. Large CPR clearcut areas in boreal forest were found to have a significant negative effect on martens, in that they could not tolerate more than 30-35% cutover within their home range. Buffer strip management between harvested strips in the CPR cuts did not provide suitable alternative habitat for martens. Conversely, other studies have failed to identify structural variables that reliably differentiated areas of low versus high marten use. Spruce budworm defoliated stands have been found to provide suitable marten habitat, with vertical structure provided by large snags and surviving live trees. Fluctuation in prey abundance can be an important source of environmentally-driven variation in marten density in northern boreal forests. However, prey abundance may not necessarily reflect prey availability, as structural habitat cues may increase marten hunting efficiency in more complex habitats. Further, many marten studies are to some degree confounded by active furbearer trapping going on within research landscapes, increasing the levels of non-natural mortality.

Studies of ungulate responses to GTR in the boreal forest have been limited to its effects on forage availability and security cover relative to clearcutting, and primarily have been for moose. Partial harvesting can increase the short-term availability of forage for moose, but this may be negated if some regeneration methods are applied post-harvest. The retention of patches of residual trees scattered throughout a harvest area can increase security cover for moose, reflected in an increased evenness of browsing activity across the cutblock relative to clearcut blocks.

Boreal amphibians appear to be poorly studied as a group. The two studies that were included in the review examined adult amphibian responses to stand-level structural retention in the boreal. These studies indicated that boreal amphibians are resilient habitat generalists. Contrary to studies from other regions, boreal amphibians were little affected by clearcutting or retention and showed no association with any of the structural variables measured. However, neither study examined the

potential influence of adjacent breeding habitat quality. A non-boreal study indicated that large (> 0.8 ha) patches of live residual trees, but not individual trees, could act as short-term refugia for red-legged frogs.

Similar to Fisher and Wilkinson (2005), this review found that, relative to the boreal bird literature, there is a limited body of literature on mammalian responses to stand-level residual tree retention and it is of such variable quality that it is difficult to identify patterns across taxa. In general, retention of live residual trees at harvest appears to be of most benefit to wildlife that nest or forage in the tree layer (e.g., foliage-gleaning and cavity-nesting birds, bats, and arboreal squirrels), and species that directly and/or indirectly (e.g., marten prey) require security cover from predators (e.g., small mammals and ungulates). There are indications from some songbird, squirrel and amphibian studies that patches of live trees perform better at short-term life-boating than scattered individual trees, and that the larger the patch the stronger the effect, but more studies are required to confirm this. A number of studies, particularly those relating to boreal songbirds and small mammals, illustrate the difficulties faced by researchers in teasing out the structural attribute wildlife are responding to when many of the attributes are highly correlated (e.g., large live trees, snags, CWD), when retention of an attribute results in short-term and long-term responses of other attributes (e.g., overstorey retention and shrub response; live tree retention and snag and CWD recruitment), and when retention practices can encompass multiple structural variables. This will be discussed further in following sections.

3.2.2 Snags

The literature is replete with studies demonstrating the importance of large snags to cavity-nesting and arboreal foraging birds and mammals in natural forests and recommendations to retain these features in harvested stands (e.g., Angelstam and Mikusinski 1994; Schieck, Stuart-Smith, and Norton 2000; Imbeau and Desrochers 2002; Fisher and Wilkinson 2005; Olsen, Hannon, and Court 2006). However there are very few studies that have examined the response of wildlife to snag retention in boreal forests. Snags and their associated fauna present unique challenges to researchers and managers. The spatial and temporal complexity of their dynamics makes them difficult to study. In broad terms, their distribution and abundance are a function of stand age and disturbance history. They are generally rare at a landscape scale but may be locally abundant, as a consequence of wildfire or insect outbreak. Similarly, populations of snag-dependent wildlife species have distributions and abundances that are functions of stand age and disturbance history, making them difficult to study with standard census methods. For forest managers, issues of worker safety often result in the removal of most existing snags within and adjacent to a cutblock, while removal of most live standing timber in commercial harvesting operations negates the possibility of recruitment of snags at levels anywhere near those produced by natural disturbances. As such, most of the studies described below represent situations where snag retention occurred incidentally as a component of residual retention harvesting practices. In addition, the longer-term studies incorporate wildlife responses to snags recruited as the regenerating stand ages. Where available, snag abundances reported in the studies are presented in Table 3.9.

3.2.2.1 Birds

Short-term responses

Hobson and Schieck (1999) contrasted bird communities in forests 1, 13-15, and 22-28 years-old following wildfire or harvest. The two treatment types contained similar amounts of residual live trees immediately post-disturbance (~ 6% of pre-disturbance canopy trees), but markedly different quantities of snags, with basal areas 1 year post-fire of 35.5 m²/ha, but only 1.9 m²/ha 1 year post-harvest. They found greatest differences between bird communities immediately post-disturbance. Bird communities in one-year post-fire stands were dominated by species that nest and forage in large snags, whereas in post-harvest stands of the same age, communities included species that typically

nest and forage in open grass or shrubby habitats. Of note, three-toed and black-backed woodpeckers and brown creeper were found to only occur in one-year post-fire stands. Five other cavity-nesting or snag-foraging species had their highest densities one-year post-fire, but also occurred in one-year post-harvest stands.

In a similar study that encompassed a broader range of ages of stands (up to 60 years post-fire or harvest) and focused on small and large residual tree patches, Schieck and Hobson (2000) found that bird communities two years post-fire were different from those present two years post-harvest. All sizes of patches two years post-fire were dominated by species that nest in tree cavities, and many of these cavity-nesting species had higher densities two years post-fire than they had in continuous old forest. Residual patches in harvested stands were dominated by birds typically associated with open and parkland habitats. These differences were largely attributed to characteristics of the habitat matrix surrounding the patches rather than characteristics of the patches themselves. There were abundant large snags in and around patches two years post-fire, whereas patches retained in harvest areas of the same age were surrounded by grass, herbs, shrubs and regenerating trees.

In a meta-analysis of three independent studies of bird community response to the type and amount of trees, snags and shrubs retained at harvest in the boreal mixedwoods of Alberta, Schieck, Stuart-Smith, and Norton (2000) found that of the 54 bird species examined, 34 bird species with relatively high densities in old-growth plots appeared to have higher densities in harvest plots when many residual trees and snags were retained and when they were retained in clumps. The degree of similarity between harvest and old-growth bird communities was related to densities of large deciduous trees, large coniferous trees, snags, and the proportion of trees retained in clumps. In one of the studies, they found that snag density accounted for slightly more variation in similarity between harvest and bird communities than did density of residual trees. But in general, the authors could not separate the relative importance of large live trees and snags as their densities were highly correlated. Retention levels across the three studies ranged from 2-40% canopy cover, densities of large snags in harvest areas ranged from 4.3-27.4/ha, and all three studies examined the period 1-2 years after harvest.

Although limited in number, these studies suggest that short-term responses of bird communities to wildfire and harvesting are markedly different when snag retention levels in harvested areas are relatively low, but these short-term differences can be lessened with increasing retention levels (up to 27.4 snags/ha). For some species, however, retention levels are less important than the type of snag retained. Fire-associated species such as three-toed and black-backed woodpeckers are dependent on a continual supply of freshly killed trees, so retaining existing, older snags during harvest would be of little value to these species.

Long-term responses

In the longer term, bird communities of post-fire and post-harvest habitats in mixedwood forests begin to converge over a 30-year period as structural conditions of stands converge (Hobson and Schieck 1999; Schieck and Hobson 2000). Most convergence can be attributed to loss of snags from post-fire stands as they fall and become part of the forest floor rather than to enhancement of forest structure in harvested stands. Cavity-nesting species generally decline, and may be absent, during mid-seral stages for both disturbance types, but become more common > 76 years post-fire as recruitment rates of large snags increase (Schieck and Song 2006). There were no post-harvest studies for this period.

In a study of snag-associated birds in naturally disturbed and managed forests of eastern boreal forests, Drapeau et al. (2002) found that decreased species richness and abundance of snag-associated birds apparent in 20-year-old clearcut areas, persisted in stands horse-logged 80 years ago relative to burned stands of similar age. Snag availability peaked immediately post-fire, and this corresponded to the period of highest occurrence of primary cavity nesters such as the black-backed woodpecker. However, contrary to other studies, they found that snag availability remained relatively static at significantly lower levels throughout forest succession (> 200 years after fire) in the naturally disturbed black spruce forests studied. The distribution and abundance of primary cavity-nesters reflected this pattern. Even though availability of snags remained low in naturally disturbed stands, they were significantly lower again in equivalent aged harvested stands, as was the proportion of cavity-nesting birds, particularly secondary cavity-nesting birds. So, depending on forest type, impacts of harvesting can be quite long-lived on snag-associated bird species, even once snag recruitment in the regenerating stand has begun.

3.2.2.2 Mammals

Mammalian response to snag retention has received even less attention. In their review of mammalian responses to forest fire and harvesting in the North American boreal forest, Fisher and Wilkinson (2005) concluded that presence of CWD, live residual trees and snags facilitate convergence of mammal communities to a pre-disturbance state for both disturbance types. With the exception of bats, arboreal sciurids, and marten which will directly use snags for nesting and/or foraging, mammalian species associations with snags in old-growth forest may be a product of the correlation of large snag availability with large live trees, abundant CWD, and canopy gaps, as no direct ecological association is apparent between snag availability and most mammal species reviewed by Fisher and Wilkinson (2005). Indirectly, the relevance of snag retention to small mammals will likely be as a result of their role in infusion of CWD into the disturbed area, particularly in the first few decades after disturbance.

3.2.2.2.1 Small Mammals

Fuller, Harrison, and Lachowski (2004), compared abundances of small mammals (mice, voles and shrews) among partially harvested (40-50% dispersed retention, averaging 13 m²/ha) regenerating commercial clearcut areas (residual basal areas of 0.81-2.44 m²/ha), and mature multi-aged stands in Acadian forests of eastern North America (a transition zone between northern hardwood forest and the northern boreal forest). Basal area of snags was significantly different between the three stand types, with mature > partial harvest > clearcut. They found that partially harvested stands supported densities of mice and voles comparable to mature stands, despite reduced canopy closure, lower densities of coniferous trees and saplings, and decreased basal area of deciduous trees and snags. The maintenance of small mammal populations was attributed to the maintenance of understorey and coarse woody debris characteristics in partially harvested stands, yet the authors included retention of large snags as a recommended practice in clearcut areas in order to “functionally approach characteristics of partially harvested stands” (Fuller, Harrison, and Lachowski 2004, p. 384).

3.2.2.2.2 Arboreal Squirrels

Holloway (2006) studied habitat use, diet, nest-use, home range size, and resource selection of two species of flying squirrels in recently shelterwood harvested and unlogged forest. She found that Northern flying squirrel densities were significantly lower on shelterwood sites and related this to lower densities of large snags, spruce and hardwood trees and lower understorey stem densities on shelterwood cuts. Southern flying squirrel, on the other hand, showed little evidence of a negative response to partial harvesting and it appeared that they may tolerate lower snag densities by nesting in natural and abandoned woodpecker cavities in live trees.

Table 3.9 Snag Abundances in Studies Comparing Wildlife Responses to Natural and Post-Harvest Levels of Snag Density and/or Basal Area

Study	Faunal Group	Forest Type	Forest Age (years)	Snag Abundance				Harvest Method
				Natural		Harvested		
				No./ha	Basal Area (m ² /ha)	No./ha	Basal Area (m ² /ha)	
Hobson & Schieck 1999	Birds	Mixedwood	1	35.5	1.9	4.3	1.9	Clearcut with residuals
Schieck et al. 2000*	Birds	Mixedwood	1-2			4.3		Clearcut with residuals
			1-2			15.8		Clearcut with residuals
			1-2			27.4		Partial
			>100	Not provided				N/A
Drapeau et al. 2002	Birds	Black spruce	1		12.5		No data	N/A
			20		3.1		0.5	Clearcut
			100		3.0		1.6	Horse-logged
			> 200		2.0		No data	N/A
Fuller et al. 2004	Small mammals	Mixedwood	1-3			174.0	1.8	Partial
		Regenerating clearcut	12-22			45.0	0.23	Clearcut with residuals
		Mixedwood	Mature	299.0	3.9			N/A
		Deciduous	Mature	188.0	1.6			N/A
		Coniferous	Mature	328.0	4.9			N/A
Holloway 2006**	Flying squirrels	Deciduous	3-10			3.0		Selective
			13-18			6.0		Selective
		Coniferous	135-148		10.1			N/A
			3-10			4.7		Shelterwood
		100		11.1			N/A	

*figures are for large snags > 20 cm dbh

**figures are for large snags > 25 cm dbh

3.2.2.2.3 *Bats*

Forest-dwelling insectivorous bats rely on forests for food and roost trees. As summarized by Patriquin and Barclay (2003), habitat use by foraging bats is influenced by forest harvesting directly via effects on flight (Sleep and Brigham 2004) and indirectly through effects on prey and roost abundance. Bat roosts tend to be found in large-diameter live and dead trees, and under the canopy of mature deciduous trees (e.g., the hoary bat), often in older “uncluttered” stands (authors summarized in Fisher and Wilkinson 2005). Erickson and West (2003 in Fisher and Wilkinson 2005) suggested that, based on structural studies of stands in western Oregon and Washington, bats should be able to use stands of any seral stage, provided the appropriate roosting structure (i.e., trees and snags) were present. Jung et al. (1999) compared bat use of several forest types in Central Ontario, of which one was a boreal-type mixedwood. In this study, multivariate habitat models suggested that in uncut forest of varying types, bat detection rates were insensitive to changes in roost site availability. However, models suggested that between logged and uncut stands, the availability of potential roost sites may be an important determinant of bat activity for smaller *Myotis* spp. and larger bats when canopy is absent.

3.2.2.3 *Summary of Wildlife Responses to Snag Retention*

In summary, there is insufficient information to draw firm conclusions on the role snag retention may play in mitigating short- to medium-term responses of snag-associated wildlife to harvesting. It is clear that the quantity and quality of snags immediately post-disturbance can have a marked influence on presence and/or abundance of a variety of bird species, particularly cavity-nesters and arboreal foragers, and some specialist mammal species such as the northern flying squirrel. There was some indication that increased levels of snag retention can decrease differences between bird communities post-fire and post-harvest, but this effect will likely only be apparent for the first 30 years after disturbance by which time most snags will have fallen. In addition, even the highest post-harvest snag-abundances studied still fall at the bottom end of the range of snag production post-fire (estimated at 50-2,500 stems/ha – Perera, Buse, and Routledge 2007), so emulation of most of the natural range of snag abundances post-disturbance is unlikely to be achievable. In the longer term, it appears that recruitment of large snags from live residual trees retained at harvest, plus contributions from the regenerating stand play a key role in convergence of post-fire and post-harvest bird and mammal communities in mid- and late-seral stages.

3.2.3 *Understorey*

A well developed understorey vegetation layer provides a wealth of foraging and nesting opportunities, as well as security cover from predators for a wide range of wildlife species, from birds to ungulates. The development of a complex, multi-layered understorey layer as stands age, often associated with the high biodiversity values of old-growth forests (e.g., NCASI 2005), is largely governed by dynamics of the overstorey. The removal of overstorey trees through harvesting or wildfire generally results in an increased abundance of shrubs through early successional phases, although significant differences exist between the disturbance types at the initiation stage, with a delay in post-fire understorey regeneration due to dominance of fire-adapted herbs (Hobson & Schieck 1999). However, increased abundance may be associated with a simplification of understorey structure. During mid-successional phases in relatively even-aged forest, canopy closure can result in a sparse understorey layer dominated by shade-tolerant species, until self-thinning and small-gap dynamics begin to open up the canopy, promoting an increase in complexity in the understorey vegetation. Shrub-associated wildlife is expected to follow these general trends, with peaks in abundance in early- and late-successional forests. It can also be expected that wildlife responses to changes in understorey structure post-harvest may be modified by varying levels and/or configurations of overstorey retention at harvest, or by stand management practices in mid-successional forests, such as thinning, that reduce overstorey cover.

The maintenance of a complex understorey during and after harvesting is often seen in conflict with maximising timber production and the successful regeneration of commercially important timber species, leading to the application of herbicides or brushing to suppress understorey vegetation in the short term. As such, it is not surprising that there are few harvesting or silvicultural practices that specifically aim for understorey retention at harvest. An exception is CPR (clearcutting with protection of regeneration), a modified form of clearcutting used in boreal forests in Quebec. In this technique, skidding trails are equally spaced 10-15 m apart and generally occupy no more than 33-40% of the harvested area (Potvin, Courtois, and Belanger 1999). Coniferous trees and trembling aspen with a dbh ≥ 10 cm are harvested from the retained strip between the skid trails, while smaller stems of these species and non-commercial tree species are not. Unlike a conventional clearcut, where logging machinery has free access, CPR leads to better protection of advanced regeneration, and the shrub, herb and moss layers between the trails. A variation of this method is MUP (mixedwood understorey protection), a potential alternative to clearcutting under investigation in boreal mixedwood forests of Alberta (Fisher and Bradbury 2006). Using a skid trail system similar to CPR (but more widely spaced at 25 m apart), MUP harvesting selectively removes large mature deciduous trees from the canopy, retaining some mature and immature trees in the overstorey and understorey, and promoting release of understorey conifers. This review incorporates studies of wildlife response to harvesting treatments such as these that directly aim to retain (or at least better protect) forest understoreys, as well as studies where wildlife response has been associated with understorey response to retention of other structural attributes such as live trees.

3.2.3.1 Birds

It has been suggested that canopy cover, and tall and low shrub layers are the most important vegetation parameters for maintaining bird communities (Crawford et al. 1981 in Norton & Hannon 1997). Yet, there are surprisingly few studies of the responses of birds to indirect understorey retention as a consequence of stand-level structural retention practices, and none of practices that directly aim to retain understorey characteristics at harvest.

Short-term community-level responses

Studies of short-term bird community responses to GTR have produced conflicting results in terms of the relative influence of understorey structure in modifying responses of birds to harvest. Norton and Hannon (1997) found that the abundance of shrub-inhabiting birds decreased with increasing levels of GTR, although they noted that approximately one-third of retained trees occurred as scattered individuals or in clumps too small to have an intact understorey. Conversely, Harrison, Schmiegelow, and Naidoo (2005) found that abundance of shrub-nesting species increased with increasing GTR, despite significant concomitant declines in shrub density and cover in some stand types. Both of these studies analysed vegetation and bird community data separately, so correlations between patterns in the data sets are purely speculative. In their study of bird community responses to the type (e.g., deciduous, coniferous, mixed), amount and dispersion of trees, snags and shrubs retained at harvest, Schieck, Stuart-Smith, and Norton (2000) explicitly analysed the relationship between understorey structural characteristics and bird community patterns. They found no relationship between high shrub cover and the degree of similarity of bird communities in harvest and old-growth stands. They also noted a high degree of inter-correlation between a number of structural characteristics studied, especially trees, snags and shrubs. Tittler and Hannon (2000) also found no relationship between understorey vegetation characteristics and levels of nest predation in cutblocks with varying levels of GTR.

Short-term species-level responses

At the species level, Kvasnes and Storaas (2007) examined the effects of clearcutting and selective harvesting on short-term availability of food and cover from predators in capercaillie (grouse) brood habitats in southeastern Norway. Capercaillie young are heavily dependent on Lepidoptera larvae in the shrub layer as a food source during the first few weeks of life. They are also extremely vulnerable to predators during this period, so their survival is largely dictated by availability of an understorey layer containing both a sufficient high-protein food source and cover from predators. Kvasnes and Storaas (2007) found no significant differences in larvae availability or understorey vegetation characteristics (vegetation height, field layer visibility, field layer cover, etc.) between uncut and selectively cut forest. Clearcutting resulted in a denser and taller shrub layer than in uncut forest, but due to absence of canopy cover, it was still considered too open to provide effective security cover. A significant shift in arboreal invertebrate prey from Lepidoptera larvae to less preferred spiders was also observed. They concluded that selective harvesting preserved food availability for capercaillie through maintenance of much of the understorey layer and maintained more security cover than clearcut areas through the retention of both overstorey and understorey vegetation. No details were provided on the level of overstorey or understorey retention resulting from the selective cuts.

Long-term community-level responses

Hobson and Schieck (1999), in their study of post-fire and post-harvest stands with low levels of residual live trees, found that 22% of the variation in bird species density over the 28-year chronosequence studied was explained by basal area of residual snags (negative trend with stand age), density of regenerating trees (negative), the dbh of regenerating trees (positive), and density of shrubs (positive), but the relative importance of each of these could not be determined. They concluded that the convergence of bird communities 14 years post-disturbance was in part due to higher densities of species that nest and forage in shrubs. Interestingly, they found that shrub layers grew more rapidly in post-harvest post-fire stands, resulting in denser shrub layers 14 years after disturbance, and for the tall shrub layer this effect was still apparent 28 years after disturbance. They suggested this as one reason for the lack of complete convergence of bird communities by 28 years post-disturbance.

3.2.3.2 Mammals

3.2.3.2.1 Small Mammals

Understorey structure plays a key role in providing security cover to small mammals from terrestrial and avian predators. Small mammal community responses to understorey structure have been studied in the context of partial harvesting of mature stands, thinning of mid-successional stands, and post-harvest regeneration treatments following CPR. However, it can be difficult to determine whether small mammals are responding to the vegetation characteristics of the stand, CWD (which may also be important for security cover), or both (Pearce and Venier 2005).

Short-term responses

Uneven-aged selection harvesting of mixed stands in Acadian forest was found to have negligible effects on densities of deer mice, red-backed voles, and short-tailed shrews in the short-term, whereas regenerating clearcut stands (11-20 years old) had significantly lower abundances of mice and voles relative to mature mixed stands (Fuller, Harrison, and Lachowski 2004). The authors attributed maintenance of small mammal populations in partial cuts to promotion of abundant understorey vegetation caused by the reduced canopy, which resulted in security cover (20% higher) than in mature mixed stands. As no relationship between the responses of the small mammal community and CWD levels was found, they concluded that the understorey structure resulting from partial cutting was providing more cover than that provided solely by CWD.

Small mammal community responses to three different regeneration treatments, following CPR were investigated by Gagné, Bélanger, and Huot (1999) in boreal balsam fir stands of Quebec. They compared the effects of natural regeneration, planting followed by herbicide release, and planting followed by brush-saw cutting on small mammal species richness and abundance. They found that species richness was unaffected by any of the regeneration treatments; however, red-backed vole abundance was significantly lower for two growing seasons following herbicide release, due to reduced ground vegetation cover (24% less) relative to other treatments.

Long-term responses

Homyack et al. (2005a), in their study of the effects of pre-commercial thinning on small mammal communities, found that increased abundance of red-backed voles and masked shrews was related to changes to the understorey following PCT. Understorey stem density was 1.4 times greater in mid-successional stands treated with PCT compared to unthinned stands. They also found that the density of understorey stems increased over the first five years after PCT. No difference between the total amount of CWD in thinned and unthinned stands was observed. Similar to Fuller, Harrison, and Lachowski (2004), they concluded that development of a more structurally complex understorey as a consequence of opening the canopy was a key driver of responses by small mammals to PCT, and the lack of a response to CWD quantity suggests that CWD may not be limiting to small mammals in the Acadian forest. As noted by Pearce and Venier (2005), it may be that it is the amount of security cover that is more important to small mammals than the type of cover, so CWD and understorey vegetation may interact in supplying suitable cover.

3.2.3.2.2 *Arboreal Squirrels*

Similar to small mammals, arboreal sciurids may also be expected to benefit from promotion of a substantial tree and shrub response in the understorey that can be associated with partial harvesting. These benefits may accrue in a similar fashion to the protective shrub cover afforded by canopy gaps in old forests which provide protective shrub cover for flying squirrels foraging on the ground (McDonald 1995 in Fisher and Wilkinson 2005).

Partial harvesting techniques generally promote not only live tree retention in the overstorey, but may often produce a substantial tree and shrub response in the understorey and/or enhanced CWD retention; these can result in interspecific competition which may confound the responses of arboreal sciurids. As noted by Carey (2003), dense understorey promotes chipmunks, which are known to reach highest abundances in response to high understorey stem densities (Bennett, Henein, and Merriam 1994, Zollner and Crane 2003 in Holloway 2006). Holloway (2006) also found a positive chipmunk response to selection and shelterwood harvesting due to enhanced understorey development. Chipmunks will compete for food resources such as hypogeous fungi and insects associated with CWD. Harvesting systems that promote structure for arboreal sciurids but also optimal conditions for ground sciurids may create response systems that are difficult to discern. Similar conflicts could occur with small mammal competition for resources.

3.2.3.2.3 *Snowshoe Hare*

Snowshoe hares require dense forest understoreys, adequate vegetative structure and habitat interspersions (review in Fisher and Wilkinson 2005) to provide for foraging opportunities as well as thermal and security cover. Stand-level structural retention practices designed to maintain or promote understorey integrity are anticipated to promote hare use as well. Snowshoe hares are a keystone species in the boreal forest in their role as an important prey species for a number of vertebrate predators (Keith 1963, Boutin et al. 1995, and Krebs 1996, in Ferron, Potvin, and Dussault 1999, and in Potvin, Bertrand, and Ferron 2005 and in Potvin, Breton, and Courtois 2005). As such, a number of studies have focused on determination of habitat associations of snowshoe hares in areas affected by

timber harvesting, and development of proposed management guidelines to enhance hare populations in these habitats (see list in Darveau, Huot, and Bélanger 1998). Understorey density and height are critical habitat variables; density has been positively associated with overwinter survival and stands are highly suitable when shrub heights exceed 1 m (see Fisher and Wilkinson 2005). Coniferous stands may provide greater thermal and security cover than in deciduous stands during winter; dense deciduous shrubs may also offer similar protection (Wolfe 1980; Wolfe et al. 1982; in Fisher and Wilkinson 2005). Brocke (1975 in Potvin, Courtois, and Belanger 1999) showed that young regenerating conifer stands (mean tree height 3.5 m) are where hares spend the day and where they escape predators. Guay (1994 in Darveau, Huot, and Bélanger 1998) found that shrubs and saplings with 2- to 3-m-high stems yielded the most significant correlations with hare pellet densities.

Numerous studies have found that snowshoe hares are either absent or uncommon for several years following logging (see list in Ferron, Potvin and Dussault 1998). Thompson et al. (1989) reported winter hare tracks were least abundant in recent (< 5 years old) clearcut areas as compared to older harvested and uncut stands presumably due to reduced winter browse availability. Studies have also found activity to be restricted to edges where dense understorey is available (Fisher and Wilkinson 2005). Burgason (1977 in Fisher and Wilkinson 2005) found hares returning to regenerating spruce-fir stands in Maine after 6-7 years, reaching peak densities after 20-25 years. Latitude, length of the winter season, and snow depths are anticipated to influence the rate of forest recovery and snowshoe hare response to logging in the more northern reaches of snowshoe hare range.

In the boreal, a number of studies have focused on effects of clearcut logging on snowshoe hare use and abundance (see review in Fisher and Wilkinson 2005). With the 1996 advent of new forest harvesting guidelines in Quebec requiring clearcut with protection of regeneration (CPR), a number of experimental and retrospective studies of hare response to harvesting have been initiated, examining both short- and long-term responses to harvesting and stand tending practices.

Key findings on the short- and long-term responses of snowshoe hare to understorey retention are summarised in Table 3.10.

Short-term responses to understorey protection

Potvin, Courtois, and Belanger (1999) noted that species with mid-size home ranges up to 25 ha, such as snowshoe hare, were excluded from recent clearcut areas harvested by CPR in 1992 in the black spruce dominated stands of southwestern Quebec. As part of this research initiative, Ferron, Potvin and Dussault (1998) reported on snowshoe hare use and habitat suitability of CPR areas as compared to uncut controls, with two years of pre-harvest and four years of post-harvest data. They used pellet counts combined with radio-telemetry to assess the effects of harvesting on snowshoe hare activity in the boreal.

At the time of the study, provincial logging standards resulted in a landscape matrix dominated by large (≤ 250 ha) clearcut areas interspersed with forest strips ranging in width between 100 and > 500 m, as well as small forest blocks (< 10 ha) distributed throughout the clearcut (totalling 4% of the block area) connected or not with the strips, and surrounded by larger tracts of continuous forest. At the stand level, hares became almost absent in CPR clearcut areas (cutover and regenerating) one, two and four years after logging; a significant decrease compared with controls (Potvin, Courtois, and Belanger 1999).

At the microhabitat level, before logging hares were located in stands with younger trees (i.e., tree basal area was significantly lower than in uncut stands, but not number of stems/ha), denser understorey, and significantly more woody debris than uncut control sites. Stands used by hares before logging and uncut control sites both had equal lateral cover (~ 70% visual obstruction; suitable for hares) (Litvaitis, Sherbourne, and Bissonette 1985; Ferron, Potvin and Dussault 1998).

After logging, CPR cuts produced habitat unsuitable for snowshoe hares in the short-term and hares sought out and relocated to nearby habitat that was similar to the habitat they occupied pre-harvest (Ferron, Potvin and Dussault 1998). Hares continued to be in sites with high woody debris and lateral cover equivalent to that in sites used before logging, though the remnant stands to which hares moved after logging were older than stands selected before logging (Ferron, Potvin and Dussault 1998). Sites selected by hares after logging were significantly different than the CPR sites; the understorey of CPR sites was sparser than sites used after logging for coniferous (12.0 vs. 71.4 %) and deciduous (0 vs. 36.0 %) components. More importantly, lateral cover was significantly less developed on cutover sites than on sites used by hares after logging (mean 38 vs. 69%), mainly due to changes to the coniferous component of the understorey, but also from a drastic change in the overstorey as the number of stems and basal area decreased to about 10% of their former values. Basal area of black spruce in cutovers versus sites used by hares after logging was 0.5 vs. 6.5 m²/ha, and total stems/ha in cutover versus after logging use areas was 92 vs. 898. As a result, lateral cover was only 38% in cutover sites; much lower than the 70% level considered suitable for hares. Recovery from logging is anticipated to be relatively slow in black spruce dominated stands (as compared to mixedwood or balsam fir-leading); Ferron, Potvin and Dussault 1998 suggested that lateral cover will not become suitable for hares, particularly in winter, until at least 10 years following CPR, and it might take over 30 years for hares to increase to peak densities (i.e., for cutover areas to recover as suitable habitat for hares).

Further, several studies have examined the effects of pre-commercial thinning (PCT) on snowshoe hare abundance and habitat use. The reduction of tree stem density has a number of silvicultural goals, but has been found to reduce snowshoe hare habitat suitability in the short term, as measured by track counts and pellet counts (Ausband and Baty 2005; Homyack et al. 2005b), and live mark-recapture techniques (Griffin and Mills 2004). However, it would seem that hare can easily move to nearby areas of suitable habitat, and leaving some unthinned habitat (20%) can maintain habitat use over the short term (Griffin and Mills 2004).

Table 3.10 Summary of Key Findings of Short- and Long-Term Snowshoe Hare Responses to Understorey Retention Harvesting Practices (Non-boreal studies are highlighted in italics.)

Region(s)	Forest Type(s)	Temporal Scale	Key Finding(s)	Reference(s)
Quebec	Black spruce-leading forest & mixedwoods.	Short-term (ST)	CPR cuts produced unsuitable habitat for snowshoe hares in the short-term, and hares relocated to more suitable habitat.	Ferron et al. (1998); Potvin et al. (1999).
Quebec	Black spruce-leading forest & mixedwoods.	ST	Snowshoe hares depend on residual forest in clearcut landscapes, even when modified CPR harvesting is used.	Ferron et al. (1998), Potvin et al. (1999); de Bellefeuille et al. (2001).
Quebec	Black spruce-leading forest & mixedwoods.	ST	Remnant stands to which hares relocated were older than stands selected before logging, and were significantly different that CPR stands (CPR stands had sparser understoreys and less lateral cover).	Ferron et al. (1998).
Quebec	Black spruce-leading forest & mixedwoods.	ST	Snowshoe hares can adapt to their new environment over short period (home range size increased, but survival rate did not decrease).	Ferron et al. (1998).
Quebec	Balsam fir-leading mixed forest; Black spruce-leading forest & mixedwoods.	ST	Residual buffer strips (up to 300 m wide) provide marginal, low quality habitats for snowshoe hares in all seasons.	Darveau et al. (1998); Potvin et al. (2005a).
Quebec	Black spruce-leading forest & mixedwoods.	ST	Residual strips used by snowshoe hares were generally wider (100 m wide) and had > 20% shrub canopy cover, and were more often adjacent to a forest patch > 25 ha, but hares avoided strip edges.	Potvin et al. (2005a).
Quebec	Balsam fir-leading mixed forest.	ST	CPR & PCT can produce favourable results for snowshoe hare habitat attributes.	<i>Etcheverry et al. (2005).</i>
Quebec	Black spruce-leading forest & mixedwoods.	Long-term (LT)	Logged mixedwood stands offer some habitat conditions for hare 10 years post-CPR, but will probably take another 10 years (i.e., 20 years post-harvest) to become optimal, and this was related to recovery of lateral cover and height of regeneration.	Potvin et al. (2005a).
Quebec	Black spruce-leading forest & mixedwoods.	LT	Snowshoe hares started to recoccupy logged coniferous stands 10 years post-CPR but the stands still had poor habitat conditions for hare because of lack of cover; it may take > 30 years for hare densities to recover.	Potvin et al. (2005a).

Daily movements immediately after logging (obtained by telemetry) were temporarily twice as great as prior to logging (i.e., exploration period) after which their movements stabilized. Home range size increased after logging (to 27 ha from 17 ha pre-logging). Survival rate did not decrease, but this is likely because hares avoided open areas (CPR cuts and regenerating stands) after cutting and adjusted to their new environment over a short period (Ferron, Potvin and Dussault 1998). Given the aforementioned composition of the landscape matrix, with leave strips and residual patches, there was sufficient residual forest available within the surrounding landscape matrix within which hares could find suitable habitat after logging. Ferron, Potvin and Dussault (1998) concluded that snowshoe hares are dependent on residual forest in clearcut landscapes, even when modified CPR harvesting is used. Therefore shape, size and distribution of leave strips and uncut blocks are critical to maintain hares.

Short-term use of residual forest

Given the understorey habitat requirements of snowshoe hares, the observation that even modified harvesting to protect understorey does not provide for suitable hare habitat in black spruce-leading boreal forest, and the apparent reliance of hares on residual forest in a clearcut matrix, does a landscape matrix of unsuitable recent (< 10 years) clearcut areas separated by 60-100-m buffer strips represent viable hare habitat? Potvin, Bertrand, and Ferron (2005a) attempted to identify stand-level attributes of buffer strips important for snowshoe hares in black spruce dominated, clearcut boreal forest landscapes in south-central Quebec, where uncut residual forest makes up about 30% of the productive land area, mainly composed of riparian and upland strips. The forests under study were also dominated by black spruce, with the presence of balsam fir and other coniferous and deciduous species. Potvin, Bertrand, and Ferron (2005a) noted that until the shrub layer reaches 2-3 m in logged sites, snowshoe hares must find habitat in residual forest units if the population is to be maintained in clearcut landscapes.

Using a track count index, Potvin, Bertrand, and Ferron (2005a) reported hares were more common in wider residual strips (> 100 m). Buffer strips with hares present were about 20% wider on average than where hares were absent (86 vs. 72 m), with signs of hare presence at least 2 to 4 times higher in strips wider than 100 m compared to narrower ones. Hares avoided strip edges; track counts were three times higher ($P = 0.016$) in the portion of a strip that was > 20 m from the clearcut edge than in the portion 0-10 from edge. Buffer strips where hares were present were more often adjacent to a forest patch (> 25 ha) than those where hares were absent (74% vs. 43%). Hares were also much more abundant in strips that had > 20% shrub canopy, often associated with greater balsam fir basal area. Lateral cover was quite uniform among surveyed buffer strips. There was no difference in attributes related to snowshoe hare habitat between riparian and upland strips, other than upland strips were generally wider and this conferred them an advantage; relative density of hares was three to four times higher in upland strips than in riparian strips (Potvin, Bertrand, and Ferron 2005a).

Track counts were five times lower in forest strips than in control sites located in continuous uncut forest. Hare density in clearcut landscapes was reduced to less than 10% of the density found in uncut landscapes, based on relative densities derived from this study (Potvin, Bertrand, and Ferron 2005a). In addition, Cusson (2000) in Potvin, Bertrand, and Ferron (2005a) reported (based on telemetry data) that summer hare survival tended to be lower in forest strips than in large forest blocks (width ≥ 200 m). This suggests that buffer strips were marginal, low-quality habitats for snowshoe hares in all seasons (Cusson 2000 in Potvin, Bertrand, and Ferron 2005a; Darveau, Huot, and Bélanger 1998), and reliance on residual forest for suitable habitat in a clearcut matrix will result in substantially reduced hare populations. Potvin, Courtois, and Belanger (1999) suggested that for black spruce-leading boreal forest in their study area of south-central Quebec, leaving uncut forest

strips > 100 m wide in areas with good shrub cover with presence of balsam fir might maintain hares at moderate densities in large clearcut landscapes.

Darveau, Huot, and Bélanger (1998) found residual forest strips to be low quality snowshoe hare habitat. They evaluated the effects of strip width and stand thinning on habitat components and hare use in riparian forest strips in boreal balsam fir managed landscapes in the Laurentian Mountains of eastern Quebec over a six-year period post-treatment. Strip widths ranged from small (20, 40 and 60 m) to large (> 300 m); thinning removed 33% of stems > 10 cm dbh. Based on coniferous and deciduous shrub densities, all riparian forest strips and adjacent cutovers remained low quality habitats for six years following clearcut conifer logging. Contrary to Potvin, Bertrand, and Ferron (2005a), who recorded enhanced hare use in wider, larger residual forest strips, browse and pellet surveys recorded low sustained use over the six years in all seasons and all types of strips regardless of width or treatment. In this study landscape, intermediate forest stages were absent, and regeneration in clearcut areas was too low (< 2-3 m) to offer suitable hare habitat; hares using mature remnants should have relied on available habitat in forest riparian buffer strips but results did not support this supposition. Darveau, Huot, and Bélanger (1998) raised the question of potential sampling error, but also noted that whether the hare populations in the study area were cyclical or not was still in question. If timber harvesting coincided with “high” hare populations in the study area and sampling for hare habitat use was done in “low” years, then results might infer low quality habitat in riparian forest strips based on evidence of low use.

De Bellefeuille et al. (2001) investigated refuges for snowshoe hare on a landscape dominated by clearcut areas. They found that hare colonization of regenerating sites was delayed in their humid boreal forest study area. Sites were in the seedling stage 7–9 years after cutting, and hares avoided them year-round because of inadequate protective cover. During the seedling stage, hares were found in the remaining forest which occupied at least 25% of the area of each home range. They concluded that retention of residual forests was essential to maintain local populations on an area dominated by commercial clearcut areas.

Influences on short-term responses

Differences in methods of detecting both wildlife responses and habitat quality can influence the evaluation of harvesting effects, as well as the benchmarks against which the effect of logging is evaluated. In addition, there are biogeographic differences in canopy and ecosystem conditions across the boreal forest. As an example, Etcheverry, Ouellet and Crête (2005) studied how two common silvicultural treatments (CPR and Precommercial Thinning, or PCT) affect abundance of small mammals and snowshoe hares in mixed forests of eastern Quebec typical of the transition zone between northern hardwood and boreal forests. Stands were dominated by balsam fir with a mixture of conifers and deciduous trees species; black spruce was not present. PCT is applied approximately 10 years after disturbance, reducing the density of young overstocked stands to accelerate growth of residual poles. The study was a retrospective of existing treated stands. Investigators looked at stands ≤ 10 years post-treatment (both CPR and PCT) and established stands > 10 years post-treatment (deciduous and conifer dominated); established stands had trees 40-60 years old. Hares were trapped and marked and capture rates were used as an estimate of hare abundance and use. In these mixed, balsam fir-dominated stands, Etcheverry, Ouellet and Crête (2005) found that understory protection and thinning produced favourable results for hare habitat attributes. Lateral cover was higher in CPR and PCT stands (92% and 100%, respectively) than in established conifer or deciduous stand (42 and 36% respectively). Hare abundance was positively related to presence of coniferous canopy and to biomass of coniferous foliage in the understory. Hare abundance remained relatively uniform in all strata (treated and established) during summer, indicating that vegetation within all strata was sufficient to maintain hares, which are generalists in terms of habitat requirements during the summer

(Etcheverry, Ouellet and Crête 2005). Though not significant, hares tended to be more abundant in established conifer stands and CPR cutovers.

Long-term responses

In Alberta, snowshoe hares were most abundant in 20- to 30-year-old mixedwood stands rather than mature or old stands (Roy, Stelfox, and Nolan 1995 in Fisher and Wilkinson 2005). In these older regenerating stands, hare density was positively related to density of small trees, shrubs, saplings and willow, and was negatively related to density of large trees. In general, winter hare activity is higher in coniferous stands of this age than deciduous because of superior thermal and protective cover. Monthey (1986) in Fisher and Wilkinson (2005) observed greater hare activity in 12- to 15-year-old than in 7- to 9-year-old cutblocks, and suggested that hare activity should return to high levels in 20-30 years. Thompson et al. (1989) observed that hare tracks were more abundant in the 20+ age class.

Hare abundance decreases as a stand matures and canopy closure increases; the timing of decreasing quality is relative to the biogeography, climate, landscape position, and site potential of the boreal forests of interest. Roy, Stelfox, and Nolan (1995) in Fisher and Wilkinson (2005) found low hare abundances in 50- to 65-year-old mixedwood stands in Alberta. However, hares were abundant in 40-year-old mixedwood stands in Newfoundland (Thompson and Curran 1995).

Potvin, Breton, and Courtois (2005b) returned to the CPR cutovers first reported in Ferron, Potvin and Dussault (1998) and Potvin, Courtois, and Belanger (1999) to examine snowshoe hare response to clearcut recovery ten years post-harvest. They returned to permanent sample plots established in the CPR cutovers prior to harvest and conducted pellet counts. None of these plots occurred within the residual forest strips; results apply only to ground harvested by CPR. Results were monitored at the scale of the forest stand (10-20 ha each). Ten years after harvest, the tree layer had changed little, with scattered white birch forming the dominant component of the residual tree layer. Over 10 years, shrub layer and available browse had increased in clearcut areas. The number of stems of coniferous shrub layer reached about 40% of that on uncut controls and coniferous browse nearly doubled. A six-fold increase in deciduous browse was recorded, attaining nearly four times that of uncut controls (12,300 vs. 3,800 stems/ha, $p = 0.01$). The deciduous shrub layer was three times higher than that found in uncut stands (1,200 vs. 450 stems/ha). Lateral cover in CPR exceeded 55% but still remained much lower than in uncut stands (75%), and regeneration was shorter than 3 m on average. Logged mixed stands had higher lateral cover (62% vs. ~55%) and taller regeneration (> 4 m vs. < 3 m) compared to logged black spruce coniferous stands.

In control stands, relative density of hares from 1991 to 2002 shows pattern typical of cyclic species, with peaks in 1991 and 2002. Snowshoe hare started to reoccupy logged coniferous stands within 10 years post-harvest, but relative density was still less than half that of uncut stands (13.9 vs. 29.1 pellets/plot; Potvin, Breton, and Courtois 2005b), confirming that logging still had a significant effect after 10 years. At the stand scale, mean pellet density per stand in 2002 was related to lateral cover ($p=0.05$) and height of regeneration ($p=0.05$), both of which were trailing in recovery as compared to shrub and browse layers, and both of which relate to winter thermal and security cover for hares. Lateral cover had the closest relationship with hare density and sites with $\geq 60\%$ lateral cover were intensely used by snowshoe hare; but few areas exceeded the 70% level considered suitable (Litvaitis, Sherbourne, and Bissonette 1985 in Fisher and Wilkinson 2005).

Potvin, Breton, and Courtois (2005b) reported that logged mixedwood stands already offer some habitat conditions for hare, but it will probably take at least 20 years post-harvest to become optimal. In contrast, they also noted that logged black spruce stands still have poor habitat conditions for hare 10 years post-harvest because of lack of cover; they will take even longer to increase hare densities (> 30 years) – much longer than reported for southern parts of the snowshoe hare range. Results from

other northern studies indicate that cutovers < 10 years old do not constitute suitable habitat (de Bellefeuille et al. 2001) and 13-27 years are needed for cutovers to become suitable, with black spruce stands taking longer to do so than balsam fir stands (Jacqmain 2003 in Potvin, Breton, and Courtois (2005b).

3.2.3.2.4 Marten and Fisher

Little research has been done on response of fisher to harvesting in the boreal forest. Recent work in south central British Columbia has noted avoidance of areas with understoreys that are too complex, with >80% closure of low shrubs presumably impeding hunting success for prey species such as hares (Weir and Harestad 2003).

Most literature for marten reports on structural characteristics of sites either used or selected in retrospective examinations of marten habitat use patterns and distributions. One exception is the experimental treatment versus control study of pre- and post-harvest short term response of various wildlife species to CPR harvesting in western Quebec, by Potvin, Courtois, and Belanger (1999). They found that within their home ranges, martens avoided clearcut patches except when patches had a substantial understorey of dense shrub layer and coniferous regeneration (Potvin 1998 in Potvin, Courtois, and Belanger 1999).

Sturtevant, Bisonette, and Long (1996) constructed a conceptual model of stand-level dynamics from an empirical study of forests in western Newfoundland and related this to the habitat requirements of resident marten. They recommend preventing stands from entering the stem exclusion phase using thinning techniques to promote understorey vegetation and provide a potential small mammal resource. In addition, supplying logs at ground level will further increase habitat potential for voles and allow marten to access this prey resource in winter. Ultimately, this type of stand-level management should be incorporated into an overall landscape-level management strategy.

In 2003, Hodson et al. (2004) set baited track plates in forests logged from 1960 to 2000, as well as in primary forests stratified into mature conifer (80+), mature deciduous (60+) and old growth (121+) in the Temagami-Algonquin region of central Ontario. A greater proportion of track plates in deciduous mixedwood and deciduous forest types had marten detections relative to those in coniferous and conifer mixedwood stands, but sample size was too low to evaluate statistical significance. The mature hardwood site, which had greatest number of detections, lacked the CWD observed in younger deciduous stands (within a 1970s logged site), but had a substantial conifer understorey density which may offset the limited overhead cover that results under a deciduous canopy in leaf-off conditions.

Payer and Harrison (2003, 2005) examined marten use in relation to forest structure in an industrial forest (2003) and in an adjacent unharvested reserve (2005) in the transitional forests of Maine, on the boundary between the boreal and northern hardwood forests. In the industrial forest, spruce budworm-defoliated stands provided suitable marten habitat; vertical structure was provided by large snags and surviving live trees in combination with plentiful CWD and understorey vegetation. These characteristics offset the reduced live-tree basal area of defoliated stands as compared to mature stands.

Estimates for forest structural characteristics in areas occupied by martens in an intensively managed industrial forest (Payne and Harrison 2003) were suggested as conservative minimum structural thresholds for martens (these were uniformly exceeded across the wilderness forest). In the industrial study area, suitable marten habitat had approximately 100 m³/ha CWD (interquartile range: 52-170), including 900 sound to moderately rotten downed logs/ha with a minimum diameter of 7.6 cm; root masses (63/ha), standing dead trees (160/ha) and stumps (290/ha) which also contributed to available

CWD; basal area $\geq 18 \text{ m}^2/\text{ha}$ for trees $\geq 7.6 \text{ cm dbh}$; $\geq 75\%$ overhead canopy; and dense understorey vegetation (approx 15,000 woody stems/ha).

3.2.3.2.5 *Ungulates*

The preference of moose for young seral stages is attributed to increased availability of forage in the form of grasses, shrubs and regenerating trees following wildfire or harvest. Forage availability is an important factor affecting moose habitat use, irrespective of scale (Mansson et al. 2007). Therefore, management practices that affect forage distribution may have an effect on spatial distribution of moose. In general, the extensive use of clearcutting in the boreal forest has increased the quantity of forage available to moose in the landscape. However, the rate at which browse regrowth occurs is an important predictor of moose abundance post-disturbance (Fisher and Wilkinson 2005). Immediately following clearcutting, cover is often lacking and food availability may be reduced due to mechanical disturbance of the shrub and ground layers. As such, positive impacts of harvesting on moose habitat may take a number of years to accrue. Stand-level management practices, such as clearcut with protection of advanced regeneration (CPR), that aim to protect and/or enhance the regeneration of understorey shrubs, are anticipated to benefit moose through the increased availability of forage immediately post-harvest.

Short-term responses

In their study of short-term responses of 12 wildlife species to CPR, Potvin, Courtois, and Belanger (1999) found that moose avoided areas where the shrub layer and coniferous regeneration were scattered. They studied moose abundance, movement, survival and habitat selection two years pre-harvest and two years post-harvest in three 52-106 km² blocks logged in 100-250 ha clustered patches separated by 60-100m wide residual strips, and an uncut control block of 126 km², located nearby. Harvested area within the blocks ranged from 34-50% and was completed within a year. The study blocks comprised seven stand-types as well as CPR clearcut areas, with black spruce-dominated and mixedwood stands generally the most common. Moose were studied at the scale of the block. Moose density was measured by aerial survey in mid-winter and telemetry was used to monitor habitat use, movement, and survival.

They found that moose density declined 20-30% in the two year period after logging. Moose generally kept the same home range (estimated at $\sim 56 \text{ km}^2$), but preferentially used uncut parts of the landscape. At the forest block-scale, densities of moose were primarily related to the proportion of deciduous and mixed stands within each block, and the amount of edge between food and cover. They concluded that CPR did not maintain suitable habitat for moose in the short-term and predicted it may take 10-15 years for moose habitat (i.e., a dense shrub layer) to recover. As the study did not include a traditional clearcut treatment, it is not possible to draw any conclusions on the relative performance of CPR in influencing moose responses to understorey protection.

Long-term responses

In a rare instance in ecology, Potvin, Breton, and Courtois (2005b) re-sampled study areas 10 years after harvest. They predicted that moose densities would have increased during this period but would likely still be lower than in “optimal habitats”, defined as the most productive young forests of equivalent age. Aerial surveys to estimate moose densities were conducted in two of the blocks surveyed previously. These blocks covered 52-99 km², and harvesting levels had increased to 47-71%. At the same time, significant changes were made in Quebec to hunting regulations, with the institution of selective harvest. To control for this confounding factor the uncut control block was re-surveyed. In addition, vegetation measurements were re-taken in five harvested coniferous stands and

five harvested mixed stands to track vegetation changes over the same period. The original measurements were not reported in Potvin, Courtois, and Belanger (1999).

Ten years after CPR, moose density had increased by 54-87% in the two harvested blocks (Potvin, Breton, and Courtois 2005b). Over the same period, moose densities in the control block increased 63%. Based on this and similar increases reported from neighbouring areas, they concluded that in the block with the smaller increase in density, the change was likely attributable to changes in hunting regulations, whereas in the other block they attributed 25% of the increase to a positive response to CPR. Although the authors did not statistically relate changes in moose abundance to vegetation changes over the same period (probably due to the different spatial resolution of the datasets), reported changes in understorey vegetation characteristics indicated a significant recovery of moose forage in the 10 years since harvest. In logged coniferous stands, the shrub layer increased markedly and deciduous browse exceeded that available in similar uncut stands, although lateral cover was still lower than in uncut stands. Logged mixed stands, which had maintained much of their pre-logging character, had continued to improve or maintained a better condition relative to coniferous stands. Available browse remained exceptionally high in those stands.

3.2.3.3 Summary of Wildlife Responses to Understorey Retention

Despite the fact that understorey vegetation has been identified as one of the key parameters for maintaining bird communities, there have been surprisingly few studies that have specifically examined this in boreal forests. Studies of short-term bird community responses to understorey retention have produced conflicting results. Research in aspen-white spruce mixedwoods has shown that abundance of shrub-inhabiting birds can increase or decrease with increasing levels of GTR, while other studies have found no relationship between understorey attributes and the degree of similarity of bird communities in harvest and old-growth stands or levels of nest predation. At the species level, selective harvesting can preserve food and security cover availability for grouse through maintenance of the understorey layer, whereas clearcutting significantly decreases both. No long-term studies of bird responses to understorey retention were found, but long-term comparisons of bird communities post-fire and post-harvest have implicated the faster recovery of low and tall shrub layers for the lack of complete convergence of bird communities 28 years post-disturbance.

Understorey structure can play a key role in providing security cover for small mammals; however, it can be difficult to determine whether small mammals are responding to understorey vegetation characteristics, other attributes such as CWD that also enhance cover, or both. A number of studies from the boreal forest have found that small mammal communities are maintained, or some species increase in abundance in response to harvesting practices that maintain or promote understorey structure. Similarly, some species decline in response to regeneration practices that reduce ground vegetation cover. None of these studies, however, monitored small mammal survival as a more direct measure of the effectiveness of understorey retention in providing enhanced security cover relative to clearcut areas.

Studies of arboreal squirrel responses to understorey retention in the boreal forest revealed that GTR practices can result in a substantial tree and shrub response in the understorey that can result in interspecific competition which may confound the responses of arboreal squirrels. Dense understoreys can promote chipmunks which will compete with squirrels and small mammals for food sources such as hypogeous fungi and insects associated with CWD.

Understorey density and height are critical habitat variables for snowshoe hare, so stand-level structural retention practices designed to maintain or promote understorey integrity are anticipated to promote hare use as well. Yet, in most cases, clearcut with protection of regeneration resulted in significant short- and long-term negative impacts on hare habitat, with estimates of habitat recovery

in the order of 20-30 years post-harvest, depending on forest-type. No traditional clearcut blocks were available for comparison, but Fisher and Wilkinson's (2005) review of snowshoe hare responses to harvesting suggests that CPR performs no better at maintaining or regenerating suitable hare habitat. The exception was a study conducted in forests of the transition zone between northern hardwood forest and the boreal, which found that CPR, followed by PCT, can produce favourable habitat conditions for hares. As such, there may be bioregional influences on snowshoe hare responses to similar harvest practices. Maintenance of snowshoe hare populations in the short term appears to be dependent on availability of remnant stands in harvested landscapes, so rates of harvesting across multiple stands in the landscape may be more critical than stand-level retention practices for this species.

Most studies of marten responses to understorey structure have been retrospective. In general, these studies have found that complex understorey structure can off-set reductions in canopy cover due to CPR harvesting, leaf-off conditions in a deciduous canopy, and spruce budworm defoliation. One study constructed a conceptual model of stand-level dynamics related to marten habitat requirements. This study recommended preventing second-growth stands from entering the stem exclusion phase by using thinning techniques to promote understorey vegetation and provide a potential small mammal resource.

Similar to snowshoe hares, moose avoided recent CPR cutblocks due to the sparse shrub layer and lack of overstorey which reduced both forage availability and security cover relative to uncut portions of their home ranges. Moose densities declined 20-30% within two years of harvesting, but recovered 10 years post-harvest. The recovery in moose densities was matched by a significant recovery of moose forage over the same period.

The limited number of studies of understorey retention, scattered across many wildlife groups, makes it difficult to identify any universal patterns in wildlife responses to understorey structures. The role of a well developed understorey in the provision of security cover appears to be significant for ground-foraging and nesting birds, small mammals, snowshoe hare, and possibly moose. Interactions between understorey structure and other structural attributes such as live trees and CWD were apparent for small mammals, arboreal squirrels and ungulates, reflecting a need for manipulative experiments to isolate the relative influence of multiple structural attributes on wildlife responses.

3.2.4 Coarse Woody Debris

In most boreal forest types, volumes of coarse woody debris (CWD) are highest immediately post-fire and in old growth, roughly exhibiting a U-shaped curve (Figure 3.15). Clearcutting can often produce CWD volumes at levels that approximate those found in early post-fire environments (Pedlar et al. 2002). However, clearcut areas lack the substantial pool of potential CWD in the form of snags created by fire that is infused into the stand over subsequent decades (represented by the hump in each peak in Figure 3.13). In addition, harvesting and silvicultural practices often result in CWD that largely consists of shorter broken or fragmented pieces in human-created accumulations such as roadside piles. Stand-level management practices that aim to protect existing and new CWD at harvest and/or that aim to enhance the future recruitment of CWD through retention of large live trees and snags should have beneficial effects for many CWD-associated wildlife species.

In terrestrial systems, CWD provides a range of ecological services to wildlife, including sites for nests, dens and burrows; invertebrate prey; hiding cover for predators and protective cover for their prey; moist microsites for amphibians; and travel-ways across streams, across the forest floor, and beneath and through the snow (Stevens 1997). Vertebrate wildlife closely associated with these ecological roles of CWD include small mammals, snowshoe hare, some squirrels, beaver, mustelids, and bears (Lofroth 1995).

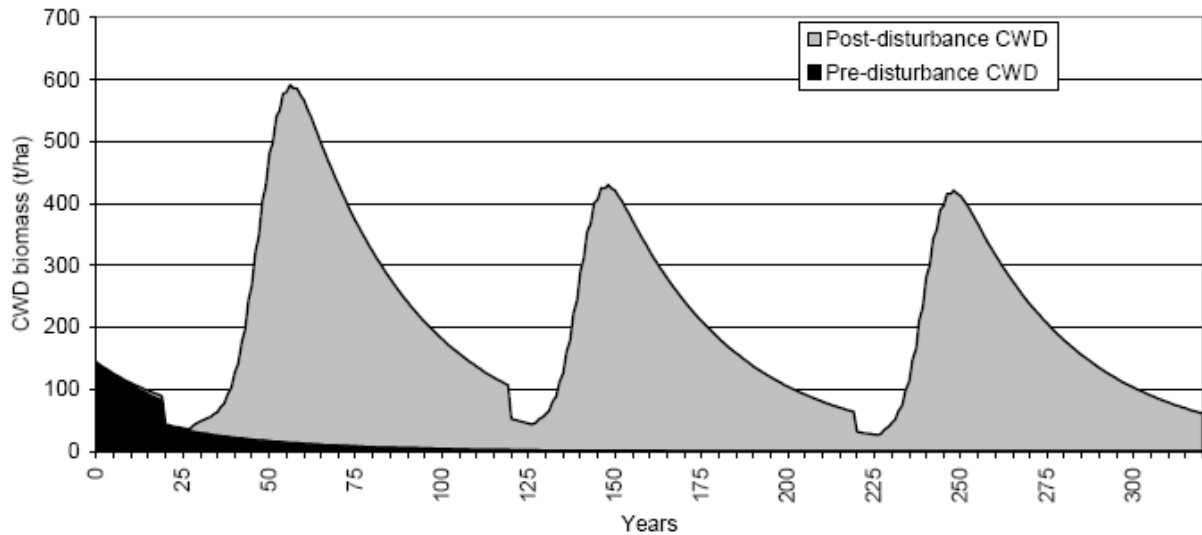


Figure 3.15 Schematic Diagram of CWD Dynamics in a Stand Subject to a Catastrophic Wildfire at Age 150 Years and Then a Series of Catastrophic Wildfires at 100-Year Intervals (reproduced from Grove, Meggs, and Goodwin 2002, p. 18)

3.2.4.1 Birds

Few boreal bird species are considered dependent on CWD, but some ant-dependent woodpeckers (e.g., black woodpeckers) are known to use logs as a feeding substrate where snags aren't readily available (Rolstad, Majewski, and Rolstad 1998). Nevertheless, the potential influence of CWD in modifying responses of boreal bird communities to GTR has received some attention.

Harrison, Schmiegelow, and Naidoo (2005) estimated percent ground cover of CWD in their study of bird community responses to varying levels of GTR. They found a significant negative linear trend in CWD quantity with increasing GTR levels in all the forest cover types they examined. However, no relationship between this pattern and bird community response was examined. Similarly, Tittler and Hannon (2000) found no relationship between CWD quantity and levels of nest predation adjacent to and within clumps of retained trees. Hobson & Schieck (1999) was the only bird study found that showed a significant influence of CWD on bird assemblages of post-fire and post-harvest stands in a chronosequence of ages post-disturbance. Immediately post-disturbance, CWD levels were twice as high on post-harvest sites (464 m³/ha) compared to post-fire sites (232 m³/ha). By 14 years post-disturbance, no significant difference remained, with CWD levels stabilising at around 280-320 m³/ha. In terms of bird community responses, they found that 17% of the variation in the number of bird species present in stands one year post-fire, 14 and 28 years of both disturbance types, and one year post-harvest was explained by the percent ground cover and volume of CWD. However, there was no obvious ecological relationship between CWD and the species predicted to have their highest abundances one year post-harvest.

It is likely that boreal bird responses to CWD will be restricted to a few specialist birds such as woodpeckers and possibly grouse; responses may be weak relative to other vertebrate groups such as mammals, but the ecological roles of CWD in relation to birds has received little attention in boreal forests or elsewhere.

3.2.4.2 *Mammals*

3.2.4.2.1 *Small Mammals*

Coarse woody debris has been recognised as a structural element of forested stands of particular importance to small mammals. CWD provides subnivean access in winter, habitat for invertebrates (an important food source), and escape cover from predators.

Short-term responses

Small mammal responses to CWD retention have been equivocal. Hannon (2005) reports on a Landscape Structure and Biodiversity Project (LSBP) from New Brunswick—a cross-taxal, cross-regional study that examined the relative contributions of stand versus landscape structure and composition in determining the presence/absence, abundance, and species dynamics in managed and unmanaged forest landscapes (Bowman et al. 2000, 2001 in Hannon 2005). Vegetation structure and composition at the stand level (primarily variables related to the quantity of shrubs and CWD) explained much of the variation in abundance patterns of red-backed voles, deer mice, short-tailed shrews, and woodland jumping mice. Similarly, Ecke, Lofgren, and Sorlin (2002) found higher species richness of small mammals and higher total abundance of voles in stands with abundant tall shrubs and CWD in heavily managed coniferous forests in Sweden. In this study, increased species richness and abundance were associated with young and mid-successional forests (0-30 years) regenerating after clearcutting, not older selectively cut forest (41-50 years old) or selectively cut old forest (> 100 years old).

Etcheverry, Ouellet and Crête (2005) found that small mammal responses to PCT, CPR and uncut 40- to 60-year-old second growth in Acadian forests of southern Quebec were species-specific, with some showing a positive association with CWD and others showing no association. In general, species richness (across the 12 species trapped) and relative abundance of small mammals were lower in PCT than in CPR or closed stands in the ten years following PCT. Red-backed voles occurred at significantly higher abundances in closed coniferous forest and CPR stands, and were significantly less abundant in PCT stands. They exhibited a preference for coniferous canopy cover and high CWD levels. CPR generated significantly higher percent ground cover of CWD than was observed in PCT stands, and slightly higher than that observed in closed coniferous forest. These results conflict with those of Homyack et al. (2005a) (see below). In terms of other small mammal species, deer mice were not influenced by treatments, but again densities were associated with the presence of CWD. Short-tailed shrews were most abundant in PCT and CPR stands in one of the study areas, but no relationship with any of the habitat variables was detected.

Contrary to predictions, manipulative experiments of CWD levels on cutblocks have failed to elicit a significant short-term response of small mammal communities to varying levels of CWD quantity. In a study of small mammal responses to varying combinations of CWD and GTR in boreal mixedwood forests (described in detail in Section 3.3.1.2.), Moses and Boutin (2001) found no relationship between relative changes in abundances, survival and reproductive activity after treatment and CWD quantity. They did, however, find a significant treatment effect, with favourable responses of some small mammal species to residual patches of undisturbed trees and associated understorey vegetation. Their results suggested that, at least in the short term, the retention of CWD alone was insufficient to maintain pre-disturbance small mammal populations in this forest type.

Craig et al. (2006) found similar results in a study of the response of deer mice to CWD manipulations in low and high elevation temperate coniferous forests of southern interior British Columbia. They compared three levels of CWD retention on small (1.4 ha) treatment sites within replicate clearcut and uncut stands. “Low” treatments were created by removing all intact pieces and crushing well decayed pieces, using an excavator on clearcut sites and by hand on uncut sites.

“Medium” treatments were not manipulated beyond standard harvesting practices on the clearcut sites, with removal by hand of approximately 50% of the CWD across diameter, length and decay classes at the low elevation study area and no manipulation at the high elevation study area due to impractically high CWD levels. To create “high” treatments in the clearcut sites, CWD that would normally have been removed from site (e.g., snags) was retained and evenly distributed across the treatment area. In uncut “high” treatments, CWD was not manipulated at the low elevation area, whereas CWD was recruited into the high elevation study area by felling approximately 12 snags. Using mark-recapture of deer mice to assess population densities, survival and reproductive rates, they found that populations responded positively to harvesting at the low-elevation but not at the high-elevation study area. At low elevations, population dynamics of deer mice were not associated with patterns of vegetation cover, but were positively associated with decreasing CWD volumes. No significant relationship between population dynamics and vegetation cover or CWD was observed at the high elevation study area. The response of deer mice at the low elevation sites was opposite to that expected from the manipulation. They concluded that CWD was not a necessary habitat component for deer mice on low elevation, densely vegetated clearcut areas within three years post-harvest.

Long-term responses

Whether the lack of response by small mammals to manipulations of CWD persists into the long term is unclear. Homyack, Harrison, and Krohn’s (2005a) study of the effects of PCT on small mammal communities across a chronosequence of stands up to 16 years post-treatment suggests they may. Small mammal responses were not related to CWD density and they found no significant difference in CWD quantities in thinned and unthinned stands or with time since thinning. They attributed positive responses of red-backed voles and masked shrews to the partially open canopy and more structurally diverse understorey produced by PCT. Both Fuller, Harrison, and Lachowski. (2004) and Homyack, Harrison, and Krohn (2005a) suggest that the lack of an association between small mammal responses to CWD in the treatments the authors studied may be an indication that CWD is not limiting in these systems, such that changes in understorey structure play a more pronounced role in providing security cover to small mammals. Manipulative studies that explicitly incorporate varying levels of understorey retention/removal, along with CWD and overstorey treatments should help inform this.

3.2.4.2.2 *Arboreal Squirrels*

Partial harvesting techniques generally promote not only live tree retention in the overstorey, but may enhance immediate and long-term CWD retention within a stand. The life requisites of arboreal sciurids demand a supply of live and dead trees in stands for short-term supply, as well as CWD for food source (e.g., hypogeous fungi and insects), and shrub cover for protection during foraging. Some hypogeous fungal species that are critical dietary components of flying squirrels are found exclusively on CWD (Wheatley 2007). Flying squirrels in old mixedwoods in boreal northern Alberta were positively associated with intermediate decay stages of CWD, which support fungi and lichen (Roy, Stelfox, and Nolan 1995 in Fisher and Wilkinson 2005). Live residual trees provide for long-term recruitment of CWD into a stand which in turn provides cover, travel paths, burrow sites and a substrate for arboreal sciurid food such as fungi and lichen (see review in Fisher and Wilkinson 2005). However, the potential for these responses to occur in a forest harvesting situation remain speculative as no studies of arboreal sciurid responses to short- or long-term CWD retention in harvested stands could be found.

3.2.4.2.3 *Marten and Fisher*

The American marten and fisher are large predatory mustelids typically associated with live tree canopy closure and abundant woody cover not generally found in young successional forest stages (see authors in Fisher and Wilkinson 2005). Fisher prefer mature forests with large coarse woody debris (CWD); stands with a deciduous component offer more complexity with regards to standing and downed wood, which provides habitat for prey species as well as sites for resting, cover and thermoregulation. Weir and Harestad (2003) report that for fishers in south central British Columbia, large pieces of CWD were used for thermal cover during extended periods of severe cold (< -20 degrees Celsius).

CWD requirements

As noted in the discussion of marten response to live tree retention, older forests offer more abundant and varied CWD (e.g., stumps, logs, brush, and root balls), enabling subnivean access to hunt small mammals. Large diameter resting and denning trees used in summer are also plentiful in older forests. Although marten may forage in a wide variety of conditions during winter, requirements for resting sites appear more specific, with the vast majority of resting sites associated with large logs, stumps and dead trees (see Watt et al. 1996). Chapin, Harrison, and Katnik (1997) and Payer and Harrison (2000) in NSAMRT (2006) found these structures also existed in younger stands that had been affected by spruce budworm in Maine.

Marten are more successful when hunting in old forest, but it is not yet clear whether the habitat offers more prey, or the physical structure renders prey easier to catch (NSAMRT 2006). Marten search out the natural hollows and air spaces that form around CWD as access sites to subnivean small mammal populations. Marten must have access to reliable prey source throughout the winter months. Downed logs and other CWD typically supplied by late-successional forests provide access by maintaining interstitial spaces beneath the snow layer (see Sturtevant, Bisonette, and Long 1996). CWD may also function as structural cover for forest vole populations, providing structure necessary for the construction of protective runways and subnivean conduits. However, some (Thompson and Colgan 1994 in Watt et al. 1996) believe that the important role of large prey items such as hare decreases the importance of CWD in northeastern boreal forests.

As noted earlier, recent scientific literature presents anecdotal and experimental evidence that martens require structure associated with latter successional stages, but not necessarily old forest itself (Sturtevant, Bisonette, and Long 1996), and may be able to sustain themselves in regenerating forests with sufficient suitable structure (see authors in Fryxell et al. 2004). Several authors (in Sturtevant, Bisonette, and Long 1996) note that subsequent second-growth forest from boreal clearcutting is often of much lower habitat quality due to absence of structural complexity. However, immediately after clearcutting, there is a pulse of CWD and a strong herbaceous growth response providing abundant cover for voles and hares. If managed appropriately, second-growth forests could provide marten with a temporal window of habitat supplying key structural attributes linked to cover and prey (Bissonette, Fredrickson, and Tucker 1989 in Sturtevant, Bisonette, and Long 1996).

Martens were rarely found in harvested 40- to 60-year-old second-growth stands of balsam fir in Newfoundland, preferring older stands (Thompson and Curran 1995 in Fisher and Wilkinson 2005). This difference in use was not due to canopy cover, but to differences in structure on the forest floor that provided habitat for meadow voles, an important food for martens in that province.

Short-term responses

Potvin, Belanger, and Lowell (2000) analysed winter home ranges to measure marten habitat selection in 1992 and 1993, immediately post-logging, in a black spruce-dominated clearcut boreal landscape (123 km²) in western Quebec. The landscape consisted of a centre of cutover matrix (74 km² or 60%) surrounded by contiguous uncut forest. Forty-four percent of the landscape was regenerating stands, much of which dated from 1992 when 28% of the block was clearcut with CPR. The residual forest within the landscape was fragmented and composed of narrow corridors 40-100-m wide along streams and permanent brooks or between individual clearcut areas, and small patches of uncut forest reserves, non-commercial young stands and non-productive areas. Telemetry data were analysed at the landscape scale (i.e., home range composition measured against random mosaics) and stand scale (i.e., use vs. availability within home ranges) with individual animals as the sample units. Within-stand habitat surveys were used to characterize coarse woody debris (CWD), coniferous saplings and trees, and lateral cover (i.e., visual obstruction).

Marten did not select or avoided recently cut stands and mid-age black spruce stands where CWD was highest (Potvin, Belanger, and Lowell 2000). Various authors have reported that the most important structural elements for marten habitat in winter are CWD and coniferous saplings (e.g., Potvin, Belanger, and Lowell 2000). However, the amount of woody debris was low in black spruce forest and deciduous forests; CWD volumes were lower in older stands (> 80 years) than younger ones. Black spruce stands do not have structural advantages for martens when they approach maturity (Potvin, Belanger, and Lowell 2000).

When studying winter hunting behaviour of Ontario marten, Thompson and Colgan (1994) in NSAMRT (2006) found that despite less subnivean access points available in logged forests, and fewer investigations of same, marten hunted beneath the snow with similar frequencies to uncut forest. This implied that CWD was not limiting, since marten hunt mostly for snowshoe hare in the winter in this region of Ontario, and take small mammals incidentally (Thompson and Colgan 1994 in NSAMRT 2006). Although most studies suggest that CWD levels must be above some minimum threshold, Gosse, Cox, and Avery (2005) found that Terra Nova National Park marten in Newfoundland did not select for stands with higher debris volumes. Similar to the Ontario results, the authors suggested that snowshoe hare populations were unusually high during the study, so marten may not have needed subnivean access. However, other authors have proposed that a lack of selection for CWD may only indicate that CWD in all habitats studied rest above minimum thresholds. NCASI (1999) and Bissonette, Fredrickson, and Tucker (1997) point out that in their study areas, debris was above minimum thresholds in forests > 12 m tall. Chapin, Harrison, and Katnik (1997) observed marten showing no cover type selection when choosing resting sites suggesting CWD levels surpassed thresholds levels.

NCASI (1999) noted that CWD alone was insufficient to influence habitat use, and despite provision of CWD, marten will not use regenerating clearcut areas until a threshold of overstorey development is reached (between 14 and 18 m³/ha).

Stand-level modeling and management

Sturtevant, Bissonette, and Long (1996) constructed a conceptual model of stand-level dynamics from an empirical study of forests in western Newfoundland and related this to the habitat requirements of resident marten. They recommend preventing stands from entering the stem exclusion phase using thinning techniques to promote understorey vegetation and provide a potential small mammal resource. In addition, supplying logs at ground level will further increase habitat potential for voles and allow marten to access this prey resource in winter. Ultimately this type of stand-level management should be incorporated into an overall landscape-level management strategy.

Long-term responses

Payer and Harrison (2003, 2005) conducted an examination of marten use in relation to forest structure in an industrial forest (2003) and in an adjacent unharvested reserve (2005) in the transitional forests of Maine, on the boundary between the boreal and northern hardwood forests. In the industrial forest, spruce budworm-defoliated stands had greater volumes of snags, downed logs and root masses, and included taller trees and higher basal areas of live trees than regenerating clearcut areas (Payer and Harrison 2000 in Payer and Harrison 2003). Defoliated stands provided suitable marten habitat; vertical structure was provided by large snags and surviving live trees in combination with plentiful CWD and understorey vegetation. These characteristics offset the reduced live-tree basal area of defoliated stands as compared to intact mature stands.

Overall estimates for forest structural characteristics in areas occupied by martens in an intensively managed industrial forest (Payer and Harrison 2003) were used as suggested conservative minimum structural thresholds for martens (these were uniformly exceeded across the wilderness forest). In the industrial study area, suitable marten habitat had approximately 100 m³/ha CWD (interquartile range: 52-170), including 900 sound to moderately rotten downed logs/ha with a minimum diameter of 7.6 cm; root masses (63/ha), standing dead trees (160/ha) and stumps (290/ha) also contributed to available CWD; basal area ≥ 18 m²/ha for trees ≥ 7.6 cm dbh; $\geq 75\%$ overhead canopy; and dense understorey vegetation (approx 15000 woody stems/ha).

Structurally mediated responses

Andruskiw (2003) and Andruskiw et al. (2008) conducted an investigation into habitat-mediated variation in predation risk of marten prey species in the jack pine and black spruce-leading forests of northwest Ontario. Marten investigate breaks in the snow surface around CWD structural elements and smell or listen for prey at the upper openings of subnivean access points (i.e., any hole in the snow large enough and deep enough for a marten to enter to the forest floor (diameter ≥ 10 cm). These points are generally located around CWD, tree trunks and low hanging branches of young trees. An unlogged control landscape (1000 km², natural origin, 40-100 years old) was paired with two non-contiguous logged landscapes (200 and 800 km²) of 20- to 50-year-old regenerating stands.

One key difference between logged and unlogged forests was the abundance of CWD, with logged forests being relatively depauperate (Fryxell et al. 2004). Red-backed voles were abundant in both logged and unlogged forests and were likely at a peak in their cycle during the study period. Prey choice was simple for marten in the unlogged study forests; red-backed voles were the most abundant and used prey type due to the near absence of any larger prey. Prey choice was more complex in logged forests, where a substantial number of snowshoe hares were present (Andruskiw 2003). No attacks on hares were observed, however, and snowshoe hares were postulated to have higher pursuit and handling costs relative to the abundant voles.

In regenerating boreal forests, the amount of CWD tends to be high following forest harvest, then declines to a minimum at about 55 years, prior to second-growth senescence. Regenerating stands of 30-60 years old tend to be structurally simpler than older stands. Despite having lower levels of CWD, the availability of subnivean access in regenerating forests was not reduced relative to uncut stands ($P = 0.948$). Additional access was created in these regenerating stands by low-reaching branches of young conifer trees. However, marten hunted with less success in regenerating forest as compared to uncut forest. Encounters with small mammals per access point in regenerating forest were 41% less frequent than in uncut forest ($P < 0.001$). Marten home ranges in regenerating forest had 30% less CWD from all decay classes (1-5) combined than those in uncut forest, and 55% less when they considered only CWD in decay classes 1-3 ($P < 0.001$).

Results from Andruskiw (2003) showed that frequency of prey encounter, attacks and kills were higher in old uncut forests, despite the fact that small mammal density was similar in younger logged forests. Differences in predation efficiency were linked to the higher abundance of CWD, which seems to offer sensory cues to martens, thereby increasing the odds of hunting success. Although voles were equally abundant in regenerating versus uncut forests, predation risk differed greatly as a result of habitat-mediated variation in search efficiency due to differences in the amount of CWD. Martens were able to use this debris to better access prey below the snow surface, enhancing their hunting success. In this system, search efficiency was most affected by habitat complexity, rather than probability of successful capture once prey was encountered. Structural habitat complexity created by presence of a substantial CWD resource enhanced the efficiency of predatory search.

3.2.4.3 Summary of Wildlife Responses to CWD Retention

The ecological roles of coarse woody debris (CWD) in relation to birds have received little attention in boreal forests or elsewhere. Of the three songbird community studies that examined the relative influence of CWD, only one found a significant, but weak, relationship between CWD volumes post-fire and post-harvest and bird community composition. It is likely that boreal bird responses to CWD are restricted to a few specialist bird species such as woodpeckers and possibly grouse.

Studies of small mammal responses to CWD retention have produced conflicting results and this appears to be in part due to the redundant roles CWD and understorey vegetation can play in providing security cover. Even manipulative experiments have failed to elicit a significant short-term response of small mammal communities to varying levels of CWD quantity. However, these studies did not include manipulations of understorey structure, so it was not possible to isolate the relative influence of each attribute. As for studies of small mammal responses to GTR, all of the studies reviewed were of short duration, so it is possible that small mammal population fluctuations may have masked responses.

Arboreal squirrels utilise CWD and understorey structure in similar ways to small mammals, so could be expected to display similar responses to practices that retain CWD. However, no studies of squirrel responses to short- or long-term CWD retention in harvested stands could be found.

Marten are generally considered to display a strong association with CWD. However, marten select against recently harvested stands, which can often have equally high or higher CWD volumes as old forest, depending on forest type. Presence of high quantities of CWD alone is insufficient to influence habitat use; marten will not use regenerating clearcut areas until a threshold of overstorey development is reached. Other studies of marten use of logged forest have also found a lack of selection for CWD, particularly where snowshoe hare populations are high and marten may not have needed subnivean access to small mammal prey. In contrast, differences in predation efficiency has been attributed to higher abundance of CWD in unharvested versus logged stands (Andruskiw 2003). Although small mammal prey densities did not differ between logged and uncut forest, CWD appeared to provide a sensory cue to martens, increasing their odds of hunting success.

With the exception of small mammals, vertebrate wildlife responses to CWD retention have received little attention in boreal forests. The few studies that have been done have generally focused on the quantity of CWD and the function of this as security and thermal cover, rather than the quality, which may be equally as important in terms of short- and long-term food supply to woodpeckers, small mammals and arboreal squirrels. CWD retention and recruitment will vary depending on the configuration of retained residual trees at harvest. Comparative studies that examine configurations other than patches, such as dispersed individual trees, may be more useful in isolating wildlife responses to CWD. Studies of wildlife response to varying CWD recruitment rates are also lacking.

3.2.5 *Summary and Conclusions*

Various forms of green-tree retention and understorey protection (e.g., CPR and MUP) have been the predominant alternative practices to traditional clearcutting that have been studied in relation to wildlife responses in the boreal forest. No studies of responses to specific snag or CWD retention practices were apparent in this review. The literature on responses to GTR practices was dominated by studies of boreal bird communities, largely from western Canada.

In general, GTR practices appear to enhance both the short- and long-term habitat value of stands for the broadest array of wildlife groups. Thus, GTR practices appear to offer the most promise in eliciting positive wildlife responses. Retention of live trees at harvest has been shown to increase species richness of bird communities relative to clearcut areas, and accelerate the convergence of post-harvest and old-forest bird communities through regeneration. Foliage-gleaners, shrub-associated species and secondary cavity-nesters appear to benefit the most, but at the expense of ground-nesting and foraging species. Similarly, mammal species that nest or forage in trees, such as bats and arboreal squirrels, and species that directly and/or indirectly (e.g., marten prey) require security cover from predators, such as small mammals and ungulates, have been shown to benefit from GTR. No patterns in wildlife responses to snag retention were apparent, but this structural attribute has received the least attention in the literature. The role of a well developed understorey layer in the provision of security cover appeared to be significant for ground-foraging and nesting birds, small mammals, snowshoe hare, and possibly marten and moose. Contrary to predictions, however, CPR does not appear to perform any better than traditional clearcutting in enhancing short-term habitat values for species such as snowshoe hare or moose, generally associated with mid-successional stands (Potvin, Breton, and Courtois 2005) CWD retention was found to have a significant influence on marten habitat use and hunting success, and on their prey-base (small mammal communities) through enhanced thermal and security cover, possibly in concert with overstorey and understorey retention.

Although GTR patches appeared to result in a significant short- and long-term life-boating effect for many taxa, there have been insufficient comparative studies incorporating other configurations such as dispersed live trees or combinations of the two, to assess the relative performance of patch-retention. Similarly, although enhanced responses were evident for many wildlife groups in response to increasing levels of retention, there has been insufficient study to identify thresholds of wildlife response for any of the attributes reviewed.

The mammalian literature was more diverse, but often less directly related to the topic. Only two studies of boreal amphibian responses to structural retention were found. The avian research on GTR and NDPE was extensive, but limited in strength of inference. The strength of inference of many of the studies was limited by absence of measures of reproductive success and lack of an explicit treatment of landscape context. There was some indication of bioregional variations in wildlife responses to similar retention practices, suggesting caution should be applied when attempting to extrapolate results from one region of the boreal to another if studies have been restricted to particular regions. A number of studies illustrated the challenges faced by researchers in trying to tease out relative influence of individual structural attributes where multiple, inter-correlated structural variables are retained at harvest, reflecting the need for manipulative experiments to compliment comparative habitat use studies. Overall, there was insufficient information in the literature that could be used to identify specific stand-level structural retention practices, retention levels, or retention configurations that might elicit positive responses of wildlife across the broadest range of taxa.

3.3 Key Information Gaps

Forest managers want answers to three questions (from Hannon 2005) in relation to stand-level structural retention.

1. What should be retained?
2. How much should be retained?
3. How should it be retained?

Similar to Hannon (2005), this review has found that there is sufficient information to answer the first question (see Section 3.4 for further discussion), but key information gaps hamper our ability to answer the other two questions.

Probably the most critical information gap is a lack of knowledge of stand-level thresholds of wildlife responses to retained structures (i.e., the answer to Question 2). Hannon (2006) criticises the bird literature in particular for testing null hypotheses that allow us to determine whether a treatment has an effect, but doesn't enable us to tell managers how much is required to meet a particular management objective. The same criticism can be applied to other vertebrate groups.

Studies that examine responses to a broader range of structural retention levels are required, using focal species that are relatively easy to sample, whose associations with particular structural attributes are well-established, and that are predictably responsive to traditional harvest methods. Hannon (2006) recommended early- and late-seral stage specialists and species with large home ranges as candidate groups. Rempel (2007) recommended a suite of 13 boreal songbird species for evaluating the effectiveness of forest management strategies at conserving biodiversity. He selected species whose habitat requirements were well known and that best represented the full range of forest cover homogeneity and heterogeneity on the landscape. A similar selection process could be used to identify candidate species for examination of stand-level thresholds of response. Among the mammal species, small mammals and snowshoe hare are relatively poor candidates due to the requirement for annual sampling for a minimum of 3-7 years to determine natural population cycles independent of treatment effects, although Pearce and Venier (2005) suggest a habitat modeling and monitoring approach for small mammals as a substitute for biological response monitoring. Arboreal squirrels, marten and ungulates may be better candidates, although study designs for the latter two must be able to isolate stand- and landscape-level responses.

Although there was evidence in the review for beneficial effects of patch retention, particularly larger patches, for many species, not enough comparative studies that have examined alternative configurations such as dispersed live tree retention or combinations of the two. The issue of where retention should occur within a stand (i.e., upland versus riparian retention) was beyond the scope of this review, but warrants further attention. As such, the answers to Question 3 remain elusive.

Additional information gaps that need to be addressed include wildlife responses to snag retention, wildlife responses to old (> 60 years) cutblocks with residuals, relationships between wildlife abundance and reproductive success, response of carnivores to fire and harvest, and relationships between stand-level and landscape-level responses for wildlife species that utilise multiple stands.

Wildlife responses to snag retention have received significantly less attention in the literature compared to any of the other stand-level structural attributes reviewed. This is probably because it is the least practiced retention type due to fears for worker safety. However, studies are needed to examine modified forms of snag retention, such as high-cut stumps or stubs (up to 5 m tall) that are beginning to be retained more often in cutblocks in some regions. These structures may be useful foraging substrates for bark gleaning birds and some woodpeckers as the stand regenerates, and will contribute to CWD recruitment within the stand.

Retrospective chronosequence studies substitute space for time, allowing long-term patterns of wildlife responses to be described in the absence of decades of research. However, the ability of this type of study to look into the future has been limited by the lack of availability of older cutblocks with and without residuals. As a consequence, Schieck and Song (2006) recommend monitoring and adaptive management. However, long-term responses of wildlife may not manifest themselves for decades, while the forest landscape continues to change in the interim due to natural and anthropogenic forces. In the absence of older cutblocks, rather than abandoning retrospective studies, it might be prudent to use older post-fire stands with and without residuals as the closest analogue available. At a minimum, retrospective chronosequence studies, like those conducted by Schieck et al. need to be expanded and/or repeated to examine boreal bird responses in a wider variety of forest types and mammalian responses to stand-level structural retention anywhere in the boreal region.

Many of the studies in this review cautioned readers that it was not known how relative abundances translated into reproductive fitness. Increases in bird density following logging in the surrounding landscape can result in crowding, with lowered pairing and breeding success in bird populations (e.g., Schmieglow, Machtans, and Hannon 1997). Similarly, Harrison (2002 in Harrison, Schmieglow, and Naidoo 2005) reported that increased abundances of Swainson's thrush in partially harvested stands at the EMEND study area did not lead to increased reproductive success, as most of the increase was associated with non-reproductive juveniles. Fryxell et al. (2004) found that abundance of adult amphibians was positively correlated with reproductive fitness, but juvenile abundance should not be used as an index of habitat quality. For boreal songbird studies, a simple estimate of the reproductive status of individuals observed in point counts, such as used by Harrison, Schmieglow, and Naidoo (2005) may be a cost-effective enhancement. On the whole, this review found that studies of mammalian responses more often incorporated estimates of survival rates, and reproductive status.

As identified in the initial scoping of the literature available for review, substantial gaps in data exist for response of carnivores to fire and harvest. Predator-prey interactions can affect mammal community structure in both early and late successional stages, so this clearly needs to be addressed. Marten, snowshoe hare, and small mammal communities may be a candidate system.

With the exception of some bird species and small mammals, most vertebrate wildlife function at scales beyond individual stands, making it difficult to discern landscape- and stand-level influences on wildlife responses. No study successfully integrated the two scales in a manner that could be related back to particular stand-level retention practices. For example, Venier and Pearce (2007) examined the relative influence of stand-level structural attributes and landscape-context variables in determining boreal forest songbird communities in a logged versus unmanaged landscape. They used generalized additive models to examine the relationship of individual species with four sets of environmental data (understorey floristics, forest structure, overstorey composition, and landscape context). They found that all four types of variables were frequently used in the best species' models, but stand-level structure occurred slightly more often in the models than landscape. However, it was not the quantity of structure at the stand-level that was important, but the landscape-scale provision of that structure across multiple stands and/or remnant stands, depending on which landscape it applied to. There is no way to readily relate these results back to any particular stand-level management activity. Other studies, (e.g., Potvin, Breton, and Courtois 2005) have analysed stand-level structural attribute data separately from landscape-level population monitoring and only discussed any apparent correlations in trends. Study designs that better incorporate multiple spatial scales need to be developed.

Finally, there is a lack of monitoring studies to examine responses of wildlife for which forest management guidelines have been in place for a decade or more (e.g., marten in Ontario; ungulates in Manitoba). Given the time frame since these guidelines were released, there may be opportunities for retrospective validation studies of cutblocks spanning over 10 years or more. However, these need to be complemented by the inception of formal effectiveness monitoring programs.

3.4 Management Implications

Returning to the three questions posed by Hannon (2005):

1. What should be retained?

While there is adequate information to answer this question in a broad sense (i.e., retention of all stand-level attributes was found to elicit positive responses from many species from broad taxonomic groups, with few negative responses), a more detailed answer is dependent on the management objectives of the harvesting practice. This is something both wildlife researchers and forest managers do not appear to be clear about. Is the objective to enhance the short-term value of clearcut areas to particular wildlife species or groups? Is it to achieve convergence with naturally disturbed forests of a similar age? Is it to accelerate convergence to old forest structural conditions?

If the objective is to enhance the value of clearcut areas to wildlife (i.e., short- or long-term life-boating) then that should be achievable with the retention of any one or more of the structural attributes considered in this review. If the objective is to achieve convergence with wildlife communities associated with naturally disturbed forests of a similar age, then this may only be achieved in the long term in relation to some structural attributes. In the context of a commercial harvest, only the lower end of the natural range of variation in the quantity of live trees and snags retained post-disturbance appears to be achievable. This is one reason why post-fire and post-harvest wildlife communities in the early-seral stage are so disparate. Emulation of natural disturbance would also largely preclude practices such as CPR, which retains understorey structure that would normally be absent immediately after fire. In fact, END could probably be enhanced by the re-introduction of post-harvest regeneration burning to boreal forests, as is now occurring to a limited extent in Fennoscandia. In the longer term, post-fire and post-harvest wildlife communities appear to converge, irrespective of the presence of retained structures, but this convergence will likely be incomplete before planned rotation ages. As such, achieving convergence with naturally disturbed forest of the same age may preclude re-establishment of many species associated with old forest, if rotation ages are truncated. If the objective is to accelerate convergence towards old forest wildlife communities, then more aggressive retention practices, such as patch retention of multiple structural attributes, aimed at short- and long-term life-boating and mid-successional structural enrichment may be required.

No single stand-level structural retention practice will achieve all wildlife management objectives. Some old-forest species will respond negatively to harvesting regardless of the retention practice used, while other species, such as those associated with open ground or shrubby mid-successional habitats (e.g., snowshoe hare) will negatively respond to GTR practices relative to traditional clearcut areas. Just as the predominant use of clearcutting resulted in concerns about wildlife habitat management, neither would a wholesale shift to retention practices such as GTR be advisable. Instead, the full range of structural retention practices, including no retention, should be applied across the landscape.

2. How much should be retained?

Neither stand-level nor landscape-level thresholds in wildlife response to structural retention have been determined. Studies of boreal bird community responses to GTR indicate that as retention levels

increase, similarities between post-harvest and old-forest bird communities increase. In addition, both large and small retained patches of live residual trees have been found to increase the short- and long-term degree of similarity of post-disturbance bird communities relative to clearcut areas. So, for boreal birds at least, increasing levels of retention of residual live trees appears to provide benefits for increasing numbers of species. But, as noted above, this may come at the expense of species associated with open habitats.

In the face of uncertainty, forest managers should employ levels of structural retention within harvested stands covering the range of natural variability. The relative proportions of these varying levels of retention that should be applied across the landscape are unknown, but should also be maintained within the range of natural variability. That said, there are a number of constraints that limit the use of such natural disturbance paradigms, including economics, safety conditions, maintaining sufficient regeneration conditions, and the need to operate within socially acceptable limits. Therefore the amount of retention must be a balanced among numerous limits.

3. How should it be retained?

Retention of live residual trees in patches appears to result in the short-term life-boating of many old forest-associated bird species, arboreal squirrels, and amphibians, and the larger the patch the stronger the effect. In the long term, bird communities in large and small patches converge, so small patches can play a significant role in enriching mid- and late successional structure. Wildlife responses to dispersed live residual trees has not received equivalent attention in the literature, but may be expected to play a similar role to small patches. No information on the relative merits of various spatial configurations of the other structural attributes was found in this review.

In general, forest managers should consider a mix of retention configurations of the various structural attributes. Large patches may be easier to configure and will encompass multiple structural attributes, but there has been insufficient study of the relative merits of other configurations, particularly dispersed structures, to warrant a focus on one configuration.

Forest managers should apply caution in extrapolating the apparent success or failure of retention strategies to forest types and regions where similar studies have not been carried out. For example, studies of marten, snowshoe hare and small mammal responses to structural retention practices indicate there may be bioregional differences in wildlife response in different parts of the boreal forest.

While it was beyond the scope of this review to examine wildlife responses at the landscape level, it is at this scale that the cumulative effects of stand-level structural retention will manifest. Stand-level management practices for wildlife need to be employed in a multi-scale framework that integrates landscape-scale considerations such as the amount of old growth and early-seral burned forest in the landscape, variable rotation ages, and rate of cut. Just as stand-level retention practices may modify landscape-level wildlife responses, landscape-level management strategies may modify stand-level responses.

If forest managers are to reach a point where some stand-level retention practices can reliably be predicted to achieve wildlife conservation objectives, then formal effectiveness monitoring programs need to be implemented under an adaptive management framework. The setting of clear objectives for wildlife at the stand level, both in terms of short-term life-boating and longer-term desired future condition will be a critical first step in this process.

4.0 CONCLUSIONS

With the exception of studies of boreal bird responses to green-tree retention, the literature on vertebrate wildlife responses to stand-level structural retention in boreal forests has been largely unfocused and of highly variable quality. As such, it is not possible to make recommendations to forest managers on specific retention practices, retention levels or retention configurations that may be optimal for the broadest array of wildlife taxa. What is apparent from this review is that a strict adherence to natural disturbance pattern emulation (NDPE) as the guiding principle at the stand level may not be possible or appropriate. As a general philosophy it is useful for identifying the range of structures that have been absent or in short supply in traditional clearcut areas, but as a guide to stand-level retention practices it appears to have limited value. In the short term, marked differences remain in wildlife communities post-fire and post-harvest, with or without residual retention. In a commercial harvest setting only the lower end of the range of natural variation in the amount of structural attributes produced by natural disturbance appears achievable. A more appropriate short-term benchmark or reference point against which stand-level structural retention practices should be assessed is their performance in enhancing habitat value for wildlife beyond that available in clearcut areas. In the longer term, natural disturbance benchmarks and/or old forest benchmarks appear to become more suitable reference points against which to assess wildlife responses to structural retention. END may have more utility as a management tool at the landscape-scale.

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APPENDIX A

PRIMARY AND SECONDARY KEY WORDS USED FOR LITERATURE DATABASE SEARCHES

Matrix of primary (highlighted in grey) and secondary key words used for the search of the *Forest Science* and *Agricola* literature databases.

Forest Type/ Region	Wildlife/Response	Treatment/Event	Attribute
Boreal:	Wildlife:	Stand(-level):	Stand(-level):
Forest	Vertebrate(s)	Retention:	Structure:
Mixedwood	Invertebrate(s)	Structural	(Large) (live) tree(s)
Deciduous	Small mammal(s)	Reserve	Snag
Spruce	Bird(s)	Recruitment	(Large) dead tree(s)
Pine	Community(ies)	Variable	Coarse woody debris (CWD):
Canada(ian)	Cavity nester(s)	Patch	Down(ed) wood(y) (debris); Down(ed) woody material (DWM).
Scandinavia(n):	Cavity excavator(s)	Group	Slash
Fennoscandia(n)	Woodpecker(s)	Aggregated	Windrows
Sweden	Furbearer(s)	Green(-)tree	Stem (stand) density;
Finland	Marten	Residual	Patch:
Norway	Response(s):	Single(-)tree	Size
Russia(n)	Biological	Dispersed	Shape
Alaska(n)	Use	Overstor(e)y	(Spatial) configuration
	Availability	Understor(e)y	Vegetation (vegetative)
	Effect(s)	Volume	Composition
	Process	Silviculture:	Riparian
	Function(al)	Alternative	Dynamics
	Occupancy	Innovative	Succession(al)
	Abundance	Partial:	
	Density	Cut(ing);	
	Biomass	Harvest(ing).	
	Productivity	Patch cut	
	Habitat:	Gap creation	
	Breeding	Clear-cut:	
	Nesting	Logging	
	Denning	Management:	
	Foraging	Even-age(d)	
	Movement	Uneven-age(d)	
	Security cover	Windthrow:	
	Thermal cover	Blowdown	
	(Bio)diversity:	Thinning:	
	Richness	Variable density	
	Evenness	Precommercial	
		Commercial	

APPENDIX B

COMMON AND SCIENTIFIC NAMES OF VERTEBRATE SPECIES

Common and scientific names of all vertebrate species mentioned in this report, grouped by class and sorted alphabetically by common name.

Order	Common Name	Scientific Name
Aves - birds	Alder Flycatcher	<i>Empidonax alnorum</i>
	American Redstart	<i>Setophaga ruticilla</i>
	American Robin	<i>Turdus migratorius</i>
	Banded-tailed Pigeon	<i>Columba fasciata</i>
	Black Woodpecker	<i>Dryocopus martius</i>
	Black-backed Woodpecker	<i>Picoides arcticus</i>
	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>
	Black-throated Gray Warbler	<i>Dendroica nigrescens</i>
	Black-throated Green Warbler	<i>Dendroica virens</i>
	Boreal Chickadee	<i>Poecile hudsonicus</i>
	Brown Creeper	<i>Certhia americana</i>
	Brown-headed Cowbird	<i>Molothrus ater</i>
	Canada Warbler	<i>Wilsonia canadensis</i>
	Capercaillie	<i>Tetrao urogallus</i>
	Cassin's Vireo	<i>Vireo cassinii</i>
	Chestnut-backed Chickadee	<i>Poecile rufescens</i>
	Chipping Sparrow	<i>Spizella passerina</i>
	Clay-coloured Sparrow	<i>Spizella pallida</i>
	Common Nighthawk	<i>Chordeiles minor</i>
	Common Yellowthroat	<i>Geothlypis trichas</i>
	Connecticut Warbler	<i>Oporornis agilis</i>
	Dark-eyed Junco	<i>Junco hyemalis</i>
	Downy Woodpecker	<i>Picoides pubescens</i>
	European Starling	<i>Sturnus vulgaris</i>
	Golden-crowned Kinglet	<i>Regulus satrapa</i>
	Golden-crowned Sparrow	<i>Zonotrichia atricapilla</i>
	Goshawk	<i>Accipiter gentilis</i>
	Gray Jay	<i>Perisoreus canadensis</i>
	Hairy Woodpecker	<i>Picoides villosus</i>
	Hammond's Flycatcher	<i>Empidonax hammondii</i>
	House Wren	<i>Troglodytes aedon</i>
	Least Flycatcher	<i>Empidonax minimus</i>
	Lincoln's Sparrow	<i>Melospiza lincolnii</i>
	LoConte's Sparrow	<i>Ammodramus leconteii</i>
	MacGillivray's Warbler	<i>Oporornis tolmiei</i>
	Magnolia Warbler	<i>Dendroica magnolia</i>
	Merlin	<i>Falco columbarius</i>
	Mourning Warbler	<i>Oporornis philadelphia</i>
	Northern Flicker	<i>Colaptes auratus</i>
	Olive-sided Flycatcher	<i>Contopus cooperi</i>
Ovenbird	<i>Seiurus aurocapillus</i>	
Pacific-slope Flycatcher	<i>Empidonax difficilis</i>	

(Continued on next page.)

Order	Common Name	Scientific Name
	Philadelphia Vireo Pileated Woodpecker Pine Siskin Pygmy Owl Red-breasted Nuthatch Red-breasted Sapsucker Red-eyed Vireo Rose-breasted Grosbeak Ruffed Grouse Rufous Hummingbird Song Sparrow Sooty Grouse Swainson's Thrush Three-toed Woodpecker Varied thrush Violet-green Swallow Warbling vireo Western tanager White-throated sparrow Willow Flycatcher Winter wren Yellow Warbler Yellow-rumped Warbler	<i>Vireo philadelphicus</i> <i>Dryocopus pileatus</i> <i>Carduelis pinus</i> <i>Glaucidium californicum</i> <i>Sitta canadensis</i> <i>Sphyrapicus ruber</i> <i>Vireo olivaceus</i> <i>Pheucticus ludovicianus</i> <i>Bonasa umbellus</i> <i>Selasphorus rufus</i> <i>Melospiza melodia</i> <i>Dendragapus fuliginosus</i> <i>Catharus ustulatus</i> <i>Three-toed Woodpecker</i> <i>Ixoreus naevius</i> <i>Tachycineta thalassina</i> <i>Vireo gilvus</i> <i>Piranga ludoviciana</i> <i>Zonotrichia albicollis</i> <i>Empidonax traillii</i> <i>Troglodytes troglodytes</i> <i>Dendroica petechia</i> <i>Dendroica coronata</i>
Mammalia - mammals	Beaver Big brown bat Canada lynx Caribou Coyote Deer mouse Eastern chipmunk Eurasian marten Eurasian red squirrel Fisher Red fox Hoary bat Little brown bat Marten Masked shrew Meadow vole Moose Northern flying squirrel Northern long-eared bat Red squirrel Red-backed vole (Gapper's) Short-tailed shrew Silver-haired bat Snowshoe hare White-tailed deer	<i>Castor Canadensis</i> <i>Eptesicus fuscus</i> <i>Lynx canadensis</i> <i>Rangifer tarandus</i> <i>Canis latrans</i> <i>Peromyscus maniculatis</i> <i>Tamias striatus</i> <i>Martes martes</i> <i>Sciurus vulgaris</i> <i>Martes pinnanti</i> <i>Vulpes vulpes</i> <i>Lasiurus cinereus</i> <i>Myotis lucifugus</i> <i>Martes americana</i> <i>Sorex cinereus</i> <i>Microtus pennsylvanicus</i> <i>Alces alces</i> <i>Glaucomys sabrinus</i> <i>Myotis septentrionalis</i> <i>Tamiasciurus hudsonicus</i> <i>Clethrionomys gapperi</i> <i>Blarina brevicauda</i> <i>Lasionycteris noctivagans</i> <i>Lepus americanus</i> <i>Odocoileus virginianus</i>

(Continued on next page.)

Order	Common Name	Scientific Name
Amphibia - amphibians	Canadian toad Red-legged frog Striped chorus frog Western toad Wood frog	<i>Bufo hemiophrys</i> <i>Rana aurora</i> <i>Pseudacris triseriata</i> <i>Bufo boreas</i> <i>Rana sylvatica</i>