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**FRAGMENTATION IN THE BOREAL
FOREST AND POSSIBLE EFFECTS
ON TERRESTRIAL WILDLIFE**

**TECHNICAL BULLETIN NO. 959
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by

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PRESIDENT'S NOTE

Landscape-level considerations, such as ensuring adequate habitat for native species, are significant components of forest management planning. A key objective is to minimize adverse effects of human activities on the viability of wildlife populations in the planning area.

The term “fragmentation” is often used in forest landscape management, and has come to encompass such a broad range of concepts and effects that it has become relatively confusing and confounded. For example, “fragmentation” can refer either to changes in the relative abundance and spatial arrangement of habitat types in a landscape, or to habitat changes that have adverse effects on the welfare and viability of wildlife populations.

This report is a review of the scientific literature on fragmentation with emphasis on studies conducted in Canada's boreal forests. The authors demonstrate that concerns about habitat fragmentation have a basis in ecological theory and are supported by many field studies. On the other hand, current information is generally not adequate to support quantification of fragmentation effects on wildlife populations in forest landscapes.

Effects of forest fragmentation vary on a landscape-by-landscape and species-by-species basis, with the magnitude of effect often related to the severity and permanence of habitat disruption. Moreover, effects of fragmentation are often difficult to distinguish from the effects of habitat loss and forest succession. Proper interpretation of forest fragmentation studies requires explicit consideration of definitions and research methods.

Prescriptions to mitigate uncertain effects of forest fragmentation often take the form of constraints on the size and spatial arrangement of timber harvest units. Research is needed to evaluate the benefits and costs of such constraints. The authors recommend that future studies include less-known species and measure changes in habitat conditions in “shifting mosaics” of stand age classes in managed forest landscapes. Ideally, research designs would link fragmentation metrics to population dynamics rather than to static measures of species abundance alone.



Ronald A. Yeske

December 2008

MOT DU PRÉSIDENT

La prise en compte des éléments à l'échelle du paysage comme assurer un habitat adéquat aux espèces indigènes, constitue une composante significative de la planification de l'aménagement des forêts. Un des objectifs principaux est de minimiser les effets adverses des activités humaines sur la viabilité des populations fauniques dans la zone qui sera aménagée.

Le terme « fragmentation¹ », souvent utilisé dans le domaine de l'aménagement des paysages forestiers, couvre un si large spectre de concepts et d'effets qu'il en est devenu relativement confus et ses différentes utilisations sont parfois confondues. Par exemple, la « fragmentation » réfère soit aux changements de l'abondance relative et l'arrangement spatial des types d'habitats dans le paysage ou soit aux changements d'habitats qui produisent des effets adverses sur le bien-être et la viabilité des populations fauniques.

Ce rapport constitue une revue de la littérature scientifique sur la fragmentation en se concentrant sur des études réalisées dans les forêts boréales canadiennes. Les auteurs démontrent que les préoccupations reliées à la fragmentation des habitats trouvent leur fondement dans la théorie écologique, ce que corroborent plusieurs études sur le terrain. D'autre part, l'information actuelle n'est généralement pas en mesure de soutenir une quantification des effets de la fragmentation sur les populations fauniques habitant les paysages forestiers.

Les effets de la fragmentation des forêts varient selon le paysage et selon l'espèce. L'ampleur de l'effet est souvent reliée à la sévérité et la permanence de la perturbation de l'habitat. De plus, les effets de la fragmentation sont souvent difficiles à distinguer de ceux des pertes d'habitats et de la succession des forêts. Une interprétation juste des études de fragmentation des forêts requiert que les définitions et les méthodes de recherche considérées soient clairement explicites.

Les mesures de mitigation des effets incertains associés à la fragmentation des forêts prennent souvent la forme de contraintes affectant la taille et l'arrangement spatial des unités de bois récoltés. Des efforts de recherche sont nécessaires pour évaluer les avantages et les coûts de telles contraintes. Les auteurs recommandent que les études futures incluent les espèces moins connues et qu'elles mesurent les changements de conditions des habitats dans le contexte des « mosaïques changeantes » de classes d'âge de peuplements dans les paysages forestiers aménagés. Idéalement, les plans de recherche devraient relier les paramètres de fragmentation avec les dynamiques de populations, plutôt qu'avec les mesures statiques de l'abondance des espèces uniquement.



Ronald A. Yeske

Décembre 2008

¹ NDT : ou morcellement

FRAGMENTATION IN THE BOREAL FOREST AND POSSIBLE EFFECTS ON TERRESTRIAL WILDLIFE

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ABSTRACT

In forest management, “fragmentation” is a term often used to describe altering habitat amount and/or habitat area on a given landscape, and its effects on a host of flora and fauna. Fragmentation is often mentioned as a negative ecological consequence of timber production in Canada’s boreal forest, contributing to effects on a range of wildlife populations. The purpose of this report is to synthesize the available literature on fragmentation in the boreal and its effects on terrestrial vertebrates. The authors surveyed a wide range of scientific works originating primarily from Canada’s boreal forest, with some studies from Scandinavia and temperate North America. The results suggest that clarity and consistency is needed when examining forest fragmentation, as the term has been used in a variety of ways across the scientific literature, and has included a range of possible effects, confounding the results. Further, the report notes that the measured effects on terrestrial wildlife are scale-, landscape- and often species-specific, contributing to inconsistencies in the measured effects on populations. The authors suggest a number of research needs, including investigations into the temporal nature of fragmentation, the need for productivity- and population-level assessments, the investigation of fragmentation effects on lesser known or rare species, and a need to translate the effects of changing landscape metrics to wildlife populations.

KEYWORDS

biodiversity, configuration, fragmentation, habitat area loss, landscape management, spatial scale

RELATED NCASI PUBLICATIONS

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. 893 (December 2004). *Ecological Interactions among caribou, moose, and wolves: literature review.*

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

Technical Bulletin No. 857 (January 2003). *Wildlife and biodiversity metrics in forest certification systems.*

LA FRAGMENTATION DANS LA FORÊT BORÉALE ET LES EFFETS POSSIBLES SUR LA FAUNE TERRESTRE

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DÉCEMBRE 2008

RÉSUMÉ

Dans le domaine de l'aménagement forestier, la « fragmentation » est un terme souvent utilisé pour décrire les altérations des quantités d'habitat et/ou de zones d'habitat d'un paysage donné, de même que ses effets sur un spécimen de flore ou de faune. La fragmentation est souvent mentionnée comme étant une cause des effets négatifs sur les paysages aménagés, particulièrement dans la forêt boréale canadienne, contribuant par le fait même aux effets sur un éventail de populations d'espèces. L'objectif de ce rapport est de faire la synthèse de la littérature disponible sur la fragmentation dans la forêt boréale et ses effets sur les vertébrés terrestres. Les auteurs ont revu un large éventail de travaux scientifiques portant principalement sur la forêt boréale canadienne, ainsi qu'un certain nombre d'études sur les forêts scandinave et tempérée d'Amérique du Nord. Les résultats laissent croire qu'il est nécessaire d'examiner la fragmentation de la forêt avec clarté et consistance car ce terme a été utilisé de plusieurs façons dans la littérature scientifique, tout en incluant un éventail d'effets possibles, provoquant ainsi des interprétations qui peuvent être confondues. De plus, ce rapport dénote que les effets mesurés sur la faune terrestre se retrouvent à l'échelle du paysage et sont souvent spécifiques à l'espèce. Ceci contribue à générer des inconsistances dans les effets mesurés sur les populations. Les auteurs proposent un certain nombre de sujets de recherche, notamment des investigations sur la nature temporelle de la fragmentation, le besoin d'évaluations des niveaux de productivité et de populations, des recherches sur les effets de la fragmentation sur les espèces moins connues ou rares et le besoin de traduire les effets des changements des paramètres du paysage sur les populations fauniques.

MOTS CLÉS

Fragmentation, perte de zone d'habitat, configuration, échelle spatiale, aménagement du paysage, biodiversité

AUTRES PUBLICATIONS DE NCASI DANS CE DOMAINE

Bulletin technique n^o 857 (janvier 2003). *Wildlife and biodiversity metrics in forest certification systems.*

Bulletin technique n^o 893 (décembre 2004). *Ecological Interactions among caribou, moose, and wolves: literature review.*

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FRAGMENTATION IN THE BOREAL FOREST AND POSSIBLE EFFECTS ON TERRESTRIAL WILDLIFE

1.0 INTRODUCTION

In many parts of the world, habitat fragmentation has been identified as one of the most serious threats to biodiversity (e.g., Watling and Donnelly 2006; Reed 2004; Vitousek et al. 1997; Harris and Silva-Lopez 1992; Saunders, Hobbs, and Margules 1991). Ecological consequences of fragmentation include loss of ecosystem resilience, declines in species richness, loss of area-sensitive species, declines in population of those species which do persist, loss of genetic diversity, increased turnover of species, and invasion by exotic and generalist species (Kupfer, Malanson, and Franklin 2006; Wiegand, Revilla, and Moloney 2005; Hunter 1996; Saunders, Hobbs, and Margules 1991).

Fragmentation is a relatively well studied phenomenon, but studies to date have focused on effects in temperate¹ and tropical² regions. High quality studies from boreal regions do exist³, but in general are less plentiful and narrower in scope than those from temperate and tropical regions. Also, since initial concerns about forest fragmentation focused on landscapes in which forests are interspersed with agriculture, there are more fragmentation studies for those types of landscapes⁴ than for others⁵, including those which consist mostly of managed forests⁶.

With respect to studies of the effects of fragmentation in forested ecosystems, a high percentage have been conducted in Canada, particularly in the boreal mixedwood ecosystems of Saskatchewan and Alberta (e.g., Bayne and Hobson 2000, 2002; Hannon 2000; Hobson and Schieck 1999; Schmiegelow and Hannon 1999; Schmiegelow, Machtans, and Hannon 1997). Numbers of studies are far greater for birds than for other vertebrates (e.g., Schmiegelow and Mönkkönen 2002; Hannon and Schmiegelow 2002; Boulinier et al. 2001; Andrén 1992; Freemark and Merriam 1986).

Concerns about the possible effects of fragmentation on the boreal forest have been expressed in both the scientific and popular literature (Park, Henschel, and Kuttner 2005; Greenpeace, NRDC, and Forest Ethics 2003; Schmiegelow and Mönkkönen 2002; Imbeau, Mönkkönen, and Desrochers 2001). There has not, as yet, been sufficient research on fragmentation dynamics in boreal forests to adequately address these concerns—indeed, one of the bases for concerns is the lack of more detailed knowledge (Schmiegelow and Mönkkönen 2002). Thus, management of the boreal forest is challenging, in that strong and sincere concerns are expressed about fragmentation based on relatively little knowledge upon which to evaluate the significance of the concerns and with which to respond.

¹Hagan and Meehan 2002; Robinson et al. 1995; Terborgh 1989; Lovejoy et al. 1986

²Miles et al. 2006; Hill and Curran 2003; Lovejoy et al. 1990; Laurance and Bierregaard 1998

³e.g., Brotons, Mönkkönen, and Martin 2003; Cumming and Schmiegelow 2001; Bayne and Hobson 1998, 2000; Edenius and Elmberg 1996

⁴e.g., Austen, Francis, et al. 2001; Riitters et al. 2000; Terborgh 1989; Temple and Cary 1988; Wilcove, McLellan, and Dobson 1986)

⁵Chalfoun, Thompson and Ratnaswamy 2002; Lahti 2001

⁶e.g., Schmiegelow and Mönkkönen 2002; Reed, Johnson-Barnard, and Baker 1996; Small and Hunter 1988

This report reviews evidence related to the effects of fragmentation in boreal Canada and attempts to identify specific aspects of fragmentation that may be of concern in managed boreal forests.

The objectives of this document are

- to review the concept of fragmentation and its applicability to managed boreal forests;
- to provide an understanding of the basis for concerns regarding fragmentation; and
- to identify important knowledge gaps and appropriate areas for further research.

This review focuses on Canada's boreal forest, but studies from elsewhere, primarily the northern U.S. and Fennoscandia, which have similar forest management contexts and environments, are also included.

2.0 WHAT IS FRAGMENTATION?

2.1 Conceptual Roots

The concept of fragmentation has its roots in Island Biogeography Theory (IBT), which addresses species richness and risk of extinction in relation to island size and isolation (MacArthur and Wilson 1963, 1967). Simply put, larger islands support more species and individuals than do smaller ones. For islands of a given size, those that are more isolated tend to have fewer species and smaller populations. Risk of local species extinctions is greatest on the smallest, most isolated islands because populations are small and immigration rates are low.

There is a substantial body of empirical evidence supporting IBT for true islands. IBT has also been applied to terrestrial ecosystems in which the "islands" are not true islands (i.e., surrounded by water), but rather isolated habitats such as caves and mountain tops with distinctive flora and fauna (Watson 2002).

Extension of IBT to concerns about forest fragmentation raises questions about the degree to which "islands" of a focal habitat type (e.g., old growth) are isolated from each other by the surrounding "matrix" habitats (e.g., younger forests). Research on these questions has drawn heavily on metapopulation concepts first described by Levins (1970). Today, forest fragmentation effects are often defined in terms of interactions among groups of populations (a metapopulation) occupying patchy, non-contiguous areas of "suitable habitat" in a matrix of habitats that are to varying degrees "less suitable."

2.2 Defining Fragmentation

There is no universally accepted definition of fragmentation, which has contributed to confusion and debate regarding the effects of fragmentation. Table 2.1 provides several definitions of fragmentation found in the scientific literature of the last 20 years.

Table 2.1 Definitions of Fragmentation Taken from Recent Scientific Literature

Wilcove et al. 1986	A process during which “a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original.”
Harris and Silva-Lopez 1992	“...an unnatural detaching or separation of expansive tracts into spatially segregated fragments.”
Andr�n 1994	“The process of subdividing a continuous habitat into smaller pieces.”
Reed et al. 1996	“A change in landscape structure that typically, but not universally includes smaller sizes, smaller patch perimeter lengths, greater distances between patches, more edge habitat and less interior habitat.”
Crampton and Barclay 1996	“...removal of trees from certain parts of stands”
Bender et al. 1998	“... an event that creates a greater number of habitat patches that are smaller in size than the original contiguous tract(s) of habitat”
M�nkk�nen and Reunanen 1999	“The division of the elements in the landscape into smaller pieces.”
Villard et al. 1999	“A process through which a focal habitat is partially or completely removed, thereby altering its original configuration.”
Wiegand et al. 2005	“[Fragmentation effects are those which result] from the configuration of habitat (i.e., brought about through reduction in habitat patch size and isolation of habitat patches, sensu Andr�n 1994).”
Kupfer et al. 2006	“It is also important to clarify that forest fragmentation can refer to either the broad process of forest loss and isolation or more specifically to changes in the spatial configuration of forest remnants that are a result of deforestation.”

Depending on the definition one chooses to embrace, fragmentation may include any or all of the following effects or characteristics:

- the base (pre-fragmentation) landscape was large;
- there are landscape-level changes in configuration of habitat;
- there are stand-level changes in structure or tree species composition;
- there is a decrease in habitat area, or complete removal of habitat;
- there is an increase in edge area;
- there is a decrease in interior patch area;
- fewer patches of habitat remain;
- a greater number of habitat patches are created;
- the matrix between habitats is unlike the remaining habitats; and
- the changes are anthropogenic.

A number of authors have commented on the difficulties of studying such an ill-defined phenomenon. Bunnell (1999a) found the concept of fragmentation so burdened with ambiguity

and mixtures of various components of ecological change that he labeled it a “panchreston” which is “*a proposed explanation intended to address a complex problem by trying to account for all possible contingencies but typically proving to be too broadly conceived and therefore oversimplified to be of any practical use.*” Haila (2002) asked, “*Is a conceptually ambiguous and empirically multifaceted term fruitful as a generic description of human effects on landscapes?*” Fahrig (2003) noted that at least 40 measures of fragmentation have been used in the scientific literature, many of which are interrelated and proportional to declines in habitat area. She argues that the term “fragmentation” is quickly losing its usefulness as more and more effects of human activities are incorporated into that single term. Lindenmayer and Fischer (2006) note that the term is losing its meaning because it is frequently used as an umbrella term for a wide range of interacting processes and in fact, avoid using “habitat fragmentation” in their book *Habitat Fragmentation and Landscape Change* because of the confusion surrounding the term.

Much of the discussion around defining fragmentation is concerned with semantics and clarity and rigour of use of terms. However, at the core of these discussions is concern over the distinction of important concepts and ecological mechanisms. While there is sufficient disparity in published accounts to conclude that no single definition or group of concepts can be said to comprise the “correct” definition, there is a sufficient basis upon which to define a conceptual model for the breadth of concerns that have been cited as elements of fragmentation. The model is presented in Figure 2.1. The concepts represented by the core circle are consistent through all definitions. The farther away from the core circle one goes, the less agreement there is that the concepts are a part of the phenomenon of fragmentation. Thus, the concept of landscape configuration is common to all definitions of fragmentation, but the concept of habitat area is not universally accepted as a component of fragmentation. Concepts in the outer ring, such as the amount of old forest, and the origin of landscape change (i.e., anthropogenic vs. natural) are often noted as peripheral to the topic of fragmentation.

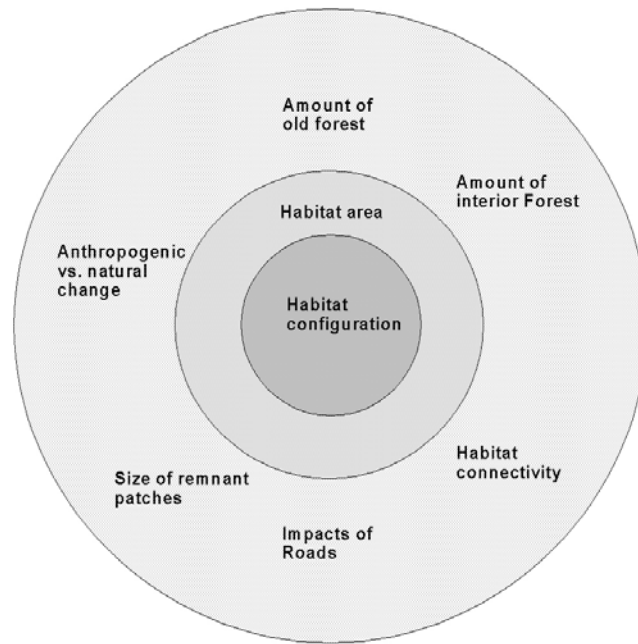


Figure 2.1 Conceptual Model of the Definition of Fragmentation in the Literature
(Elements in the outer band occur less frequently than those in the center, which are always or more frequently included.)

Figure 2.1 does not present a definition of fragmentation. Rather, it presents a model that may be useful for providing a context for discussions related to fragmentation and its possible effects. The most important and oft-cited overlapping effects are those associated with habitat area and those associated with habitat configuration—the two innermost layers of the model. This is explored in more detail below.

3.0 KEY ISSUES

3.1 Fragmentation and Habitat Area Loss

The ecological effect most often lumped in with fragmentation is decrease in habitat area. Some believe that habitat area loss is an integral component of fragmentation (e.g., Kupfer, Malanson, and Franklin 2006). Others argue that the term should only apply to effects associated with the configuration of discontinuous tracts of forest on the grounds that lumping habitat area and configuration effects together makes it difficult to 1) differentiate between their separate and ecologically distinct effects and 2) identify the component that is of most concern (Bunnell 1999b; Fahrig 1999, 2003; McGarigal and Cushman 2002; Schmiegelow and Mönkkönen 2002).

Table 3.1 provides a synopsis of several studies and meta-analyses that have compared or commented on the effects of changes in habitat area and habitat configuration. Well-designed investigations, such as those of McGarigal and McComb (1995), Trzcinski, Fahrig, and Merriam (1999), Selonen, Hanski, and Stevens (2001), and Betts et al. (2006), have been able to separate

the effects of changes in habitat area from habitat configuration. The predominant conclusion from these studies is that amount of habitat area has a greater effect on species presence and/or abundance than do changes in habitat configuration, which supports the contention that habitat area change is a phenomenon independent from fragmentation. Fahrig is the most prolific of those with this perspective (Fahrig 1997, 1998, 1999 2001, 2002, 2003; Trzcinski, Fahrig, and Merriam 1999; Bender, Contreras, and Fahrig 1998). In several publications, she argues that the largest downside of including habitat area loss with fragmentation is that it confuses debates about the relative importance of ecologically significant effects, and it may thus shift the focus of management activities toward reducing configuration changes and away from the more important goal of preventing habitat area loss. Several authors express similar positions (Villard, Trzcinski, and Merriam 1999; Bunnell 1999; Selonen, Hanski, and Stevens 2001).

On the other hand, Lindenmeyer and Fischer (2006) acknowledge that there may be some value in understanding the separate effects of habitat area loss and habitat configuration, but also point out that area loss is almost always accompanied by fragmentation, making it of questionable value to dwell on the differences.

Table 3.1 Summary of Several Studies (and meta-analyses) Comparing or Commenting on Effects of Habitat Area Loss and Changes in Habitat Configuration*

Study and Location	Brief Description	Key Results	Summary/Conclusions
Schmiegelow et al. 1997	<ul style="list-style-type: none"> Work was conducted in the boreal mixedwoods of central Alberta. The project examined the decline in number of bird species, species turnover, abundance, and effects of adjacent harvesting in isolated fragments (1, 10, 40 and 100 ha), and fragments (1, 10, and 40 ha) connected by a riparian buffer. Results from fragments were compared to results of same-sized blocks within a contiguous forest. Birds were surveyed for one season prior to fragmentation and 2 years after. 	<ul style="list-style-type: none"> 59 bird species were included in results. Species richness was significantly related to area in both fragmented blocks and blocks in contiguous forest. There were significant differences in composition of species assemblages supported by sites before and after fragmentation. Isolated fragments had higher turnover than either control sites or connected fragments. After fragmentation, isolated and connected fragments contained fewer neotropical migrants than did controls; results for resident species were equivocal. <p>Fragmentation had a significant negative effect on 7 species in isolated fragments and 6 species in connected fragments</p>	<ul style="list-style-type: none"> Authors recognize that two years of post-harvest results is not sufficient to detect mid-or long-term effects. Authors suggest that Neotropical migrants may be disproportionately prone to fragmentation and disturbance related effects because they tend to be habitat specialists; species less affected tend to be generalists. Habitat area loss may result in population declines of certain bird species, but this may not be a fragmentation effect. Area-related edge effects (e.g., a reduction in habitat quality due to changes in vegetation, competitive exclusion or replacement by species able to utilize the surrounding matrix) may exacerbate habitat area loss. <p>The magnitudes of negative fragmentation effects were small given the extent of their manipulations. Where effects did occur, they were most pronounced in the smaller isolates, and habitat specialists exhibited the greatest sensitivity.</p>
Bender et al. 1998	<ul style="list-style-type: none"> The study was a quantitative meta-analysis of the relationship between patch size and population density based on 25 studies of birds, mammals, and/or insects. None of the studies were in a managed boreal forest context similar to Canada's, but several were in boreal environments. 	<ul style="list-style-type: none"> Patch size effects were commonly observed for edge and interior species, but not for habitat generalists. This was attributed partly to a common bias in the means used to calculate animal densities which underestimates densities for edge and interior species Densities of generalist species tend not to be related to patch size. Contrary to other studies (including Schmiegelow et al. (1997), they did not find that migrant species were more sensitive to patch sizes than are generalists. 	<ul style="list-style-type: none"> They identified five predictions based on their review. <ol style="list-style-type: none"> Changes in generalist species that are not associated with only the edge or only the interior habitat should be accounted for by pure habitat area loss. The decline in population size of interior species associated with changes to habitat configuration and loss of habitat area will be greater than that predicted from pure habitat area loss alone. The decline in population size of edge species will be less than that predicted by pure habitat area loss alone. Relative effects will not be influenced by the extent of habitat area loss, but they will be affected by the pattern of habitat area loss for edge and interior species if only the small or large patches are preferentially removed. <p>As changes to habitat configuration increase within a landscape, migratory species will generally suffer less of a decline in population size than resident species.</p>

Table 3.1 Continued

Drolet et al. 1999	<ul style="list-style-type: none"> • Work was conducted in managed forest landscapes of boreal Quebec. • Birds sampled at 136 stations for one season and landscapes were characterized for 100 ha surrounding each station. 	<ul style="list-style-type: none"> • Although they recorded 38 species, they only analyzed data for 14; species which were uncommon were excluded from the analysis. • The occurrence of 7 of the 14 species was significantly related to landscape structure (which included aspects of forested area). • Independent associations with cover (habitat area) existed for only three species, but associations with configuration existed for none. • The species with the strongest relationships to landscape structure were bay-breasted warbler and solitary vireo. 	<ul style="list-style-type: none"> • The occurrence of nesting songbirds was related to forest cover at scales greater than that of the average songbird territory (ca. > 5 ha). • The authors caution that “forest remnants sufficiently large to include an average songbird territory can be inadequate for species such as the bay-breasted warbler and the solitary vireo, when embedded in a clearcut dominated landscape,” suggesting that the relationship between remaining forest cover is unlikely to be linear for several bird species.
McGarigal and McComb 1995	<ul style="list-style-type: none"> • Work was conducted in central Oregon Coast Range. • They sampled vegetation and birds in 30 watersheds (250-300 ha) of various extents of fragmentation resulting from forest management. • The analyses focused on 15 species associated with late-seral forests. • The study encompassed three years of sampling. 	<ul style="list-style-type: none"> • Different statistical methods did not always yield similar results; for example, using analysis of variance, only 2 of 15 species were affected by habitat configuration; using principle component analysis, 10 of 15 species occupied landscapes that differed from “average” landscape configuration; partial correlations with residual configuration indices either with or without first taking habitat area into account were significant for 12 of 15 species. • In general, the authors conclude that variation in bird abundance among landscapes was more strongly related to changes in habitat area than habitat configuration with the exception of some “edge” species. • The relationship between abundance and configuration varied dramatically among species. 	<ul style="list-style-type: none"> • Landscape structure (area and configuration) at the patch scale typically explained less than half of the variation among landscapes and therefore the results at one scale are not necessarily applicable to another. • The authors also note that the “matrix” in their work was managed forest, and so their results are not comparable to those in agricultural settings • This paper is often cited as one which definitively shows that habitat area is more important than configuration; the careful and detailed statistical analyses used both strengthen the overall conclusion (that area is more important than configuration) and draw attention to the authors’ caveats regarding the conclusions • Caveats: <ul style="list-style-type: none"> ▪ Only 15 species were included in analyses. ▪ The spatial scale of investigation was limited. ▪ Habitat classification was community centered, not organism-centered. ▪ Uncommon species, and those with patchy distributions were not included in the study. • The authors caution about generalizing the results to non-related circumstances.

Table 3.1 Continued

<p>Trzcinski et al. 1999</p>	<ul style="list-style-type: none"> • Work was conducted in southern Ontario and southern Quebec, mostly in Great Lakes-St. Lawrence Forest. • Bird abundance was studied in 94 landscapes, 10 x 10 km each. • Landscapes ranged from 2.5–55.8% forested. • The analysis focused on 31 bird species normally affiliated with forests. • The study used multiple logistic regression based on forest cover and a fragmentation index. 	<ul style="list-style-type: none"> • The relationship between forest cover and probability of presence was positive for all 31 species, and statistically significant for 25. • For 4 species the probability of presence decreased with increasing fragmentation; the probability increased for 2 species. • Forest cover explained a larger proportion of the deviance and had a larger logistic regression coefficient than did forest fragmentation for 24 of the 25 bird species that responded significantly to either effect. • Bird species presence was strongly associated with forest cover, although for some species, the relationship was not statistically significant. • There was no general relationship between the presence of forest bird species and fragmentation. 	<ul style="list-style-type: none"> • This work took place mostly in landscapes where forests were interspersed with agricultural land uses and not in boreal environments; however, the results strongly indicate that habitat amount rather than configuration are the stronger influence on bird species abundance. • The authors suggest that the negative effects observed in [other studies in comparable landscapes] may be due to habitat removal and not habitat fragmentation. • They also note that their work was at the landscape scale and is not necessarily applicable to the patch scale. • Authors also note that rare species were not included in their study and hypothesize that they may be rare because they are the most sensitive to landscape change and cannot adapt.
<p>Villard et al. 1999</p>	<ul style="list-style-type: none"> • The study took place in mixed forest/agricultural landscapes near Ottawa, ON. • The study included 3 different areas in the region comprising 33 different landscapes (6.25km²), with forest cover ranging from 3-68%. • The study related forest cover and 3 configuration metrics to presence/absence of 15 forest bird species for each of two years. 	<ul style="list-style-type: none"> • All three configuration variables were correlated to cover. • Landscape structure (cover and configuration together) was a significant predictor of presence over both years of the study for 9 of the species. • Only 3 species were not related to landscape structure in either of the two years. • Forest cover and configuration (considered independently) were equally good predictors of species presence. 	<ul style="list-style-type: none"> • The authors argue that the effect of forest cover on bird species presence might include a configuration effect, and that the configuration effect is clearly evident. • “The fact that our approach was conservative with regard to configuration effects make even more compelling our finding that cover effects were not clearly dominant.” • The authors note that the range of cover included in their study (3-68%) includes landscapes with greater habitat than the 20-30% benchmarks at which configuration effects start to occur as described by Andren (1994) and Fahrig (1997), implying that configuration may be important not just when most of a species’ habitat is gone. • However, they do note that their landscape’s scale (6.25 km²) is different from the scale of other studies which have considered larger areas. • They note that they found little evidence of sharp thresholds at which configuration effects become important. • In spite of their finding that configuration effects can be important, they strongly support Fahrig’s (1997) conclusion that habitat area loss, rather than configuration should be the focus of conservation efforts.

Table 3.1 Continued

<p>Selonen et al. 2001</p>	<ul style="list-style-type: none"> • The study examined Siberian flying squirrels in southern Finland, and compared habitat use in managed forests vs. a national park. • The Siberian flying squirrel is a different genus from those found in Canada, but has similar ecology. • All forests were patchy, but in the park there were fewer sapling stands and clearcuts than in the managed forests. • They radio-tracked 47 squirrels over 4 years. 	<ul style="list-style-type: none"> • Male squirrels inhabited a greater number of patches in more fragmented than continuous landscapes; females had much smaller home ranges which were completely in non-fragmented patches. • Home range size was larger for individuals that lived in several small patches than for those that lived in few large patches. 	<ul style="list-style-type: none"> • Males were able to inhabit areas where mature forest was separated by cuts and young forest, by expanding their “normal” home range size to compensate for fragmentation; • In a patchy landscape, with few and scattered suitable patches, females “may face difficulties” in finding new habitats in the face of fewer large-enough patches; males appear more elastic in their response • These results suggest that decline in area of preferred forest is a more important reason for the decline of flying squirrel population than landscape connectivity. • Female squirrels require a suitable large [habitat] patch. That decline in area of suitable habitat, rather than the effects of patch isolation may lower the density of females and reduce their reproductive output.
<p>Brotans et al. 2003</p>	<ul style="list-style-type: none"> • The study was a meta-analysis/review of 9 studies from Fennoscandia relating bird population densities to area. • Six of the studies were in forests fragmented by peat lands and some agriculture, and 3 studies were of forested islands in the Baltic sea and inland lakes. • The spatial arrangement of the forest patches was similar in the 6 land-based fragments and the 3 island fragments so the authors conclude there is basis for comparing the results. 	<ul style="list-style-type: none"> • The relationship between bird density and patch size was significantly correlated for islands, but not for habitats surrounded by a terrestrial matrix. Correlation coefficients estimating overall patch-area effects (PAE) on islands were significantly positive; but this relationship did not exist on terrestrial landscapes. • For species which occurred in both habitats (i.e., on islands and on inland forests), the results for islands were consistently stronger (indicating a stronger PAE) than for the inland fragmented forests. 	<ul style="list-style-type: none"> • The results indicate that there is an ameliorating effect of fragmentation on fragmented inland “islands” of habitat related to the surrounding matrix of habitat. • These results are similar to Schmeigelow and Mönkkönen (2002) who showed that the effects of fragmentation in a landscape dominated by forestry differ from those observed in a landscape dominated by agriculture. • Although this study found that interior forest specialists had larger PAEs (i.e., a stronger response) than did generalists on true islands, they found that the size of inland fragments had no consistent overall effect for either specialists or generalists, suggesting that there was little difference between the two in their ability to use the resources from the matrix generated by forestry. • The authors suggest that this could mean that boreal birds may be well adapted to use, or move across heterogeneous landscapes provided that the quality of the matrix is sufficient. • However, we note that Mönkkönen and Welsh 1994 hypothesized European bird species may be more resilient to fragmentation effects due to their longer association with human settlements and that sensitive species may have already been extirpated there, so it may not be possible to extrapolate this finding from Fennoscandia to North America.

Table 3.1 Continued

<p>Fahrig 2003</p>	<ul style="list-style-type: none"> The study reviewed 100 papers on fragmentation to catalogue fragmentation effects and to examine the extent to which habitat configuration was confounded with habitat area loss. 	<ul style="list-style-type: none"> Of the 100 papers examined, only 17 were empirical studies of habitat configuration, the others all were clouded with habitat area loss. Of the 17 studies, the author identified design issues with 8 which limited their utility. Of the 9 in real landscapes, only one was in a boreal setting (Drolet and Destrocher 1999 – reviewed above). The overall results of the 17 studies is that habitat area loss has a much larger effect than configuration on biodiversity measures. For those studies which did find a configuration effect, it was at least as likely to be positive as negative. 	<ul style="list-style-type: none"> The author describes that many statistical indicators of fragmentation include aspects of both configuration and habitat area loss. The author notes that theoretical studies suggest that habitat configuration can affect where an extinction threshold occurs relative to habitat amount. The overall conclusion of the paper is that decline in habitat area is a much more important ecological phenomenon in limiting populations and species presence/absence than is habitat configuration. Lindenmeyer and Fischer (2006) are critical of this work because it did not distinguish between different species' unique habitat requirements.
<p>Betts et al. 2006</p>	<ul style="list-style-type: none"> The study examined the response of blackburnian warbler (BLBW) and ovenbird (OVEN) to different forest amounts and configuration over two years The study took place in the Greater Fundy Ecosystem of New Brunswick, in the Acadian Forest Region. The study used a “stratified sampling design that reduced the confounding effect of habitat amount and configuration.” 	<ul style="list-style-type: none"> For both species, statistical models which included only local-scale variables were not good predictors of bird presence. Occurrence of BLBW was best predicted by the amount of poor-quality matrix. Patch size was an important predictor of occurrence for OVEN. 	<ul style="list-style-type: none"> The fact that occurrence and re-occurrence of both species were strongly influenced by landscape characteristics at scales greater than the individual territory indicates little support for the notion that birds respond in proportion to habitat availability. “The results support the notion that landscape pattern is important for some species only when the amount of suitable habitat is low.” Because OVEN responds to patch size, manipulating the pattern may reduce negative effects for it, but this is not the case for BLBW which responded most strongly to amount of poor-quality matrix.

* Experimental studies included in this table examined habitat area loss and fragmentation effects, although not necessarily in managed boreal forests; meta-analyses included in this table included examination of at least one study in boreal environments.

Contributing to the confusion is that, although in some cases the effects of habitat area loss and changes in habitat configuration may be independent, the same elements of habitat change most often cause both. While it is possible for habitat to be altered with no significant change in configuration, if, for example, a contiguous block of habitat is temporarily or permanently changed on a landscape, habitat cannot be divided without an area of habitat change causing the division.

While the general conclusion that habitat area loss has a more deleterious effect on wildlife than changes in configuration seems justified based on research to date, the possible effects of changes in configuration should not be trivialized.

- Very few studies addressing the effects of habitat area loss vs. configuration changes have been conducted on taxa other than songbirds.
- Studies upon which this conclusion is based invariably exclude rare species from their analysis (McGarigal and McComb 1995; Schmiegelow, Machtans, and Hannon 1997; Drolet, Desrochers, and Fortin 1999; Trzcinski, Fahrig, and Merriam 1999).
- Several studies cited above did find that some species were affected by changes in configuration. Therefore, generalizations may lead to important considerations being overlooked for these species. Schmiegelow and Mönkkönen (2002) express similar concerns regarding the “indiscriminant generalization of empirical observations.”
- Important elements of experimental design remain inadequately addressed in boreal contexts. Most studies examining fragmentation have been short term (<3 years) and few studies have examined the relative responses to fragmentation by comparing guilds or ecological types (such as the responses of generalists vs. specialists or edge- vs. core-sensitive species) (Bissonette and Storch 2002).

When the effects of habitat area loss and configuration changes are assessed independently, the effect of habitat area loss is almost always considered the greater of the two. However, as long as researchers and managers who assess and act upon such results are cognizant of their implicit definition of fragmentation (i.e., that it includes habitat area loss as well as configuration), the concern that managers may focus solely on managing habitat configuration without maintaining habitat amount may not be warranted.

Many of those interested in forest ecology do not distinguish between habitat area loss and habitat fragmentation per se to the same extent as do many academic writers (e.g., Wildlands League 2006; Lee, Gysbers, and Stanojevic 2006). The concern regarding appropriate partitioning of responsibility for undesirable changes in habitat quality between two related effects may seem moot and even immaterial to the broader notion of habitat degradation. For clarity, however, all those concerned about habitat management, habitat area loss and fragmentation are best served by explicitly defining the interpretation of fragmentation used in their publications and or campaigns. While this is becoming the case for scientific publications, such rigour has yet to find its way into the popular media. Indeed, given the nature of many popular publications, it may never. This increases the need for scientists to clearly articulate the nature of the effects they are investigating, and for forest managers to articulate both the potential effects for which they are managing, and the concerns to which they are responding.

3.2 The Question of Scale

One of the challenges in clarifying the effects of fragmentation is dealing with questions of scale. What is the scale of the scientific investigation, or the scale at which species use the landscape or at which fragmentation effects are manifested? On what scale does forest management (or other events) affect the landscape?

Fahrig (1999, 2003) has suggested that habitat fragmentation is a landscape-scale process. This means that in the typical study of the effects of fragmentation on biodiversity, the researcher relies on a sample size of two: one continuous landscape and one fragmented landscape. The small sample size ensures that any inferences made about the effects of fragmentation will be weak because any apparent effects of fragmentation could be due to other differences between the landscapes. Fahrig (1999) recommends overcoming this problem by conducting studies on the landscape scale, in which the landscape is the unit of observation. This would require the inclusion of numerous independent landscapes in the study, with each landscape serving as an individual data point.

Fahrig (1999, 2003) also discusses the “patch-scale problem,” which arises when fragmentation is measured at the patch scale rather than the landscape scale. If a study is conducted at the patch scale, it means that the sample size at the landscape scale is only one, making it impossible to make any inferences at the landscape level. Indeed, many studies of the effects of fragmentation are conducted at the patch scale, where use of patch size as a measure of habitat fragmentation contains the implicit assumption that patch size is independent of habitat amount on the landscape scale. This assumption may not be correct and can lead to misinterpretation of results. For example, although for some outcomes there may appear to be a correspondence between patch- and landscape-scale effects, the landscape-scale interpretation of patch size effects is actually a function of the landscape context of the patch.

The focus of research at the patch scale also contributes to the common use of the term fragmentation to represent both habitat area loss and changes in habitat configuration. Studies at the patch scale are too small to differentiate between the effects of area loss and configuration change (Fahrig 1999).

Landscape connectivity is another issue that must be considered when discussing the relationship of scale to the effects of fragmentation on wildlife. Like fragmentation, connectivity is difficult to precisely define and quantify, but With (1999) proposes that connectivity should be assessed from an organismal perspective and be based on the scale at which organisms interact with the scale of fragmentation in the landscape. In the simplest terms, high landscape connectivity exists if organisms can move easily among habitats in the landscape and low connectivity exists if the habitats or configurations of habitats resist movement through the landscape (Bunnell 1999a; With 1999). Obviously, the degree of connectivity will be a function of both the type of organism and the scale of fragmentation. It is tempting to equate loss of connectivity with fragmentation, but as With (1999) points out, connectivity is not an inherent quality of a landscape, since the same landscape may be connected (i.e., not fragmented) from the perspective of one species but disconnected (i.e., fragmented) from the perspective of another. A landscape that appears fragmented to a salamander may not be perceived as such by a wolf because the two function at different scales. Similarly, Harris and Silva-Lopez (1992) note that fragmentation may make sense from a structural perspective (i.e., the amount and spatial distribution of vegetation), but from a functional perspective (i.e., how a species interacts with the landscape) the scale of reference should take the species of concern and its scale of habitat use into account.

Bunnell (1999a) warns against generating confusion over the meaning of the word fragmentation by choosing to scale the environment according to our own perceptions. He points out that because models do not handle gradients well, researchers often conceptualize a landscape composed of sharply defined patches and then analyze as if those sharp contrasts were real. But, he cautions, there is little evidence that other vertebrates define patches the way we do. This is illustrated by Lahti (2001) in a review of literature on the “edge effect on nest predation” hypothesis. Lahti (2001) notes that the majority of studies have not found higher nest predation near habitat edges and speculates that this “may be due to the fact that nest predators range

indiscriminately across borders between habitats which are similar in physiognomy, not recognizing them as habitat discontinuities.”

Questions of scale also arise in the consideration of ecological thresholds (discussed in Section 3.3). Lindenmayer and Luck (2005) note that while habitat area loss and habitat fragmentation are multi-scale issues, studies on ecological thresholds have typically been focused at a single spatial scale. They point out that different thresholds may manifest at different spatial scales.

Management of the boreal forest takes place at the stand, landscape, and forest scales. The stand is the traditional unit of manipulation (i.e., stands are harvested and regenerated). However, with the recent emphasis on emulation of natural disturbances, management focus is broadening to incorporate landscape-scale considerations. See, for example, Ontario's Natural Disturbance Pattern Emulation Guideline (Ontario Ministry of Natural Resources 2001) and that province's efforts to develop a landscape guide for forest managers. Thus, it is becoming prudent for managers to consider fragmentation effects at a variety of scales during forest management planning processes.

3.3 Thresholds

Like “fragmentation,” the term “threshold” may also be defined in several ways. Within the context of species loss related to loss of habitat area, threshold may be generally defined as the degree of habitat area loss beyond which there is a disproportionate decline in population (Groffman et al. 2006). However, Betts, Forbes, and Diamond (2007) make a distinction between the fragmentation threshold hypothesis and the extinction threshold hypothesis. The fragmentation threshold hypothesis states that thresholds in species occurrence related to landscape-scale habitat area loss are the result of an increasing influence of fragmentation effects below some level of habitat amount (Andrén 1994). The extinction threshold hypothesis attributes those thresholds directly to loss of habitat area, with an increase in the effects of habitat area loss below some minimum habitat amount (Betts, Forbes, and Diamond 2007). Further, Betts, Forbes, and Diamond (2007) note that researchers should be able to differentiate between these two by examining the statistical interaction between habitat configuration and habitat amount. A lack of interaction would be associated with the extinction threshold hypothesis.

Andrén (1994) reviewed over 30 studies on birds and mammals in habitat patches in landscapes with different proportions of suitable habitat. He concluded that where the proportion of suitable habitat in the landscape remains above 10-30%, population declines are generally in proportion to the amount of habitat lost. However, consistent with the fragmentation threshold hypothesis, he found that when 70-90% of suitable habitat area was lost, fragmentation configuration effects began to play a role and losses in species or declines in population size were greater than expected from habitat area loss alone.

Work by Fahrig (1997, 1998) and Trzcinski, Fahrig, and Merriam (1999), on the other hand, appears to lend more support to the extinction threshold hypothesis. Fahrig (1997, 1998) used a spatially explicit simulation model, first in an effort to estimate the relative importance of habitat area loss and habitat configuration in population extinction, and then in an attempt to identify the specific conditions under which fragmentation affects population survival. The model indicated that, in general, when breeding habitat covers more than 20% of the landscape, fragmentation had no effect on survival (Fahrig 1997, 1998). Further, the model indicated that even once breeding habitat was reduced to less than 20%, fragmentation affected population survival only if 1) the average between-generation movement distance of the organism is 1-3 times the expected nearest distance between breeding sites; 2) the habitat is not ephemeral; 3) the organism has high breeding site fidelity; and 4) the mortality rate in the non-breeding habitat areas is much higher than the mortality rate in breeding habitat areas (Fahrig 1998). Trzcinski, Fahrig, and Merriam

(1999) tested for an interaction between habitat amount and habitat configuration in effects on densities of songbirds in southern Ontario and Quebec and found none, a characteristic of extinction thresholds rather than fragmentation thresholds.

Based on findings like those of Andrén (1994) and Fahrig (1997, 1998), some have suggested that population extinctions can be avoided simply by setting some benchmark level of required landscape cover above a 20-30% threshold (Lindenmayer and Luck 2005). However, others question the use of such general thresholds. Lindenmayer and Luck, in a 2005 review, listed three reasons why land managers should avoid setting benchmark levels for landscape cover. First, they noted that there is little consistency in results of studies of threshold levels of landscape cover. For example, Mönkkönen and Reunanen (1999) reanalyzed the data used in Andrén's (1994) analysis and found that landscape composition and configuration had a significant bearing on the threshold level. Similarly, Betts, Forbes, and Diamond (2007) found that the nature of the threshold response was highly species-specific.

Second, Lindenmayer and Luck (2005) believe that the use of such threshold levels is a misapplication of the original threshold theory. Threshold theory suggests that species will be lost at a greater rate below a specified threshold level, but species losses and population declines can still occur above that level, just at a slower rate. For this reason, some warn that the uncritical application of general thresholds will lead to the loss of sensitive species (e.g., Mönkkönen and Reunanen 1999; With and King, 2001).

Third, Lindenmayer and Luck (2005) point out that for most landscapes, patterns of habitat area loss are not random and do not leave habitat cover of uniform quality. Thus, the percent habitat cover that is required to maintain viable populations of most species will vary with the quality of the remaining habitat.

Others question whether landscape thresholds exist at all. Villard, Trzcinski, and Merriam (1999) found a continuous relationship (rather than a step function, which would have implied the existence of thresholds) between abundances of 15 bird species and forest cover in 33 landscapes in eastern Ontario. In a modeling study, With and King (2001) examined the simulated response of birds with different sensitivities to habitat area and edge effects in various landscape configurations. They concluded that there is a general lack of threshold-like responses to habitat area loss and fragmentation.

Some researchers believe that there is not yet adequate information to demonstrate the existence of thresholds, but stop short of questioning their existence. Fahrig (2003) noted that several theoretical studies, including her own (Fahrig 1997), predicted the existence of an extinction threshold, but reported that there have been very few direct empirical tests of that hypothesis. The interpretation of many studies intended to test the extinction threshold hypothesis is complicated by difficulties encountered when attempting to separate the effects of multiple variables such as patch size, patch isolation, and habitat amount (Fahrig 2003).

A recent study by Betts, Forbes, and Diamond (2007) was designed specifically to look for threshold levels of habitat in landscapes and to characterize any thresholds they identified as either fragmentation or extinction thresholds. The authors studied the occurrence of 15 bird species in the Fundy ecosystem of New Brunswick using a new statistical approach designed to use presence/absence data to identify thresholds. They found evidence of thresholds in songbird responses to habitat amounts at local or landscape scales for 14 of the 15 species examined. For all but two species, data supported the extinction threshold hypothesis. For the other two, black-throated blue warblers (*Dendroica caerulescens*) and Ovenbirds (*Seiurus aurocapilla*), the fragmentation threshold hypothesis was supported.

3.4 The Role of the Matrix

Most work related to this topic in the boreal forest deals with forest birds, and therefore the following discussion focuses on those taxa.

Early studies of forest fragments in North America were conducted in landscapes in which forested woodlots were surrounded by agricultural areas (Galli, Leck, and Forman 1976; Whitcomb, Whitcomb, and Bystrak 1977; Freemark and Merriam 1986; Wilcove, McLellan, and Dobson 1986; Temple and Cary 1988). Since for many forest birds, land between the woodlots was essentially unusable habitat, it is no surprise that the findings of these studies were consistent with the theory of island biogeography, where the diversity of bird species in individual fragments was related to fragment size and/or isolation. Haila (2002) noted that studies such as these are based on a conceptualization of landscapes in which forested ecosystems are viewed as islands of habitat embedded in an uninhabitable matrix of non-forest.

In the context of managed forests, however, it may not be accurate to consider harvested areas between mature forest as the “hostile sea” (Bunnell 1999b) envisioned by the theory of island biogeography. In managed forests, the matrix between areas of mature forest may not be a completely unusable environment. Further, the usefulness of the matrix as habitat and for facilitation of movement between areas of mature forest will increase over time. Thus, short-term demographic isolation may occur for some immobile species, but it is unlikely that genetic isolation will persist.

The two most important aspects of contrast between the matrix and the subject habitat are the extent to which the matrix impedes movement and the extent to which the matrix can be used as habitat. A body of water severely impedes the movement of small mammals and offers no habitat value at all, and so it is not surprising that studies of small mammals on archipelagoes (e.g., Pokki 1981) have found good concordance between the principles of island biogeography and their distribution. The context is clearly very different for use of the matrix by wildlife in managed boreal forests.

Brotons, Mönkkönen, and Martin (2003) reviewed a series of studies that tested for the effect of patch area on the density of forest birds in islands and forest fragments. They restricted their review to studies conducted in two distinct boreal forest landscapes in Fennoscandia: 1) mature forest fragments embedded in a matrix consisting of a mosaic of forest stands of different ages, peatlands, and cultivated areas; and 2) forested islands along the Baltic coast or in lakes. The spatial arrangement and shapes of the islands closely resembled the forest fragments observed in the terrestrial studies. Brotons, Mönkkönen, and Martin (2003) concluded that forest fragments do not function as true islands because the surrounding matrix provides useful resources and enhanced connectivity. They also cautioned against applying the patch-oriented approach of island biogeography to predict how species use heterogeneous landscapes and hypothesized that bird species in boreal forests may be well adapted to use or move across heterogeneous landscapes, provided that the quality of matrix is sufficient.

Schmiegelow and Mönkkönen (2002) showed that the effects of fragmentation in a forested landscape differed from those observed in a landscape dominated by agriculture. They emphasized that the quality of the matrix was key in affecting the abundance and distribution of forest birds in the overall landscape.

Edenius and Elmberg (1996) looked at landscape-level effects of modern forestry on bird communities in northern Sweden and found relatively small negative effects on relative abundance of species. They hypothesized that the lack of fragmentation effects was due to the lack of significant contrast between the matrix and the unharvested forest.

Gap crossing experiments with boreal songbirds found species-specific differences in the willingness of birds to venture into the open from forested habitats and/or cross gaps of various distances in response to play-back calls (St. Clair et al. 1998; Desrochers and Hannon 1997; Bélisle and St. Clair 2001). Although birds generally preferred to travel in corridors or through contiguous forest, most species did at least occasionally venture into open areas, suggesting that open areas are not impenetrable barriers. Nonetheless, the disinclination of some species to venture into the open is cited by Schmiegelow and Hannon (1999) as potentially contributing to fragmentation effects on songbirds in managed forests.

Natural disturbances such as insect outbreaks, windthrow and fire have produced patchy heterogeneous environments in boreal forests with many habitat and stand types of varying size and juxtapositions. In boreal areas, bogs, rock outcrops and senescing stands also contribute to the forest's patchiness. Brotons, Mönkkönen, and Martin (2003) note that the matrix in managed forests can be very similar to the matrices created by natural disturbances. Indeed, in recent years, efforts have been made across much of Canada's boreal forest to emulate natural disturbance patterns during forest management, with attention given to patch size, shape, and distribution over the landscape and residual structure (Ontario Ministry of Natural Resources 2001; Song 2002). Given the patchy nature of the boreal forest, many of its wildlife species are adapted to heterogeneous environments (Cotterill and Hannon 1999). Noss (1991) suggested that edge effects are not as prominent in heterogeneous forests that have gaps and greater internal patchiness than homogenous forests. Similarly Andrén (1995) suggested that nest predation is more prominent in fragmented homogenous forests than in patchy forests with many natural edges.

In recognition of the importance of the influence of the matrix on the effects of fragmentation, and that the view of a hostile matrix is not universally applicable in fragmented environments, Rodewald (2003) and Kupfer, Malanson, and Franklin (2006) argued that ecologists should move from an island-based perspective of fragmentation to one that puts greater emphasis on the matrix and its role in fragmentation processes. Similarly Fischer and Lindenmayer (2006) argued for a "continuum model" of landscape processes which emphasizes gradations in habitat and the local distribution of biota.

From the above discussions, it seems that the matrix created by boreal forest management may minimize the effects of fragmentation. However, there may be specialist species that are less well adapted to the boreal forest's disturbance-driven nature and may thus be more sensitive to forest management. In addition, there are clearly differences between naturally disturbed patches and management-created patches and adaptations to naturally created patchy environments may not ensure adaptability to heterogeneous environments created by forest management activities (Thompson 1992; Niemi et al. 1998).

3.5 Temporal Aspects of Fragmentation

It is well established that the boreal forest is a disturbance-driven ecosystem. Most literature cites fire return times of 80–150 years as normal for the boreal forest, although both shorter and longer return times are noted for some boreal ecosystems (Heinselman 1981; Johnson 1992; Foster 1983; Lynham and Stocks 1991). In addition, wind and insect-driven disturbances create an environment in which change is a dominant aspect. Fragmentation in boreal landscapes is a natural dynamic process in which patch configuration and other characteristics change

continuously. It seems reasonable, therefore, to hypothesize that most organisms inhabiting such an environment would be adapted to rapid succession of patchy environments and habitat fragmentation. This rationale has been used by several authors to explain the resilience of many boreal species. For example, Bayne and Hobson (1998) expected, but failed to find, edge effects on boreal red-backed voles in the Prince Albert Model Forest in Saskatchewan and speculated that the high degree of natural fragmentation by fire and insect disturbance in the boreal forest of western Canada has resulted in better adaptation for dealing with edges.

DeMaynadier and Hunter (1998) and Boulet and Darveau (2000) cite the ephemeral nature of clearcut edges as one reason for the minimal edge-effects observed in managed boreal forests compared to the more readily detectible effects at forest/agriculture interfaces. Harris and Reed (2002) found that effects of edges on songbirds, primarily black-throated blue warblers (*Dendroica caerulescens*), in landscapes fragmented by forestry in Maine were ambiguous, possibly because of the transient nature of edges in forests managed for wood production.

Schmiegelow and Mönkkönen (2002) cited the transient nature of boreal successional stages as a potential ameliorating influence on the effect of fragmentation in these dynamic landscapes, as seen in experimental work in western boreal mixedwoods by Schmiegelow, Machtans, and Hannon (1997). NCASI (2004) noted that several studies in Canada's western boreal mixedwoods found equivocal results regarding the role played by buffer strips and corridors in facilitating movement of songbirds (Machtans, Villard, and Hannon 1996; Schmiegelow, Machtans, and Hannon 1997; Hannan and Schmiegelow 2002; and Robichaud, Villard, and Machtans 2002). Several of those authors suggested that the limiting factor in use of corridors seemed to be that the contrast between corridors and the harvested matrix disappears with time.

Schmiegelow, Machtans, and Hannon (1997) believe that the evolutionary advantage of being adapted to change in boreal environments is supported by work from Palearctic forests where dominant species tend to be habitat generalists. However, Angelstam (1992) speculated that the dominant species tend to be generalists simply because the long history of human-induced habitat change in Palearctic forests has already led to the extirpation or extinction of species sensitive to fragmentation.

With respect to the concepts of island biogeography and the role of the matrix, Kupfer, Malanson, and Franklin (2006) noted that in most studies of fragmentation, the matrix is treated not only as inhospitable, but also static. In contrast to the matrix between true islands or even the agricultural matrix between woodlots in settled landscapes, the matrix in managed boreal forests is ephemeral. The contrast between harvested matrix and unharvested forests is most obvious immediately after harvest. Even if the matrix presents a barrier and inhospitable habitat for some species, its effect can be expected to moderate or diminish as the harvested lands succeed back to mature forest. Within 5-10 years after harvest, saplings are usually well established. Within 20-30 years, depending on the stand types, young trees occupy the sites and within a few decades, crown closure is usually complete. With each passing year, the matrix becomes less and less distinct from the surrounding forest. It is in this context that the terminology around fragmentation effects becomes somewhat confounded; if habitat is not permanently removed, but regenerates over time, the term "habitat area loss" may be misleading. Habitat area may be lost, but the loss is temporary. Further, the "lost area" becomes habitat for other species, and in fact could be qualified as "habitat area gained" for early successional species, but will again shift back to late successional forests over time, as in a shifting habitat mosaic (Pickett and White 1985), which helps maintain connectivity in terrestrial systems and reduce the overall fragmentation effect (Wimberley 2006).

4.0 FRAGMENTATION AND ROADS

One of the main ecological effects of roads is landscape fragmentation (e.g., Trombulak and Frissell 2000; Forman et al. 2003). The reported effects of roads include increased animal mortality via collisions, impeded wildlife movement, disruption of water flows, and increased erosion. The discipline of road ecology has arisen in recent years in response to concern about these effects. Because roads bisect the lands through which they run, many of the effects of roads are encompassed by various definitions of fragmentation. Although most of these would likely fit into the outer bands of the definition of fragmentation modeled in Figure 2.1, effects associated with direct changes in landscape configuration likely fit well in the narrow definition represented by the inner circle.

Several studies, primarily from the western United States, investigated effects of roads in concert with effects of forest harvest and clearcutting on landscape metrics that may serve as proxies for fragmentation (Miller et al. 1996; Reed, Johnson-Barnard, and Baker 1996; Tinker et al. 1998; Saunders et al. 2002; McGarigal et al. 2001). For the most part, the studies found that road construction/use had a significant effect on metrics such as core area, amount of edge, patch size distribution, and patch shape. In several cases, these effects were stronger than those caused by harvesting.

However, Miller et al. (1996), in a study of forest roads and landscape structure in the southern Rocky Mountains, found that the effects of roads on landscape patterns are localized along the roads themselves and that both average stand size and patch shape were related more to topography than road density. Miller et al. (1996) concluded that the relationship between road density and landscape structure in the southern Rocky Mountains is not easily quantified. They stated that while roads may alter the spread, frequency, and intensity of disturbances on the landscape, their effects on landscape structure are modified by the influence of topography and probably a variety of other factors that also affect stand size and shape.

No comparable studies from boreal Canada were found in the literature. The road density of several of the studies mentioned above is comparable to that in managed boreal forests, as was the density of clearcuts, and therefore the results may be applicable to Canadian boreal forests as well.

All of the above cited studies were based on GIS analyses. Each study extrapolated effects of changes to landscape metrics base on published results of other studies. They inferred that measured changes could be related to detrimental changes in air pollution, the creation of habitat barriers, increases in direct vehicular fatalities, increased disturbance by human activities, the introduction of exotic species, changes in microclimate, changes in inter-species interactions, increased competition for resources, decline in amounts of core habitat, etc. Consistent with the discussion above, these effects, although not all related to fragmentation per se, are among those frequently lumped in with fragmentation.

An important point is that road networks, not just individual roads, should be considered in assessing the effects of roads on fragmentation (McGarigal et al. 2001; Lugo and Gucinski 2000). Tinker et al. (1998) noted that the spatial distribution of roads may affect landscape structure within a watershed more strongly than road density. Similarly, Reed, Johnson-Barnard, and Baker (1996) found that roads evenly distributed across a landscape may have a greater effect on core area, patch size and amount of edge than those clustered in a small area of a watershed. This is important because road density is often used as an index of the potential ecological effect of roads (Miller et al. 1996; Ontario Ministry of Natural Resources 2004). By focusing on road density rather than metrics such as road distribution, road quality, traffic pattern and volume, the potential

for some effects may be exaggerated or underestimated. Unfortunately, these measures are often unavailable for forest access roads in the boreal, making it difficult to assess the transferability of study results.

As noted previously, the relationship between changes in the various landscape metrics and ecological effects must be validated in order to substantiate or refute concerns raised in the studies. Additional research is required in order to determine whether and how changes in metrics used in these studies result in effects on wildlife species.

5.0 POSSIBLE EFFECTS ON VERTEBRATE FAUNA

The literature contains a moderate amount of information on the effects of fragmentation on boreal wildlife species. Logically, the broader the definition of fragmentation used, the more effects are possible, and so the further one proceeds from central concept in Figure 2.1, the more literature is available, assuming these related but peripheral aspects have been examined. This section focuses on effects associated with landscape configuration, but also includes topics for which there are well documented concerns related to the outer concentric circles of Figure 2.1.

5.1 Bats

Crampton and Barclay (1996) examined habitat selection by little brown bats (*Myotis lucifugus*) and silver-haired bats (*Lasionycteris noctivagans*) in fragmented and unfragmented aspen mixedwood stands in northern Alberta. Their definition of fragmentation, “the removal of trees from certain parts of stands,” was based on intra-stand harvesting. While this is not consistent with more broadly used definitions, bats do perceive changes of this scale in their environment and therefore the definition seems appropriate for this study. The researchers examined habitat use related to openings in the forest and concluded that in general, edge habitats created by harvesting are preferred for foraging over the mid portions of clearcuts and dense aspen forests. They hypothesized that the less cluttered structure of edges provide for good navigation and prey (insect) densities.

Similarly, Grindal (1996) examined habitat use by several species of bats that he classified as either open-adapted [big brown bat (*Eptesicus fuscus*), silver-haired bat, hoary bat (*Lasiurus cinereus*)], or clutter-adapted [little brown bat, yuma bat (*Myotis yumanensis*) long-eared bat (*Myotis evotis*), long-legged bat (*Myotis volans*), California bat (*Myotis californicus*), northern long-eared bat (*Myotis septentrionalis*)] in southern British Columbia, south of the boreal portion of the province. He found that foraging activity was significantly greater along edges than in clearcuts or forest habitat for clutter-adapted bats, and that open-adapted bats preferred both edges and clearcuts for foraging.

Little additional research in Canada on the effects of fragmentation on bats in forested environments has been reported. From these few studies, no conclusion regarding effects of fragmentation at larger spatial scales on bats is possible, but it does seem that edge habitats and open areas are important for foraging, and that the juxtaposition of forest and open areas may be ideal.

5.2 Small Mammals

Although there is evidence to suggest that roads have an inhibitory effect on movement of some small mammals, these cases are either in other landscapes⁷ (primarily the prairies), or on roads with volumes of traffic considerably greater than those normal for forest access roads (Oxley, Fenton, and Carmody 1974). Merriam et al. (1989) found that white-footed mice tended to cross small roads in deciduous forest fragments much less than anticipated based on frequency and distance of movement within the areas adjacent to the roads. They concluded that while the roads were not absolute barriers, they did effectively inhibit movement.

Merriam et al. (1989) also looked for genetic variations between white-footed mouse populations in 11 forest fragments that were in the same 375 km² area, but geographically isolated from one another by medium intensity farmland and roads. They found no evidence of genetic isolation in spite of the fact that the fragments did appear to be effectively isolated patches.

Selonen, Hanski, and Stevens (2001) studied landscape configuration effects on Siberian flying squirrels (*Pteromys volans*), inhabitants of spruce-dominated boreal forests from Finland to eastern Siberia and Japan. They found that home range size for females was not influenced by any of the measured landscape variables. Females typically live within a single patch and have home ranges smaller than those of males. One study area contained nest boxes, use of which produced a high density of females. At this site, the primary determinant of male space use appeared to be density of females. When data from the other study sites were analyzed, the researchers found that male home range was larger for individuals that lived in several small patches than for those living in one or a few large patches. In addition, males were able to inhabit areas where mature forest was separated by cuts and young forest because they were able to move between patches of preferred habitat.

Selonen, Hanski, and Stevens (2001) noted that a lack of nest cavities may be a problem for flying squirrels. They also concluded that loss of preferred habitat area is more detrimental than loss of landscape connectivity, because the female flying squirrel requires a suitably large spruce patch, deciduous trees for food, and access to cavities for nesting.

Holloway and Malcolm (2007) examined habitat use by northern flying squirrels (*Glaucomys sabrinus*) in Algonquin Provincial Park, Ontario. The park contains both unharvested areas and harvested areas that contain uneven aged stands with single- and multiple-tree canopy gaps produced by removal of about one-third of the overstory basal area every 20-25 years. The researchers initially planned to capture squirrels in both unharvested and harvested areas and fit them with radio collars for tracking. However, after 1545 trap nights of effort, no northern flying squirrels were captured in harvested areas, so all squirrels followed in the study were captured in unharvested areas of the park.

The researchers found that male squirrel home ranges were nearly three times larger than female home ranges and that nest sites were typically located outside the core areas of highest squirrel activity, often near the edges of the home range (Holloway and Malcolm 2007). Core areas differed from the peripheral areas of the home range primarily by having greater densities of spruce trees, understory stems, and declining trees ≥ 25 cm dbh. When they compared habitat in home ranges of the squirrels to that of random locations in the same areas that were outside any home ranges, the researchers found a number of significant differences. Basal area, tree species richness, snag density, and the density of hardwoods ≥ 25 cm dh were all lower in areas being used by squirrels, while understory density and density of food-producing shrubs, spruce trees,

⁷ Swihart and Slade 1984; Kozel and Fleharty 1979; Meserve 1971

and declining trees ≥ 25 cm dh were significantly higher. Holloway and Malcolm (2007) concluded that old conifer forests are important habitats for northern flying squirrels, who appear to have a preference for areas with old, senescing trees with a mosaic of canopy gaps. Spruce also appears to be a key feature of squirrel habitat, since high spruce density was characteristic of core areas. These researchers concluded that partial harvesting, such as practiced in the park, had a negative impact on several structural features important to squirrel habitat, such as the density of dead/diseased trees, and understory and spruce density.

5.3 Herptiles

There are relatively few species of herptiles in Canada's boreal forest, and very few studies of their ecology or of the effects of forest management. In a review of the effects of habitat fragmentation on amphibians, Wind (2000) included only one study specifically from boreal Canada among 14 studies reviewed in detail and approximately 50 citations. Studies from temperate North American forests are much more common (e.g., Brooks, Brown, and Galbraith 1991; deMaynadier and Hunter 1995; Gibbs 1998a, 1998b; deGraaf and Yamasaki 2002; Marsh and Beckman 2004; Marsh et al. 2005).

Studies of the effects of management and roads in forests on amphibians have tended to focus on the effect of edges and the relative inhospitability of recently-harvested areas. In her literature review, Wind (2000) noted amphibian abundance is generally lower in open areas and second-growth stands than in mature forests due to changes in microclimate. If harvested areas and naturally disturbed sites do represent temporarily inhospitable habitats for amphibians, fragmentation effects may be observed.

Seburn, Seburn, and Paszkowski (1997) documented source-sink dynamics for leopard frogs (*Rana pipiens*) in the Cypress Hills of Alberta, noting the importance of source ponds in the metapopulation dynamics in local areas. Gill (1978) documented similar dynamics for red-spotted newts in Virginia. Both studies used stand-level observations extrapolated to the landscape scale, and both authors noted that factors such as relative locations of ponds, and distances and habitat between ponds, play a strong role in structuring metapopulations of amphibians. Waldick (1997) specifically focused on effects of forest management and noted that the limited dispersal abilities of amphibians may preclude dispersal across clearcut and plantation habitats. She suggested that lower adult breeding populations in clearcuts versus the surrounding mature forest is evidence that fragmentation and clearcutting may impose constraints on populations.

DeMaynadier and Hunter (1998) examined whether clearcut edges affect the abundance of 14 amphibian species in forests in Maine. They found that such effects exist for four species: the red-back salamander (*Plethodon cinereus*), spotted salamander (*Ambystoma maculatum*), blue-spotted salamander (*Ambystoma laterale*), and wood frog (*Rana sylvatica*). They noted that the inhospitable nature of openings may affect the landscape dynamics of these species. They also found a higher portion of immature animals in recently harvested areas adjacent to mature stands and suggested that such sites may serve as sink habitats for nonbreeding "floaters" that are excluded from mature forest territories. In contrast, they found no such effect for four species: eastern red newt (*Notophthalmus viridescens*), pickerel frog (*Rana palustris*), leopard frog (*Rana pipiens*) and American toad (*Bufo americanus*). They also noted that the temporary nature of forest openings needs to be taken into account in considering the longer-term effects of forest management. The spatial distribution of harvest units also should be considered, as typically only a small portion of the landscape is harvested in any given year.

While there is a strong sense in the literature that patch dynamics as affected by forest management operations are important in affecting amphibian populations⁸, there is also explicit recognition that this is a poorly understood aspect of amphibian ecology⁹, particularly in boreal settings¹⁰, and that species-specific differences prevent generalizations about the effects of forest management on amphibians.

Salamanders' slow rate of travel and multiple resource needs (i.e., breeding habitat distinctly different from other habitat needs) make them vulnerable to road kill mortality. In addition, forest roads may form an impediment to movement for some species of amphibians, most notably northern red-back salamanders. Marsh and Beckman (1984) noted that while roads may create only narrow openings in the forest canopy, the edge effects can be at least as strong as those from clearcuts or other types of edges. Gibbs (1998a), working in Connecticut, and Marsh et al. (2005), working in Virginia with similar methods, both found that terrestrial salamanders enter roadside habitats less frequently than they do forest habitats. Marsh et al. (2005), considering the results of their and others' studies, concluded that "there is now substantial evidence that most forest roads are partial barriers to terrestrial salamander movement."

Most studies of effects of roads on frogs have examined road kill, although frogs have been included in some studies of barrier effects. There is no evidence of significant frog mortality on roads of use levels comparable to those in Canadian managed forests and no evidence of those roads forming significant barriers to movements. DeMaynadier and Hunter (2000) found no barrier effect of roads on the species of anurans they examined: wood frog (*Rana sylvatica*), green frog (*Rana clamitans*), pickerel frog (*Rana palustris*), and American toad (*Bufo americanus*). Gibbs and Shriver (2005) noted that frogs' greater mobility may make roads a less daunting obstacle for them to cross than they are to salamanders. Similarly, Wyman (1991) noted that frogs exhibit relatively little reluctance to cross roads.

Brooks (2007) looked at the constraints on conserving reptiles in Canada and identified traffic mortality as the single most important issue. He did not, however, consider forest management or the boreal area in particular. Turtles, most particularly snapping turtles, were noted as being especially vulnerable to road mortality due to their low reproductive rates and propensity to nest in roadsides. Gibbs and Shriver (2002) noted that the works of others¹¹ have been used in calibrating models that suggest that relatively small (2-3%) increases in mortality can have negative effects on population growth rates. In this context, land with road densities of greater than 1 km/km² and rates of travel greater than 100 vehicles/lane/day were thought to contribute excessively to annual adult mortality thresholds of land turtles. Type, quality, and permanence of road were not considered in this analysis. In the context of the boreal forest, road densities in Ontario's boreal forest range from 0.21-0.52 km/km², with rates of travel varying from 0-20 haul trucks per day, varying with season and operations, with increased rates where forests are routinely accessed by the public.

⁸ e.g., Waldick 1997; Rosenburg and Raphael 1986; deMaynadier and Hunter, 1995, 1998; Wind 2000

⁹ DeMaynadier and Hunter 1995

¹⁰ Wind 2000

¹¹ Doroff and Keith 1990; Brooks, Brown, and Galbraith 1991; Congdon, Dunham, A.E., and van Loben Sels 1993

5.4 Meso-Carnivores

Meso-carnivores (e.g., skunks, mink, marten, fishers, lynx, coyotes, etc.) represent a large group of mammalian predators, and exhibit a range of responses, from negative to positive, to forest fragmentation (Goodrich and Buskirk 1995). Generalist meso-carnivores, such as raccoons (*Procyon lotor*), coyotes (*Canis latrans*), striped skunks (*Mephitis mephitis*) and red foxes (*Vulpes vulpes*) tend to exhibit positive population shifts in response to forest fragmentation, and occasionally urbanization (Adkins and Stott 1998; Oehler and Litvaitis 1996; Parker 1995; Rosatte 1987). Kurki et al. (1998) note that a number of researchers have reported that human-induced changes in boreal landscape composition have led to widespread changes in natural community structure, which have, in turn, resulted in rapid changes in interactions between species in these new communities. Some of these researchers have expressed concerns that these changes will negatively impact some species. For example, increased populations of generalist meso-carnivores in fragmented forest landscapes may result in increased predation pressure on vertebrate prey (Kurki et al. 1998). However, there is little evidence that the density of generalist predators is related either to fragmentation of forest *per se* or fragmentation of mature forest as a result of clearcutting (Kurki et al. 1998). Species with large home ranges and a preference for more mature forest conditions, such as American marten (*Martes americana*), and Canada lynx (*Lynx canadensis*) have not fared well in circumstances where sufficient late seral stage characteristics (e.g., sufficient denning sites, coarse woody debris, snags) and/or habitat area have not been maintained on a landscape (Hargis, Bissonette, and Turner 1999; Koehler and Aubry 1994).

Published literature on the relationship between lynx and bobcats and roads is scarce. Lovallo and Anderson (1996) found no avoidance of lightly travelled roads. Three other articles have noted that lynx regularly cross secondary and low-volume roads and use roads for hunting and travel (McKelvey et al. 1999; Mowat, Poole, and O'Donoghue 1999; Koehler and Aubry 1994).

A considerable number of studies examining marten habitat use have led to an understanding that residual forests are important to marten in most circumstances, but there have been considerably fewer examinations of the effects of fragmentation on their persistence.

Chapin, Harrison, and Katnick (1998) examined the influence of landscape pattern on habitat use by marten in northern Maine. They tracked 65 radio-collared marten in an industrial forest landscape with patches of residual forest (height >6 m) ranging in size from < 1 to 3,400 ha interspersed with recent (1-7 yrs) clearcuts and regenerating forest (8-15 yrs). The study area abutted a state park where no harvesting was permitted. They found that residual patches used by marten were on average 18 times larger than patches with no observed use and closer to the park. They detected no difference in edge index between used and unused patches, indicating that the shape of the patches did not influence use by marten. The study was conducted using grid cells ranging in size from 10-250 ha and across the range of spatial scales examined, the amount of residual forest and size of patches were positively related to use of grid cells by resident marten. The authors suggested that isolation of residual patches interacts with patch size to influence spatial distribution of marten in landscapes with extensive clearcutting. Soutiere (1979) and Steventon and Major (1982) also examined marten habitat use in Maine and concluded that marten use residual patches at a level disproportionate to their presence, but did not determine the relationship, if any, between patch use and patch area.

The finding of Chapin, Harrison, and Katnick (1998) that area of residual patches was a dominant influence on marten use is comparable to that of Snyder and Bissonette (1987), who found that only 5 of 51 captures of marten in western Newfoundland occurred in forest patches smaller than

15 ha. The authors concluded that larger residual patches are key habitat components for marten in extensively clearcut areas.

Potvin, Bélanger, and Lowell (2000) analyzed home range characteristics of 33 marten radio-collared in a managed forest landscape in boreal western Québec, originally documented by Potvin and Breton (1997). In addition to characterizing habitat use in relation to stand ages and types, they assessed home range characteristics using a series of configuration metrics (McGarigal and Marks 1995). They found that fragmentation was lower in random mosaics than in those occupied by marten home ranges, but that core habitat area in uncut forest, which is related to the size and shape of patches, was much higher in home ranges. A contrast edge metric, which measured the proportion of the perimeter of uncut forest patches in direct contact with open/regenerating areas was significantly lower in home ranges (although this metric was correlated with the core area metric). They concluded that martens are “fairly intolerant” of habitat fragmentation and cannot tolerate more than 30-35% cutovers in their home ranges.

Thompson and Colgan (1994) radio-tracked 36 marten in 2 uncut and 10 logged forested landscapes (5-30 years since harvest) for 4½ years in northwestern Ontario. They found that distances between home range core areas, defined as those areas used most frequently and that contained den sites and known resting sites, were greater in logged forests than in unlogged forests. They attributed the difference to greater food availability in the unlogged areas, since martens in uncut forests captured up to 119% more prey biomass than those in logged forests. They also speculated that larger home ranges in logged forests reduce the energetic efficiency of animals in those habitats. In years when food was scarce, the mean distance between core areas was significantly greater than in years of abundant food.

The habitat requirements of marten encompass a range of characteristics. However, the precise role that fragmentation plays, independent of factors such as forest age, composition, availability of coarse woody debris, access to subnivean habitats, and food availability, is difficult to discern. Clearly, fragmentation is a factor affecting habitat preference and use by marten in managed forests, but martens can exist in intensively managed landscapes if other habitat requirements are met and, most importantly, if patches of sufficient size are maintained (Thompson and Colgan 1994; Chapin, Harrison, and Katnick 1998). Because martens locate their home ranges in relatively unfragmented portions of a given landscape, their relationship with fragmentation may be somewhat scale-dependant. Landscape management approaches, such those described by Bissonette, Fredrickson, and Tucker (1989) and Watt et al. (1996), that factor in an array of habitat requirements are critical in providing for the habitat needs of marten. Such management approaches have been applied with some success, creating large unharvested habitat cores for marten amidst forest harvesting areas, which has helped to sustain marten in some jurisdictions (e.g., Watt et al. 1996).

5.5 Large Ungulates

There are a number of large ungulates in the boreal forest, including white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*), caribou (*R. tarandus*) and moose (*Alces alces*). For ungulates as for other taxonomic groups, the effects of fragmentation are often species- and life-history specific. Moose, more so than deer and elk, are thought to select habitat primarily on the availability of forage, which may increase after forest harvesting (Telfer 1978). Moose have often been found to respond positively to fragmentation, with increased foraging opportunities at forest edges resulting in increased populations (Schneider and Wasel 2000). Similarly, the creation of edge habitat and small openings creates abundant browse for white-tailed and mule deer, resulting in population increases. Such changes to the herbivore community can alter the successional dynamics of forest regeneration (Rooney

and Waller 2003). While the effects of fragmentation per se are not well documented for elk, the effects of roads are thought to be significant. Lyon (1983) suggested that road densities greater than 1.2 km/km² reduced habitat suitability for elk.

In the boreal forest, the majority of studies examining the effects of fragmentation on ungulates have focused on woodland caribou. Boreal populations of woodland caribou are known to be sensitive to human disturbance (Racey et al. 1991; Cumming 1992; Courtois et al. 2004; Vors et al. 2007). Understanding the effect that fragmentation may have on caribou populations is challenging because of the complex ecology of the species and the variety of factors thought to play a role in that ecology.

The notion that predation plays an important role in affecting woodland caribou populations has received considerable recent attention, as reviewed by NCASI (2004), and forest fragmentation has been hypothesized to be a contributory factor in predation effects (Bergerud 1974; James 1999; Rettie and Messier 2000; Voigt et al. 2000; Dyer et al. 2001; Courtois et al. 2004). The basic hypothesis is that in areas where caribou are the only ungulates, they do not exist at sufficient densities to support large predator populations and can thus maintain viable populations. However, in areas where commercial-scale logging has occurred, the younger forest matrix and fragmentation of habitats has increased habitat for other ungulates, primarily moose, but also white-tailed deer and elk. As a result, predator populations have increased and predation pressure on caribou has exceeded the species' ability to persist (Simkin 1965 in Bergerud 1974; Bergerud 1974; Darby et al. 1989; Racey et al. 1991, 1999; Chowns 2003; Schaefer 2003).

Caribou may also be adversely affected by the existence of forest roads. Several studies of caribou behaviour in response to forest roads have suggested that while the evidence is not conclusive, caribou appear to use linear features to facilitate movement, but are inhibited by vehicular traffic, possibly as a result of increased noise disturbance (Banfield 1974; Bergerud, Jakimchuk, and Carruthers 1984; Curatolo and Murphy 1986; Murphy and Curatolo 1987; Cumming and Hyer 1998; Yost and Wright 2001; Dyer et al. 2001, 2002). Very lightly traveled roads may not pose a disturbance, or may even provide some benefits, but use of the roads by vehicles above some relatively light, but as yet unidentified, threshold may act as a deterrent for use and potentially present an ecological barrier. Hunting, facilitated by northern access roads, may also have an effect on populations of woodland caribou (Johnson 1985; Dyer et al. 2001; Chowns 2003; Courtois et al. 2004).

Because of concerns about the hypothesized roles of forest management and fragmentation in the decline of woodland caribou, control of fragmentation is emphasized in boreal forest management strategies. This is both implicit and explicit in the measures advocated for Quebec (Courtois et al. 2004) and northwestern Ontario (Racey et al. 1999) for integration of caribou habitat concerns and forest management. For Quebec, suggested practices include 1) delimiting large (100–250 km²) habitat blocks and planning harvest strategies that maintain such blocks on the landscape in old forest conditions; 2) maintenance of connectivity between seasonal habitats through the provision of wide (2 km) corridors; and 3) concentration of forest harvesting in contiguous blocks so as to avoid creating forest fragments. Similar strategies are advocated for northwestern Ontario: 1) concentration of forest harvesting in large areas (> 10,000 ha) and maintenance of similar sized blocks of mature habitat; 2) provision of refugia from predation, primarily through deconstructing roads; 3) discourage conversion to hardwoods that provide browse for moose; and 4) maintenance of connectivity between summer and winter habitat by the use of wide corridors.

5.6 Large Carnivores

Few studies address the effects of forest landscape fragmentation on boreal predators. This is likely at least partly because it is difficult to study boreal predators over landscape scales at which fragmentation effects may be manifested. Nonetheless, the ecology of boreal predators is such that the effects of forest management-related landscape changes may be tempered by the manner in which these large carnivores use their environments. Many large boreal predators are capable of using, or may even require, several habitat types to meet their needs and most have large home ranges or travel widely, using the forest at scales transcending those at which fragmentation metrics are usually employed.

Inasmuch as roads constitute a fragmenting force, there is evidence of effects for some predators. McLellan and Shackleton (1988) and Mace et al. (1996) found strong evidence that grizzly bears (*Ursus arctos*) avoid areas with road densities within the range of those found in Canadian managed forests. Black bears (*Ursus Americana*) have been noted as victims of road kill (Alt et al. 1977; Brody and Pelton 1989; Manville 1983), but the roads on which the mortalities occurred in these studies were more heavily traveled than are roads in Canada's managed forests.

There is a considerable body of work which has found that access management is an important feature of bear management. For example, Horejsi (1989) and Knick and Kasworm (1989) found that road-mediated mortality, primarily from hunting, is a significant cause of tenuous population dynamics for some grizzly populations. Although roads do not form barriers to bear movements, available evidence suggests that bears select habitat away from roaded areas.

A study from Arizona found that mountain lions (*Puma concolor*) avoided areas with active timber operations (Van Dyke et al. 1986). The authors suggested that avoidance of timber operations was at least partly due to increased road density.

Wolves (*Canis lupus*) are known to travel widely and even use lightly traveled roads as movement corridors (Murie 1944; Mech 1970; James and Stuart-Smith 2000; Dyer et al. 2001). There is a considerable amount of literature on the relationship between wolves and roads. Much of the literature from eastern North America relates to thresholds of road densities implicated in the failure of wolves to persist, and the hunting and trapping of wolves as a result of human activities facilitated by access (Thiel 1985; Jensen, Fuller, and Robinson 1986; Mech et al. 1988). However, Mladenoff et al. (1995) noted that the negative public attitudes about wolves have subsided to the point where the formerly cited threshold of persistence (about 0.6 km of road km²) is no longer relevant, suggesting that human access rather than roads themselves is a significant part of the issue. Mladenoff et al. (1995) and Mech (1995) note that wolves can move through a fragmented landscape, but establishment success is restricted to higher quality habitats. Note, however, that the fragmented landscapes referred to in the above studies were primarily areas in which forest is fragmented by settled and agricultural areas rather than through forest management.

5.7 Birds

As noted earlier, there has been considerably more research into the potential effects of fragmentation on birds than for other vertebrates in the boreal and other forest types. The issue of fragmentation effects on forest birds was discussed in considerable detail in NCASI (2004). This section brings recent publications into the discussion, but also borrows from that review. The following discussion focuses on two distinct aspects of potential fragmentation effects related to songbirds: edge effects (mostly increased parasitism and predation of nests proximal to forest edges) and the implications of decreased forest connectivity and changes in landscape configuration.

5.7.1 *Edge Effects*

Nest parasitism by cowbirds (*Molothrus ater*) and nest predation can have serious detrimental influences on forest birds in landscapes in which forest patches exist within an agricultural matrix (e.g., Gates and Gysel 1978; Wilcove 1985; Yahner 1988; Robinson et al. 1995). As nest parasitism is not an issue in managed boreal forests (NCASI 2004), this discussion focuses on nest predation.

Nest predation and parasitism have been found to have detrimental effects along forest edges in agricultural landscapes (Gates and Gysel 1978; Wilcove 1985; Yahner and Scott 1988; Robinson et al. 1995). Factors contributing to higher nest predation along forest edges and inside forest patches identified by these and other studies include

- higher densities of prey along edges, which attract higher predator densities and higher levels of predatory foraging;
- habitats adjacent to forests acting as a source of predators which forage into the adjoining forests;
- habitat edges used as travel corridors by predators, increasing the opportunistic finding of birds' nests; and
- agricultural landscapes supporting more generalist predators than forest landscapes, causing increases in predator populations.

A key question is whether or not these same dynamics exist in landscapes in which forests predominate and forest management is the primary land use. Boulet and Darveau (2000) summarized hypotheses proposed by other researchers to explain why edge-related effects are not likely to occur in managed forest landscapes in which clearcutting is the dominant agent of change.

- Clearcut areas are ephemeral, so there are no permanent changes in predator or prey populations or associated dynamics;
- Forest-clearcut edges are more abrupt than are edges in forest-agricultural matrices, making them less attractive for nesting birds and subsequently to predators;
- The abundance of generalist predators is lower in a mosaic of residual and regenerating forest than in a forest-agriculture mosaic.

In addition to these reasons, Cotterill and Hannon (1999) noted that natural edges at a variety of scales are common in the boreal forest because of its disturbance-driven dynamics. They cited the suggestions of Noss (1991) and Andr en (1995) that edge effects may not occur in patchy environments because species that inhabit them are already adapted to heterogeneous environments.

Table 5.1 provides summaries of studies that have examined nest predation at forest edges in boreal forests. Most studies in the table found no edge effect. However, the researchers noted in several cases that their tests had low statistical power.

Manolis, Andersen, and Cuthbert (2000) undertook a comprehensive review of 26 analyses of edge and fragmentation effects in 11 previously published studies set primarily in the northern and northeastern United States. Manolis and his co-authors were very critical of the designs of several studies, noting, for example, that some had considerable pseudo-replication. They were also critical of the statistical techniques employed and the low statistical power of many of the analyses. Of the 26 analyses they reviewed, 13 found edge effects, 12 did not, and one showed greater nest predation rates in unfragmented versus fragmented areas. When they excluded analyses of low statistical power that found no effect, all of the remaining studies showed

statistically significant edge effects at $p \leq 0.05$. When they excluded analyses of both low and moderate statistical power that found no effect, 13 of 19 of the remaining studies (68.4%) showed significant edge effects. The authors concluded that their data and analyses strongly suggested that clearcut-edge effects do occur in forested landscapes. It should be noted, however, that the authors only considered the statistical power of the study, a measure that minimized incorporation of false negatives. The authors did not balance this with a sensitivity analysis to minimize incorporation of false positives. Given that the analysis of Manolis, Andersen, and Cuthbert (2000) was based primarily on non-boreal studies, their findings are not automatically transferable to boreal forests. However, many of the studies they reviewed looked for effects in managed forests. Furthermore, the issue of low statistical power has been raised by the authors of several boreal studies.

Lahti (2001) reviewed studies of 55 empirical tests of edge effects on nest predation. The goal of the review was to examine the hypotheses that 1) type of edge affects the probability of having an edge effect, and 2) percent forest cover at the landscape scale influences predation levels and the existence of an edge effect. In contrast to Manolis, Andersen, and Cuthbert (2000), Lahti found no consistent evidence of edge effects at the stand scale.

At the landscape scale, Lahti (2001) sorted studies according to levels of fragmentation. If < 50% of the study area was suitable habitat, fragmentation was labeled “high.” Areas with “low” fragmentation had > 75% in suitable habitat and “intermediate” fragmentation was defined as having 50-75% of the study area in suitable habitat. Not all studies in the review provided sufficient information to be included in this assessment. Seven of 11 sites (63%) with high levels of fragmentation exhibited an edge effect in at least one test treatment, whereas only 3 of 10 sites (30%) with levels of low fragmentation showed an effect. When non-forest habitats were excluded from the analysis, the pattern was amplified. Only one of six sites in areas of low fragmentation exhibited an effect and it was characterized as equivocal. All five sites with high levels of fragmentation exhibited an effect. This assessment included only studies of clearcut and mature forest of undefined age. The author concluded that edge effects are more likely to be observed on landscapes with higher levels of fragmentation. In another review paper, Marzluff and Restani (1999) examined the results of 47 studies of edge effects from around the world, incorporating a wide variety of ecosystems, matrix types and predator communities. Although they did not categorize studies in the same way as Lahti (2001), their conclusions were similar.

Studies of the behaviour of common nest predators may provide some explanation of the findings of Lahti (2001). Red squirrels are known to be important predators of nests (Tewksbury, Hejl, and Martin 1998; Sieving and Willson 1998; Song and Hannon 1999; Boulet, Darveau, and Bélanger 2003). Based on work in southern Quebec, Boulet, Darveau, and Bélanger (2000) suggested that when forest stands are disturbed, squirrels concentrate in nearby stands, and this may increase bird predation there. In addition, Ibarzabal and Desrochers (2004) found that gray jays, also significant nest predators in boreal forests,¹² forage more intensively near forest edges in landscapes of mixed clearcuts and forest. Thus, edge effects, in the form of increased nest predation by gray jays and red squirrels, may be observed in boreal forest landscapes with high rates of natural disturbance or harvest and resultant interspersed of burned or clearcut areas with mature forest.

¹² Song and Hannon 1999; Boulet and Darveau 2000; Boulet, Darveau, and Bélanger 2003

Betts et al. (2006) examined the response of two bird species, Blackburnian warblers (*Dendroica fusca*) and ovenbirds (*Seiurus aurocapilla*), to different forest amounts and configurations. They did not make a link to edge effects per se, but did report that the occurrence of both species was strongly influenced by landscape characteristics at scales greater than individual territories, such as the amount of suitable habitat within 2 km of nest sites. Although their work was in the Acadian Forest, the bird species they studied are common in boreal areas, so their results may also be applicable in areas of the boreal where structural, temporal, and succession dynamics are similar to the Acadian forest.

The majority of studies summarized in Table 5.1 found that edge effects are not significant in managed boreal forests. However, the evidence is not consistent across studies or landscapes, probably because of both local differences in the study sites and differences in the study methodologies applied. Local differences include things like different stages of regeneration, differences in local predator communities, and different levels of harvest.

As Cotterill and Hannon (1999) and others have noted (see Section 2.4) fragmentation in the boreal forest is a transitory state. As Lahti (2001) found, there is little evidence of fragmentation effects in landscapes in which mature forests are interspersed with younger forest. Therefore, as the forest regenerates, nest predators are less likely to focus on edges either for travel, or as a result of habitat compression, reducing predation pressure on nests over time.

King, Griffin, and DeGraaf (1998), Cotterill and Hannon (1999), and Boulet, Darveau, and Bélanger (2003) point out that the nature of the predator community has an important influence on nest survival rates, and therefore local knowledge of the predator community seems to be key in predicting the potential importance of edge effects. There is also evidence, such as the study by Lahti (2001) described above, that there may be an interaction between predator effects and the extent of harvesting in the landscape. Thus, differences in the level of harvest may influence study outcomes in and of themselves, and they may also act as a factor that affects the influence of predator communities on study outcomes.

Finally, as Lindenmeyer and Fischer (2006) point out, nest predation studies have employed a wide variety of methodologies, which may have contributed to difficulties in finding consistent trends. Many studies have been confined to a short period of time (shorter than the typical incubation period of most birds) and last only one or two field seasons. In addition, most studies use artificial nests stocked with quail eggs or even eggs made of plasticine. Several authors have noted that artificial nest studies suffer from a number of methodological biases that render their results difficult to interpret (Major and Kendal 1996; Wilson, Brittingham, and Goodrich 1998).

Table 5.1 Summary of Several Studies Which Have Examined Nest Predation at Forest Edges in Boreal Forests

Study and Location	Brief Description	Key Results	Summary/Conclusions
<p>Hanski et al. (1996)</p> <p>Northern Minnesota</p>	<ul style="list-style-type: none"> • Study in boreal – hardwood transition forest • Investigated relationship between bird predation and several vegetation parameters and distance to edge in two locations in northern Minnesota. • Monitored fates of real nests detected by careful searches in forests and open areas. • Open areas which abutted forests included clearcuts, young forest, (time since disturbance not provided) power line rights-of-way, and small bogs. • Surrounding landscape was mostly forested. • Lasted 1 field season. 	<ul style="list-style-type: none"> • No evidence of edge effect was found in either forest or open habitats. • Nest predation was lower in open habitats than in forests. 	<ul style="list-style-type: none"> • Proximity of nest to edge had no effect on nesting success. • The authors suggest that lower predator densities in open areas explained the difference in predation rates between habitats.

(Continued on next page.)

Table 5.1 Continued

Study and Location	Brief Description	Key Results	Summary/Conclusions
<p>Darveau et al. (1997)</p> <p>Southern Quebec</p>	<ul style="list-style-type: none"> • Study in southern boreal forest (fir-dominated mixedwoods) • Investigated nest predation in 25 riparian buffers of 20, 40, and 60 m and 20 m thinned, control strips (> 300 m) and 15 clearcuts subjected to different regeneration practices (planting with chemical and mechanical weeding and natural regeneration without vegetation control). • Riparian sites were along rivers 5–15 m wide with < 30 % slope, and an alder fringe 1–7 m wide. • Thinning removed 33% of trees (the largest). • Stands abutting riparian strips were clearcut. • Used artificial nests placed on ground and in trees (only ground used in clearcuts). • Lasted 4 field seasons. • 3-5 years post-harvest at start of study. 	<ul style="list-style-type: none"> • For riparian buffers, the risk of predation was lowest in 20 m intact strips, intermediate in 20 m thinned and control strips, and highest in 40 m and 60 m strips. • Nests in unmanaged clearcuts had 3–10 times lower probability of predation than those in control riparian strips. • There was no difference in predation between clearcut treatments, although nests experienced high predation the first year after weeding. • Predators in riparian strips included red squirrel (39% of predated eggs), small mammals (22%), birds (14%), woodchuck (14%), and weasel, raccoon, snowshoe hare, and porcupine (10% combined)—a greater variety of predators than other similar studies have found. 	<ul style="list-style-type: none"> • A major finding was the much lower rate of ground nest predation in naturally regenerated clearcuts than in control forest strips. The authors suggest the much higher density of squirrels in riparian strips contributed strongly to this result. • The authors caution that the comparison between clearcuts had limited statistical power due to low sample size. • The authors suggest that the 20 m and control strips were less attractive to predators than were the 40 and 60 m strips, explaining the higher predation in the intermediate width strips. • The authors conclude that “[w]e have no evidence that forest management alone can lead to an increase in nest predation”, but they note that forest management in combination with other activities may affect nest predation.

(Continued on next page.)

Table 5.1 Continued

Study and Location	Brief Description	Key Results	Summary/Conclusions
<p>Fenske-Crawford and Niemi (1997)</p> <p>Northern Minnesota</p>	<ul style="list-style-type: none"> • Study in boreal-hardwood transition (aspen mixedwoods) • Examined predation along edges and up to 100 m into interior in 5 medium-age and older forests abutting 2- to 4-year-old aspen (hard edges), and in 5 medium-age and older forest abutting 13-19-year-old aspen forest (soft edges). • Predation recorded by motion-sensitive cameras. • Used artificial ground nests. • Lasted 1 field season. 	<ul style="list-style-type: none"> • Predation was greatest at the edges of both hard and soft boundaries. • Predation was higher at soft edges than at hard edges. • Eight mammalian species of predators identified. 	<ul style="list-style-type: none"> • The authors hypothesize that increased predatory activity at edges is because of increased cover or because of their use as travel routes. • The authors suggest that the higher predation at soft edges may be related to the variety of predators which preyed on the nests.
<p>Cotterill and Hannon (1999)</p> <p>Central Alberta</p>	<ul style="list-style-type: none"> • Study in boreal mixedwood forest • Compared nest predation in 11 leave patches (ave. 40 ha) and in 11 control blocks • Proximal stands were subjected to first pass in a two-pass harvesting system. • Used artificial nests placed on the ground and in shrubs. • Examined predation 1 year and 5 years after logging. 	<ul style="list-style-type: none"> • Clearcutting did not significantly affect predation rates on ground or shrub nests. • There was no edge-related increase in nest predation. • Murids were most common predator of ground nests; although murids and red squirrels were important predators of shrub nests, the predator in many instances could not be determined. • Generalist predators commonly associated with agricultural areas were not detected. 	<ul style="list-style-type: none"> • The authors note that statistical power to detect differences among treatments was low. • “There appears to be no evidence for short-term negative edge effects in this forest at the current level of fragmentation.” (Approx. 14% of the study area was fragmented by clearcutting).

(Continued on next page.)

Table 5.1 Continued

Study and Location	Brief Description	Key Results	Summary/Conclusions
<p>Song and Hannon (1999)</p> <p>Central Alberta</p>	<ul style="list-style-type: none"> • Study in boreal mixedwood forest • Compared nest predation in aspen stands adjacent to a) white spruce stands, b) clearcuts; c) seismic lines and in the interior of aspen stands. • Used artificial nests – both shrub and ground. • Lasted 2 field seasons. • Clearcuts were 1-2 yrs post-harvest. 	<ul style="list-style-type: none"> • For ground nests, there was no effect of edge type on predation in either of the 2 years of the study. • For shrub nests, the results were variable. • Predation rate was higher on shrub nests than on ground nests. • There was no edge effect at aspen/clearcut edges. 	<ul style="list-style-type: none"> • Annual variation in patterns of predation was explained by patterns of red squirrel activity. • “Clearcuts and aspen forests next to clearcuts are unlikely to provide favourable habitat for nest predators.” • The authors conclude that it does not appear that anthropogenic activity causes an increased incidence of nest predation at forest edges relative to natural edges and the forest interior.
<p>Manolis et al. (2000)</p> <p>Northern Minnesota</p>	<ul style="list-style-type: none"> • Study in boreal hardwood transition forest • Conducted natural and artificial nest studies • Natural nest study. • Examined predation of nests in forest tracts relative to vegetation and habitat variables and distance to edge. • Proximal stands were clearcut. • Stands were 3-18 yrs old. • Lasted 3 field seasons. • Artificial nest study <ul style="list-style-type: none"> • As part of 3 different experiments, artificial nests were placed at the clearcut edges and a variety of distances into the forest ranging from 0-300 m. • Stands were 3-18 years old. • Lasted 2 field seasons. 	<ul style="list-style-type: none"> • In the natural nest study, mortality rates were greater at edges than in forest interior for ground nesting birds (most of which were ovenbirds); distance to edge was the best predictor of nest success in logistic regressions. • In the natural nest study, distance to clearcut edge was not a predictor of nest success for two most common arboreal nesters, but authors note low statistical power for this determination. • In the artificial nest study, predation rates were greater at edges than in the forest interior. 	<ul style="list-style-type: none"> • The authors supplemented the analysis of their experiments with an examination of previous studies of edge effects. They noted that many studies had low statistical power and concluded that edge effect is important for many studies in forested environments. (See text for more discussion.)

(Continued on next page.)

Table 5.1 Continued

Study and Location	Brief Description	Key Results	Summary/Conclusions
Tittler and Hannon (2000) Central Alberta	<ul style="list-style-type: none"> • Examined nest predation in cutblocks with three levels of residual retention, and in forest adjacent to cutblocks. • Used artificial nests. • Lasted 1 field season. • 3 years after logging. 	<ul style="list-style-type: none"> • The level of retention did not affect predation rate in the adjacent forests, nor did it affect within-cutblock predation rate. 	<ul style="list-style-type: none"> • The authors concluded that vegetation is not a good predictor of nest predation in this area. • The authors concur with earlier studies that cutblocks do not provide habitat that increased potential predator abundance, nor did they facilitate movement of predators along forest edges, nor does amount of residual retained influence predation.
Ibarzabal and Desrochers (2001) Southern Quebec	<ul style="list-style-type: none"> • Study in southern boreal forest • Examined predation of bait stations (similar to artificial nests) in forests placed 0, 30, 60, 90, and 120 m from open areas created by recent clearcuts and power lines. • Clearcut stands were < 5 yrs old; power lines had vegetation < 1 m. • Bait stations were placed on the ground and in trees. • Lasted 2 field seasons. 	<ul style="list-style-type: none"> • There was no relation between predation and distance to edge. • Predation rates were more than twice as high for ground stations than for tree stations. • Predators included red squirrels, murids, mustelids, and birds (although total number of instances [25] in which predators were identified was low). 	<ul style="list-style-type: none"> • Major finding is the lack of edge effect.

(Continued on next page.)

Table 5.1 Continued

Study and Location	Brief Description	Key Results	Summary/Conclusions
Boulet et al. (2003) Southern Quebec	<ul style="list-style-type: none"> • Study in southern boreal forest (black-spruce dominated mixedwoods) • Compared nest predation in five 60-m wide riparian strips and in five 60-m wide non-riparian strips to five control sites. • Proximal stands were clearcut. • Used artificial nests placed on the ground and in trees. • Lasted 2 field seasons. • 1-2 years after logging. • A concurrent nest predator survey was conducted. 	<ul style="list-style-type: none"> • Proportion of depredated nests did not differ among treatments or nest heights. • Most common predators were red squirrels and gray jays. 	<ul style="list-style-type: none"> • The authors do not believe that logging modified the community of nest predators, as has been found in forest-agricultural areas, or that short-term crowding increased nest predation.

5.7.2 *Connectivity and Landscape Configuration*

Another consequence of fragmentation that may affect birds is loss of connectivity, or the effect of impeding movement by breaking forested habitats apart. The concern is that habitats, or portions of forest, which have been “disconnected” by harvesting will be unavailable for use by species that are unable or disinclined to cross harvested areas. It may seem counterintuitive that connectivity would be a concern for songbirds, many of which migrate thousands of miles between their summer and winter grounds. However, as Desrochers and Hannon (1997) pointed out, most songbirds migrate at night and move through habitats in the day. Based on work done on common garden birds in the UK,¹³ Desrochers and Hannon (1997) speculated that woodland birds may be affected by predation during daytime movements outside the cover of forests.

Connectivity has been examined in three ways: 1) the propensity of birds to use corridors; 2) the willingness of birds to cross open areas; and 3) the differential representation of birds in connected and unconnected habitats. Studies of the first two types provide evidence of bird use of and preference for corridors. While it could be argued that studies of the third type provide direct evidence for effects of reduced connectivity due to fragmentation, it is difficult to determine, without direct observations of birds, whether the results suggest a configuration effect, in which colonization of fragments is difficult, or a habitat area loss effect, in which remaining patch sizes are too small to maintain sufficient population density.

Machtans, Villard, and Hannon (1996) found that one of the two riparian management areas they examined acted as movement corridors for dispersing juveniles in Alberta’s boreal mixedwood zone, but not the other. However, the two sites differed in their configurations, making interpretation difficult. In a follow-up study at the same sites, Robichaud, Villard, and Machtans (2002) found that riparian buffer strips acted as movement corridors for adult and juvenile birds; however, the effect decreased with time after harvest of the adjoining forest.

In the same area, Hannon and Schmiegelow (2002) followed up on an earlier experiment described by Schmiegelow, Machtans, and Hannon (1997). They found that the presence of corridors facilitated travel of some resident species to connected forest patches, but that the effect was not consistent. They concluded that “corridors had limited utility for most species, at least over the short term.” Both Hannon and Schmiegelow (2002) and Robichaud, Villard, and Machtans (2002) opined that the role of corridors in facilitating travel will decrease as the abutting harvested forest grows. Therefore, from these few studies, it seems corridors do play at least a small role in facilitating travel by some songbirds, but the role may be relatively short-lived. The duration and degree of usefulness likely depends on individual species’ propensity for crossing gaps.

St. Clair et al. (1998) compared the willingness of four resident species (black-capped chickadees, white-breasted nuthatch, hairy woodpecker and downy woodpecker) to travel in three habitats (continuous forest, corridors < 10 m wide, and gaps in forest cover of 25–200 m) in response to broadcast chickadee mobbing calls. They found that chickadees were as likely to use corridors as to travel in continuous forest, but the other species were not. The authors suggest that corridor width may have limited the birds’ willingness to use them. All four species avoided gaps, but chickadees and downy woodpeckers crossed gaps more frequently.

St. Clair et al. (1998) also examined the willingness of chickadees to cross gaps or take detours through forested areas that had various edge configurations. They found that the distance birds were willing to travel in the open increased as detours became less efficient, but that a threshold existed, as

¹³ e.g., Hegner 1985, Lima and Dill 1990, Todd and Cowie 1990, Suhonen 1993

birds were apparently not willing to travel across gaps >50 m when they had a choice of traveling through forest cover.

Desrochers and Hannon (1997) conducted a similar gap-crossing assessment of five woodlands species (black-capped chickadee, *Parus atricapillus*, red-breasted nuthatch, *Sitta canadensis*, golden-crowned kinglet, *Regulus satrapa*, Yellow Warbler, *Dendroica petechia*, and red-eyed vireo, *Vireo olivaceus*). They found that the species differed greatly in their propensity to cross gaps in response to playback calls; however, all species were more reluctant to cross open areas than to travel through woodland. They concluded that woodland corridors do facilitate movements, more for some species than others. They speculated that maintaining connections among forest fragments may facilitate songbird dispersal.

As part of their corridor study, Hannon and Schmiegelow (2002) compared the abundance of several species of birds in isolated patches, in connected patches, and in reference forests, and found generally lower abundance in isolated patches. They concluded that gaps in residual forest cover created by recent forest harvesting reduced the probability of some forest birds establishing nesting territories in isolated forest patches for up to five years post-harvest. Commenting on earlier efforts related to the same research initiative, Schmiegelow, Machtans, and Hannon (1997) noted that “although we observed significant negative effects of the experimental fragmentation...magnitudes were small given the extent of our manipulations.”

It seems, therefore, that some evidence exists that woodland birds use corridors, although the results of empirical studies are somewhat equivocal (Machtans, Villard, and Hannon 1996; Schmiegelow, Machtans, and Hannon 1997; Robichaud, Villard, and Machtans 2002; Hannon and Schmiegelow 2002). Note, however, that these studies took place in a single boreal region in central Alberta. Comparable studies from other Canadian forested areas are lacking, and therefore broader conclusions must be tentative.

Also, there is evidence that some species of birds are reluctant to cross forest gaps caused by harvesting, thus reducing the likelihood that they will inhabit isolated habitat that is otherwise suitable (Desrochers and Hannon 1997; St. Clair et al 1998). On the other hand, any isolation effects that may exist in managed forest mosaics are temporary and differ by bird species and site-specific considerations. Connectivity is a species-centric quality; a landscape that one species perceives as connected may not be so to another. The results of the gap crossing experiments discussed above support this point. Bunnell (1999b) pointed out that evidence of use of corridors in forested environments does not necessarily suffice to support arguments of their importance. With (1999) noted that the debate may not be resolved because utility depends on the organism being considered. Bunnell (1999b) reviewed publications providing empirical information on the use of corridors by mammals and birds, and concluded “...while evidence for movement within corridors is accumulating for agricultural and urban landscapes, extrapolating findings and conclusions to managed forests is questionable (Small and Hunter 1988; Lindenmayer 1994). We lack evidence of the efficacy of corridors in managed forests.”

While there is relatively little evidence that lack of connectivity is a threat in managed forest landscapes (Bunnell 1999b) and empirical evidence of the utility of corridors by forest birds is equivocal, there is nonetheless evidence that some forest birds are inhibited from crossing gaps. Most authors advocate the maintenance of connectivity at least as a precautionary approach (Noss and Harris 1986; Hunter 1996; With 1999). However, a significant question for managers of managed forest landscapes is whether static corridors are required to maintain connectivity or whether high levels of connectivity can be maintained in these shifting mosaics without corridors.

6.0 SYNTHESIS/CONCLUSIONS

In its most uncomplicated sense, fragmentation refers to changes in landscape configuration. Although studies have examined ecological effects associated with landscape configuration changes in the boreal forest, these studies have tended to focus on birds. For many terrestrial species, documented effects of concern extend well into topics represented in the outer bands of Figure 2.1. Whether the term fragmentation is used to mean only landscape configuration effects or if its use includes other effects associated with anthropogenic perturbations seems to depend on the landscape context under consideration and the mental models of the researchers/authors. Several authors have issued calls for rigour in the use of term, and we echo that sentiment in this document. However, there has been, and continues to be, so much work reported under the catch-all of fragmentation, that it seems unrealistic to suppose that precision will be brought to the use of the term in the near future. Ideally, researchers will define their conception of fragmentation in their reports, and more importantly, those who use and cite the results of studies will do so with the authors' definition as context.

How one defines fragmentation influences one's perspective on the nature and extent of its effects. The broader the definition used, the greater the likelihood that effects will be identified. As noted by several authors whose works are reviewed here (Fahrig 1997; Bunnell 1999a, 1999b; Villard, Trzcinski, and Merriam 1999; Lindenmeyer and Fischer 2006), clarity in the use of terms and care in communication would help in identifying specific areas where conservation and research attention would best be directed. In many cases, concerns about fragmentation expressed in the literature or popular press would be more accurately presented as concern about habitat area loss or loss of old forest area.

Amount of habitat area loss is the effect most frequently aggregated or confused with fragmentation. When a forest is fragmented, habitat area for some species may be lost and converted to other habitat types, while at the same time the spatial arrangement is changed. Investigations that have attempted to differentiate between the effects of habitat area loss and changes in landscape configuration have generally found habitat area loss to have the more deleterious effect on wildlife. However, the potential for landscape configuration to affect species should not be discounted for several reasons: 1) almost all studies addressing the effects of habitat area loss vs. configuration have been on songbirds; 2) most studies have excluded rare species from their analyses; and 3) important aspects of experimental design, such as study duration and consideration of species assemblages, are often not taken into account.

In this document we identify some of the key issues influencing the nature and severity of fragmentation effects in the boreal forest. Among the more important notions is that fragmentation is a species-specific phenomenon. An area perceived by a songbird to be fragmented would likely not be so to a large terrestrial carnivore that uses the forest at a much different scale or even to other bird species with different habitat associations. To make sense of fragmentation effects, one needs to consider the scale at which species use their environments relative to the scale at which natural disturbance, forest management, and other disturbance agents affect the landscape, the temporal duration of habitat alterations, and other factors. Forest stands are the traditional unit of manipulation and consideration of the stand scale permits understanding of potential effects on species with relatively small home ranges. The recent focus on emulation of natural disturbances at landscape scales allows managers to consider potential effects on sensitive species that range over large areas. The broad effects of landscape change on species that use small areas of habitat are likely easier to study and predict than are those of species that use larger areas.

Another key aspect in considering fragmentation effects in the boreal forest is the quality of the matrix. The conceptual roots of fragmentation theory (the theory of island biogeography) considered the matrix to be permanent and unusable. In the boreal forest, the matrix is transitory. Harvested areas regrow and, in a span covering years to decades, good quality habitat for many species returns, or at least the area becomes much more hospitable. In addition, the matrix created by forest management is not completely unusable to all species. The “hostile sea” that characterizes the quality of the matrix in the conception of island biogeography is not an accurate portrayal of the boreal forest matrix for many species. Some species can continue to use the matrix to fulfill at least portions of habitat requirements, and many others can travel through the matrix. While the hostile sea analogy may hold for some species (e.g., salamanders), it does not apply to many others. Because the boreal forest is a patchy, disturbance-driven ecosystem, several authors have hypothesized that many of its wildlife species are adapted to fragmentation dynamics (DeMaynadier and Hunter 1998; Cotterill and Hannon 1999; Brotons, Mönkkönen, and Martin 2003; and others).

A key factor influencing the size of the footprint of forest management activity in the boreal forest is the development of access roads. Roads bisect the forest in linear patterns, rather than in the amorphous, block-like patterns associated with fragmentation caused by forest harvesting. The effects of roads are frequently considered to be fragmentation effects. Roads are not only more linear than other disturbances, they are usually much less transitory. This gives rise to a model of fragmentation in the boreal forest somewhat different from a typical fragmentation scenario. Rather than a fragmented mosaic as a conceptual model, it is more appropriate to consider a model of dynamic disturbance (harvest blocks) with less transitory elements of linear fragmentation (roads).

There have been more studies of fragmentation effects on songbirds than on other taxa, not just in the boreal forest, but in virtually every terrestrial ecosystem. Birds offer a range of benefits as study systems: they are easier and more economical to study; they can be detected by their songs and don't require the use of expensive radio-telemetry for many applications; they respond readily to changes in forest structure; and they are relatively plentiful, which facilitates the use of statistical techniques. Many studies of fragmentation effects on songbirds are set in landscapes in which agricultural uses are interspersed with woodlots. There, the matrix is more or less permanent and likely to be more hostile to forest birds than is the case in the boreal forest, and therefore those studies are not overly useful when considering fragmentation effects in the boreal forest. Studies from the boreal forest are relatively inconclusive. This is likely because of species-specific sensitivities and the local ecological context (e.g., the predator community and the community of inter-specific competitors within guilds). We hypothesize that the amount of suitable habitat remaining and the nature of the local predator community are key considerations in determining the nature and extent of edge effects on songbirds.

Table 6.1 summarizes this document's findings on the effects of fragmentation on taxa other than birds.

Table 6.1 Effects of Boreal Forest Fragmentation on Taxa Identified in This Review

Taxa	Configuration Effects	Other Effects	Notes
Bats	<ul style="list-style-type: none"> • Not studied. 	<ul style="list-style-type: none"> • Edge habitats are preferred for foraging by some species. 	<ul style="list-style-type: none"> • Little work is available from the boreal.
Small Mammals	<ul style="list-style-type: none"> • There is some evidence of effects on Siberian flying squirrels. • Possible effects on northern flying squirrels. • No evidence of effects for strictly terrestrial small mammals. 	<ul style="list-style-type: none"> • Evidence of inhibitory effect of forest roads on some species in some ecosystems; but this is unlikely to result in population/genetic level effects. • Habitat area loss studies show effects of harvesting for some species. 	<ul style="list-style-type: none"> • Little work is available from the boreal.
Herptiles	<ul style="list-style-type: none"> • Metapopulation dynamics may be affected by landscape configuration for some species. 	<ul style="list-style-type: none"> • Roads act as a barrier for some species. • Edge effects of roads are comparable to that of harvested areas. • Road kill is an important factor for turtles in other landscapes but the effect in boreal forests is not clear. 	<ul style="list-style-type: none"> • The scale of habitat use for herptiles is different than for most other vertebrates • Little work is available from the boreal forest.
Meso-Carnivores	<ul style="list-style-type: none"> • Effects appear to vary, with generalist species responding positively, while habitat specialists respond negatively. • Isolation of patches interacts with patch size to influence spatial distribution of forest-interior species on managed landscapes. • Marten have been well studied, and appear to prefer unfragmented landscapes over fragmented ones. 		<ul style="list-style-type: none"> • For some species, habitat requirements encompass a range of characteristics, among which fragmentation is an important factor. • However the precise role of configuration independent from other factors (forest age, composition, coarse woody debris) is uncertain.
Large Ungulates	<ul style="list-style-type: none"> • Effects vary by species; those which can take advantage of increased forage opportunities tend to increase; those which may be outcompeted or suffer alternative effects (e.g., increased mortality from increased predators) may decrease. • Significant work has focused on woodland caribou. Range constriction and population declines are evident but the relative contribution of increase in competitors, increase in predators, sensitivity to road traffic and hunting are difficult to determine. 		<ul style="list-style-type: none"> • Various effects likely act together to effect range and populations of caribou.
Large Carnivores	<ul style="list-style-type: none"> • The broad scale of landscape use by large predators suggests that configuration may not be a factor affecting large carnivores. 	<ul style="list-style-type: none"> • There is evidence of road effects from non-boreal ecosystems on bears (hunting/poaching) and wolves (facilitation of travel, thresholds densities). 	<ul style="list-style-type: none"> • Very little work is available from the boreal.

7.0 RESEARCH NEEDS

From the above discussions, it is evident that much remains to be done to identify whether fragmentation effects are important factors in the ecology of boreal vertebrates. Some broad information needs are identified below.

Differentiating between landscape configuration and other effects

Several authors have noted the importance of work that differentiates between the effects of changes in landscape configuration and changes in other aspects of the forest (e.g., Fahrig 1999; Villard, Trzcinski, and Merriam 1999). Such work is important so that conservation efforts can be accurately targeted. If change in habitat area is a primary agent of negative change, then focusing on limiting changes in landscape configuration will not be a productive use of conservation effort. As Table 3.1 shows, although work of this sort has been conducted for songbirds, little work on other taxa has been undertaken.

Studies integrating transitory and permanent aspects of fragmentation

Harvesting has a transitory effect on the forest. Several studies that focus on fragmentation effects related to harvesting have noted that effects are either short-term or diffuse. Roads are more permanent features on boreal landscapes and effects may be longer-term. These two aspects of fragmentation need to be integrated in considering how forest management affects boreal wildlife.

Studies translating changes in values of metrics to effects on species

There are a host of metrics used to portray landscape configuration and many studies assess the effects of fragmentation based on changes in values of such metrics. Changes in metrics are often used as proxies for changes in values of real ecological interest, but studies examining the relationship between the two (i.e., landscape metrics and population effects) are not common. To some extent this is understandable, as it is often simpler to produce computer-based assessments rather than assessments based on field studies. Although metric-based studies are informative, exploration of the relationship between the metrics and wildlife species would greatly add to their utility. It would both provide a basis for comparing results between locations and help identify the most useful of the gamut of metrics available.

Additional research attention to neglected species

Although it may seem cliché to call for more species-specific research, we found a surprising lack of studies on many taxa. Marten and caribou have been the focus of considerable research, and there is much work on songbirds. However, several taxa (predators, herptiles, bats, small mammals) are under-represented in the body of research. While work from other forest types provides some basis for extrapolation, findings of effects in other forest types has not resulted in comparable levels of effort in boreal forests.

In addition, we note that for songbirds, many of the studies reviewed here did not include rare species in their analyses because insufficient observations of these species were available to use as a basis for statistical analyses. In some cases, rare species are clearly associated with non-forest habitat, but many are true forest species. Several authors have noted that rare species may be sensitive to changes in habitat, which may be one of the reasons for their rarity (Noon, Bingham, and Noon 1979; Rotenberry et al. 1995; Hagan and Meehan 2002). Exclusion of these species from conclusions regarding fragmentation effects may give inaccurate broader perceptions. NCASI (2004) cites several ways to investigate the response of rare species:

1. Undertake specific field assessments on rare species. These are likely to be difficult and expensive because of the species' rarity.
2. Undertake meta-analyses using data from studies which have been unable to analyze rare species themselves because of their paucity of data.
3. Simulate the response of rare species based on their habitat affiliations or guild associations.

Productivity-based assessments

Many of the studies we reviewed based their assessments on surveys or counts of animals. Several authors, most notably Van Horne (1983) and Thompson (2004), have warned that density can be a misleading indicator of habitat quality. Although many authors of assessments based on abundance warn of the shortcomings of basing conclusions on studies of this type, abundance-based assessments remain more common than those based on productivity.

Population-level assessments

This research need relates to a requirement for greater refinement in the studies undertaken. It may be that some effects exist, but are trivial in the greater scheme of forest-level populations, communities, and ecosystems. For example, although some small mammals may be reluctant to cross forest roads, additional studies are needed to determine if such inhibitions are so severe as to precipitate population effects. Similarly, it may be that forest birds are reluctant to venture into openings created by forest management, but are the overall effects important relative to local- or forest-level populations?

Long-term studies

In this report we have noted that harvested areas regenerate, and therefore fragmentation effects may be transitory. The patchy and disturbance-driven nature of the boreal forest has led to the hypothesis that boreal species are adapted to fragmentation. Unfortunately, most studies have taken place over relatively short time periods (1-5 years). Studies of this duration are confounded by external influences (e.g., severe weather events), temporal complications such as the initial increase then decrease in bird abundance following forest harvesting identified by Hagan, Vander Haegen, and McKinley (1996), and random events. Short-term studies cannot detect subtle, yet potentially important, responses of wildlife to habitat changes, nor can they detect the amelioration (or exacerbation) of effects over time as the forest changes.

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