Implications for Forest Management of Bird-Vegetation Relationships in the Mixedwood Boreal Forest of Northeastern British Columbia

by

Kelly A. Squires

M.Sc. (Conservation Biology), University of British Columbia, 2003
B.Sc. (Hons.), Memorial University of Newfoundland, 1997

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Name:	**Kelly A. Squires**
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Examining Committee:

Chair: Murray Rutherford, Professor

Ken Lertzman
Senior Supervisor
Professor

David Green
Supervisor
Associate Professor
Department of Biological Sciences

David Huggard
Supervisor
Independent Researcher

Anne Salomon
Internal Examiner
Assistant Professor

Fiona Schmiegelow
External Examiner
Professor
Department of Renewable Resources, University of Alberta

Date Defended/Approved: April 10th, 2013

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Abstract

Species-habitat models have been used to quantify habitat quality and predict species distributions, with the goal to guide forest managers in setting harvest limits and designing silvicultural practices. However, considerable uncertainties exist regarding this ‘fine filter’ approach to forest management. In this thesis, I examine uncertainties concerning how management targets can be reliably derived from species-habitat models, appropriate measurement scales, and the financial costs of generating reliable habitat models. I address these uncertainties within the context of bird conservation in the mixedwood boreal forest, but several of my findings have general implications for the use of species-habitat models to inform forest management. The first concerns a major paradigm in conservation biology – the idea that non-linearity in species-habitat models reflect ‘threshold’ declines of species to habitat loss, thereby allowing targeted amounts of habitat protection to be set above thresholds. In Chapter 1, I reviewed 37 empirical studies attempting to quantify thresholds in habitat loss. I find that so far non-linearity in species-habitat models have not identified habitat amounts needed for species persistence. However, these relationships can still be used to set management targets, as they likely show changes in habitat quality. As an example, in Chapter 2, I related the densities of bird species to the gradient in forest composition. I used non-linearity in the relationship to delineate ‘good’ quality habitat for generalist species as stands comprised of more than 30% deciduous trees, representing a target for regeneration practices following clear-cutting of old mixedwood stands. The third chapter of this thesis addresses uncertainties concerning scale. Specifically, I show that good quality habitat for a keystone woodpecker species, the yellow-bellied sapsucker, can be measured at the stand scale by measurements made at fine scales - the characteristics of aspen trees chosen for nesting. Finally, I address cost uncertainties by showing that reliable habitat models can be generated using a less expensive roadside survey, but only for bird species that are coniferous or deciduous tree specialists. Generalist species will require surveys for birds and habitat in the forest interior, which is more time consuming and thus expensive but yields more reliable models.

Keywords: habitat thresholds; mixedwood boreal forest; bird-habitat relationships; nest site selection; monitoring costs

Dedication

I dedicate this work to all those who seek truth,

and to all those who teach it.

Wisdom tells me I am nothing.

Love tells me I am everything.

Between the two my life flows.

~ Nisargadatta Maharaj

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1. General Introduction

Several management strategies have been proposed to help minimize the effects of logging on forest biodiversity. Strategies that focus on reserving forests at multiple scales, and retaining important habitat features within logged forests are referred to as 'coarse filter' and 'medium filter' strategies, respectively (Lindenmayer et al. 2006; Schulte et al. 2006). These approaches typically focus on strategies to sustain habitat across space and time (e.g. Lindenmayer et al. 2006). But in order to devise strategies to sustain habitat, it is necessary to study species to determine what habitat is, and to delineate good from marginal habitat. Since the strategies are ultimately intended to conserve species, then species must be monitored in order to assess whether strategies are effective (Villard and Jonsson 2009).

Ecologists have more often identified animal habitat by measuring how species relate to their environment - most often to vegetation - rather than by measuring environmental resources and limitations directly (Johnson 2007). Though 'habitat' represents dynamic, multidimensional forms of matter and energy, the use of vegetation as a simplifying surrogate for habitat has generally resulted in models with reasonable explanatory and predictive power because many species are tightly related to vegetation (Scott et al. 2002; Morrison et al. 2006). Species-vegetation models have been particularly useful in forest management because logging causes large and measureable changes to vegetation.

Four pivotal considerations inform species-focused strategies for forest biodiversity conservation. The first concerns the choices of species on which to focus efforts (e.g. Hannon and McCallum 2004; Rempel et al. 2007). The second concerns which responses of species to their environment can be used to measure habitat quality (Scott et al. 2002; Johnson 2007). The third consideration is the 'now what?' question – once species-habitat relationships have been quantified, how should these best be used to guide management? (e.g. Villard and Jonsson 2009). Each of these three considerations has received voluminous attention in the literature - the first under the guise of the ‘focal species’ problem, the second in studies of habitat quality, and the third is the practical extension of what I refer to as the ‘habitat thresholds’ paradigm. The fourth consideration – cost - has received considerably less attention in the literature. However, the costs involved in generating reliable predictions of species relationships to habitat are often of utmost importance in the real world. These four considerations form central themes of the four chapters of this thesis.

In the first chapter, I critically review empirical tests of the ‘habitat thresholds’ paradigm. This paradigm has received considerable attention in the literature because the goal of the paradigm promises an answer to a plaguing question – how much habitat is enough to sustain species? Theoretical modeling suggests that species respond non-linearly to habitat loss, such that there is a ‘threshold’ habitat amount below which extinction is inevitable (Andrén 1994; Fahrig 2001). Quantification of thresholds in response to habitat loss may be useful to set management targets, such as the amount of forest to be retained from harvesting (Huggett 2005). A precautionary target for the amount of habitat can be set at some point above the threshold. I refer to this approach to species conservation as the ‘habitat thresholds’ paradigm. In Chapter 1, I distil three arguments for why the approach may be more useful to identify ‘good’ habitat, rather than how much habitat is needed. I provide a framework for delineating ‘good’ habitat from which to base quantitative goals for management practices.

The remaining three chapters concern management for bird conservation across logged landscapes of the mixedwood boreal forest. Extending from Manitoba to northeastern British Columbia, the mixedwood boreal forest is characterized by forest stands that are a ‘mix’ of coniferous and deciduous trees (Chen and Popadiouk 2002). In western North America, logging practices typically result in the replacement of mixedwood stands with either coniferous or deciduous stands that are less “mixed” than those they replace (Kabzems et al. 2007; Lieffers et al. 2008). Replacement occurs through planting to coniferous species like white spruce, or through natural regeneration to deciduous species like aspen and poplar.

Mixed forest compositions are likely a major evolutionary force shaping biodiversity in the boreal mixedwood forest. Some researchers have suggested that mixedwood stands are a distinct habitat type, and have identified bird species that prefer mixedwood stands over stands comprised primarily of either coniferous or deciduous trees (Hobson and Bayne 2000; Girard et al. 2004; Hagar 2007). The loss of mixedwood stands due to logging and other industrial activities may be negatively impacting bird species that prefer stands with a mixed species composition (Drapeau et al. 2000; Hobson and Bayne 2000).

In mixedwood forests, knowledge of an appropriate ratio of conifer to deciduous species at stand and landscape scales could guide reserve design, and logging and regeneration practices (Gauthier et al. 1996; Hobson and Bayne 2000). In Chapter 2, I relate the density of commonly-detected birds in old stands to the gradient in forest composition (0-100% deciduous trees). I test the hypothesis that bird species that are generalist with respect to tree species occur at higher densities in mixedwood stands, because stands containing both deciduous and coniferous trees are expected to have a wider range of resources. By applying the framework I developed in Chapter 1, I delineate ‘good’ habitat for generalist species as a quantitative guideline for ratios of coniferous and deciduous trees expected to support highest bird densities.

Chapter 3 continues with the theme of using species-habitat modeling to guide management, but three additional themes are addressed – single-species management, scale, and species responses. The focal species approach of Chapter 2 shifts from a suite of species, down to a ‘keystone’ species – the yellow-bellied sapsucker. Sapsuckers have been identified as ‘double’ keystone species because they provide both habitat and food resources used by a host of other species (Daily et al. 1993). Abandoned cavities excavated in trembling aspen trees by yellow-bellied sapsuckers provide the majority of roost sites of big brown bats (Kalcounis and Brigham 1998) and nesting sites of northern and southern flying squirrels (Holloway and Malcolm 2007). The sapwells it excavates are used for food particularly by red squirrels, rufous hummingbirds, and bees (Sutherland et al. 1982; Daily et al. 1993; Walters et al. 2002; personal observation). In Chapter 3, I address the theme of scale by measuring nest site selection of yellow-bellied sapsuckers. I applied the framework of Chapter 1 to delineate ‘good’ nest sites, and then determined whether the distribution of ‘good’ nest sites can be used to infer the distribution pattern of yellow-bellied sapsuckers at broader scales.

The third and main theme of Chapter 3 concerns the problem of using measures of species distribution to quantify habitat quality. Use-availability studies and measures of site fidelity have been used to infer habitat quality (Johnson 2007); however, these analyses alone do not provide complete measures of quality without also being related to fitness (Arlt and Pärt 2007). But populations at times may experience lower fitness for reasons unrelated to vegetation preferences, such as when predators acquire abilities to access nests (Martin 1993). Conversely, selection for vegetation may be adaptive at broad evolutionary scales, such that all individuals of a population make similar choices to meet basic requirements for survival and reproduction. In both cases, measures of reproduction would not reveal the vegetation structures that comprise habitat. To determine whether reproduction is a useful measure of habitat quality, I related nest productivity of yellow-bellied sapsuckers to vegetation structures selected for nesting from those available.

The final problem I address concerns the costs involved in quantifying habitat relationships. Management strategies based on measures of habitat quality will only be effectively derived from reliable species-habitat models. Reliability usually comes with a cost. Cost considerations of habitat modeling have rarely been evaluated in the peer-reviewed literature. In Chapter 4, I evaluate whether bird-habitat models can be reliably generated from a less expensive roadside survey using remotely-sensed habitat data. I use Cost Effectiveness Analysis to determine the incremental cost of improving roadside models using data collected from a more expensive and intensive survey of both birds and habitat in the forest interior.

2. Chapter 1

Demise of a Paradigm? Why 'Habitat Thresholds' Don't Tell Us How Much Habitat is Enough.

2.1. Abstract

'How much habitat is enough?' has been referred to as the most important question for conservation biology. One branch of research addressing this problem is rooted in the idea that quantitative goals for how much area to protect can be identified from 'thresholds' in species-habitat models - so-called 'habitat thresholds'. To provide a broad overview and critique of habitat threshold studies, I reviewed 45 empirical studies and conclude that thresholds identified from species-habitat models have not provided reliable estimates of how much land to protect. The majority of authors testing for extinction thresholds used patch-scale models of species presence-absence in relation to the amount of forest cover. Sample size equals "one" for inferences of landscape-scale processes derived from a patch-scale study; inferences are especially weak from studies of vagile species like birds, which comprised more than half (60%) of the reviewed studies. Only three studies tested alternative hypotheses explaining species responses to forest cover – two of these studies found unimodal responses of birds to forest cover, suggesting that the least amount of 'habitat loss' can occur in moderately forested areas. These results reveal that most authors may have erroneously assumed that forest cover is monotonically related to habitat loss, and that insufficient testing for alternative hypotheses has precluded strong inferences of habitat loss effects on species. In addition, authors of 51% of the studies visually identified 'thresholds' from linear models, revealing inconsistency in the interpretation of a threshold response. I conclude that the habitat thresholds paradigm has resulted in confused efforts to define management goals using the responses of species to vegetation. I suggest that researchers limit inferences and management guidelines to the scale at which species were observed. I propose a shift away from focusing on non-linearity in species responses to define ‘thresholds’, toward using the theoretical and statistical framework available from the field of Change Point Analysis. Finally, I briefly discuss roles for policy and economics to answer the question ‘how much habitat is enough?’

2.2. Introduction

The question of how much land to protect from human disturbances has been a central preoccupation of the conservation disciplines (Tear et al. 2005; Wilhere 2008). ‘How much is enough?’ has been referred to as the most important question for conservation biology (Fahrig 2003). The question often arises from the need for quantitative targets to bound development within sustainable limits, because without them developers more often win arguments for higher levels of industrial or other developments (Therivel and Ross 2007). One branch of research addressing this problem is rooted in the idea that quantitative goals for how much space to protect can be identified from ‘thresholds’ in species-habitat models - so-called ‘habitat thresholds’ (Swift and Hannon 2010). Research directed to this end has grown rapidly because it has been widely assumed that thresholds can be used to define the minimum amount of habitat required to ensure long term species persistence (reviewed in Hugget 2005; Ficetola and Denoël 2009). The end goal of the habitat thresholds paradigm is the use of empirically-derived thresholds to derive ‘management targets’ for policy makers and managers tasked with land protection and restoration. To provide a broad overview and critique of habitat threshold studies, I reviewed 45 empirical studies (Table 2.1). I argue that ‘thresholds’ identified from species-habitat models cannot be used to provide quantitative conservation goals for how much space to protect, and that the paradigm has resulted in confused efforts to use the responses of species to vegetation to define management targets. Instead of ‘how much?’ to protect, I argue that such relationships be refocused to define quantitatively ‘what?’ to protect. Finally, I briefly review the role of ecology in setting conservation targets.

2.3. Overview

The habitat thresholds paradigm proposes that species respond non-linearly to habitat loss such that there is an amount of habitat – the ‘extinction threshold’ – below which species are unable to persist in disturbed landscapes (Lande 1987; Fahrig 2001). Based primarily on Island Biogeography Theory, the configuration of remaining habitat – the number, size, and distance between habitat patches – has been proposed as the main cause of extinction thresholds (Swift and Hannon 2010). Independent of habitat loss, habitat configuration is thought to have an additional negative effect on the probability that species will persist once the amount of habitat has declined to below extinction thresholds. For example, as habitat is lost from landscapes, the distance between remaining habitat ‘patches’ usually increases non-linearly (Andrén 1994). It is hypothesized that the persistence of species with limited movement abilities begins to decline at a threshold amount of habitat below which habitat patches may be too isolated for successful colonization (With and Crist 1995; With and King 1999; Fahrig 2003; Swift and Hannon 2010).

The main empirical test for the existence of extinction thresholds is evidence of a non-linear relationship between species abundance and occupancy rates of habitat patches, and habitat amount decreasing through time or across landscapes. The amount of habitat at which the rate of decline in species abundance and occupancy rates begins to accelerate is thought to be the ‘pre-extinction threshold - close to but not at the extinction threshold, and is referred to more generally as a ‘habitat threshold’ (Radford et al. 2005; Betts et al. 2007; Zuckerberg and Porter 2010; citations for these and all other habitat threshold studies are listed in Appendix A). The attractive practical extension of such non-linearity in the relationship between species abundance and habitat loss is the concept of ‘targets’ – amounts of habitat larger than the threshold amount assumed to be required by species to maintain viable populations, which can be equated to the amount of land needed for species protection. That is, the ultimate goal of the habitat thresholds paradigm is to provide an answer to the question - how much habitat is enough?

2.4. Methods

I compiled literature from two major reviews of habitat threshold studies (Ficetola and Denoël 2009; Swift and Hannon 2010), and from cross-referencing online searches in the ISI Web of Science using the terms 'extinction thresholds', 'ecological thresholds', and 'habitat thresholds' to find more recently published studies. I limited studies to those relating species responses to habitat using empirical data to test for a 'fragmentation threshold' or 'extinction threshold', which I hereafter refer to as population threshold studies. In most studies, this objective was explicitly stated; in some studies it was implied by discussion of thresholds in reference to key literature (e.g. Andrén 1994, With and Crist 1995; With and King 1999; Fahrig 2003). I included a second type of habitat thresholds study, in which an objective was to test for thresholds in habitat use along vegetation gradients to derive management guidelines, but without reference to fragmentation and extinction thresholds and the key literature of the paradigm. I refer to these as studies of thresholds in habitat use.

From this process I compiled 45 empirical studies - 40 mensurative studies from real areas, and five experimental studies of insect responses to small fabricated 'landscapes' (< 16 x 16 m, 0.08 ha, Table 2.1). Thirteen studies were sourced from online searches, one from cross-referencing, and 31 from the two reviews. Eleven studies from the two review papers were excluded because the objectives did not include tests for thresholds, or because the study used empirical data to parameterize a model but did not otherwise empirically test for thresholds.

A landscape-scale study in which multiple landscapes were sampled is the appropriate study design for deriving inferences of population-level processes such as the effects of fragmentation on species, including tests for extinction thresholds (Fahrig 2003). Thus, I determined the scale at which population threshold studies were conducted. I defined a patch scale study as one in which the response variable was measured within one point or habitat patch, and related to responses from other points or patches varying in amount of surrounding habitat. I considered landscape scale studies to be those in which the response variable was measured across several well-distributed sites that sampled multiple habitat patches within each landscape (Fahrig 2003). I further distinguished quasi-landscape scale studies as those in which the response variable was measured from just two or three sites within each landscape. If the number of independent landscapes was not provided, I estimated the number of landscapes sampled in each study from the size of study areas, by arbitrarily defining a landscape as 50^2 km for birds and mammals, as 20^2 km for herptiles, and as 5^2 km for insects and plants. For study areas that were very large relative to the home ranges of the study species (e.g. > 200^2 km for birds), I reported the number of sampled landscapes as ‘multiple’.

2.5. Summary of Studies

Most studies tested for fragmentation or extinction thresholds (37 of 45); eight tested for thresholds in habitat use (Table 2.1; Appendix A). Half of all studies (51%) were published in just three journals - Biological Conservation (12 of 45), Forest Ecology and Management (6 of 45), and Ecological Applications (5 of 45). Only one study related species response to habitat change over time (Becker et al. 2011); in all other studies, species responses to spatial variability in habitat was assumed to equate with responses over time. The majority (60%, 27 of 45) of studies were of birds only (Table 2.1).

2.6. Why Habitat thresholds Don’t Tell Us How Much Habitat is Enough

2.6.1. Problem 1: Mismatch between scales of measurement and inference

Sample size was generally very low for deriving inferences of population-scale processes, like the existence of extinction or pre-extinction thresholds for population threshold studies in real landscapes (Table 2.1). Only one quarter of studies (8 of 32) were conducted in multiple landscapes; all other studies were conducted in an average of 2.5 landscapes (range 1 – 6 landscapes). About half (53%, 17 of 32 studies) of population threshold studies in real landscapes were patch-occupancy studies – the presence-absence of species was related to habitat at the patch scale voiding the ability to make landscape-scale inferences. The goal of the habitat thresholds paradigm is to make inferences about the effects of habitat loss on population persistence; in a patch-scale study, the sample size for making such inferences is one (McGarigal and Cushman 2002; Fahrig 2003). Though habitat was measured over relatively large areas in some population thresholds studies conducted at the patch-scale (maximum 7850 ha, Table 2.2), these studies cannot make reliable inferences of population-level processes because the number of sampled landscapes was very low. In total, only three studies were conducted both at the landscape scale and across multiple landscapes – the scale appropriate for making reliable inferences of extinction or pre-extinction thresholds (Table 2.1). A mismatch between the scale of measurement and inferences drawn from most population thresholds studies is a mirror of the same problem in the much larger parent body of fragmentation studies (McGarigal and Cushman 2002). Major reviews of fragmentation effects point out that most studies tested the effects on individuals not on populations, but most authors interpreted the results at the population scale (Andrén 1994; Fahrig 2003).

2.6.2. Problem 2: Overly-Simplistic Measures of 'Habitat'

Habitat amount was quantified as the amount of forest cover in 78% of population threshold studies (25 of 32 studies, Table 2.1). Cushman and McGarigal (2003) presented a hypothesis that calls into question the use of amount of forest cover to measure habitat amount. They predicted highest abundance of resources for forest species in landscapes with intermediate levels of forest disturbance, because the edges and openings created by fragmentation create habitat resources. Thus, the least amount of 'habitat loss' for forest dependent species may occur in areas of intermediate forest cover. Three studies showed graphically that the amount of forest fragmentation and thus the amount of edge habitat was highest at about 40%-50% forest cover (Villard et al. 1999; Imbeau and Desrochers 2002; Cushman and McGarigal 2003). Especially for shrub-foraging species, which includes many forest songbirds, increased shrub abundance at forest edges (four out of six studies reviewed in Harper et al. 2005), may provide access to abundant food, resulting in habitat gains at intermediate levels of forest cover.

Only four studies tested for a unimodal relationship of species to forest cover (Cushman and McGargial 2003; Schmidt and Roland 2006; Summerville and Crist; Becker et al. 2011, Table 2.1). Some researchers did in fact find unimodal responses of species to forest cover, but did not acknowledge that the shape of the response indicated a non-monotonic relationship between habitat loss and forest cover (e.g. Radford et al. 2005; Betts et al. 2007; Betts et al. 2010).

All but three of 37 population threshold studies were conducted within a 'patch-matrix' design based on Island Biogeography Theory. In contrast to Austin's (2007) suggestion that many species-habitat models have been created in the absence of explicit ecological theory, studies testing for extinction thresholds are firmly rooted in Island Biogeography Theory. Despite a considerable lack of evidence supporting the application of this theory to terrestrial ecosystems involving habitat islands rather than true islands (Bunnell 1999; Haila 2002; Fahrig 2003), alternative explanations to the assumptions of the theory were rarely tested. Of these 34 studies, only six studies tested whether mechanisms other than 'patch' isolation and size resulted in non-linearity in the relation between species abundance and habitat amount (Table 2.1). Confounding of habitat quality with quantity was the only mechanism tested by these studies. For instance, none of the studies determined whether clumped distributions of individuals were caused by conspecific attraction, rather than patch isolation effects. The data presented in Radford and Bennett (2004) and Jansson and Angelstam (1999) suggest that occupied habitat 'patches' were clumped together across the landscape. Conspecific attraction or patchy distribution of food resources would be viable alternative hypotheses to explain the finding in both papers that occupancy declined with increasing inter-patch distance. Interestingly, both studies were of cooperatively-breeding species. Neither study addressed these alternatives, either of which would render null their conclusion that the population was likely limited by dispersal ability.

Equating habitat with forest cover amount has likely resulted in a failure to accurately measure habitat amount in most studies testing for habitat thresholds. The overly-simplistic binary classification of landscapes into habitat islands and non-habitat has focused attention away from tests for alternative explanations for thresholds. Both issues preclude effective management applications. For example, a threshold in the relation between species abundance and habitat 'patch' size may be found, not because the species is restricted to patches and responsive to patch size, but because habitat quality is poor in areas with smaller patches. Managers would ensure patch size was larger than the threshold, but would not manage for habitat attributes the species actually requires.

2.6.3. Problem 3: A confused definition of thresholds and a dearth of targets

Many studies distill the habitat thresholds paradigm into statements like this one:

> *"…'habitat thresholds' ...can provide information on the minimum amount of habitat necessary for species persistence, and allow an objective definition of conservation targets."* (Ficetola and Denoël 2009)

The search for habitat thresholds has resulted in a confused definition of 'thresholds', and tests for 'thresholds' as an 'objective' way to define conservation targets have become confusingly over-emphasized in the literature. In 51% (23 of 45) studies, authors identified thresholds visually from *linear* regression models, mostly logistic regressions (Table 2.1; see also Swift and Hannon 2010; Ficetola and Denoël 2009). In only 13% (6 of 45) of studies were thresholds in species occurrence mentioned - values along habitat gradients below (or above) which species did not occur, which may represent 'true' thresholds in the form of abrupt ecological limits. There was no mention of occurrence thresholds even in studies in which 'thresholds' identified at arbitrarily chosen probabilities of presence in linear logistic regression models or using statistical methods to detect non-linearity were similar in value to occurrence thresholds (e.g. Butler et al. 2004, Denoël and Ficetola 2007; Jones et al. 2011).

From a management perspective, 'eye-balling' plots of species responses to habitat gradients to find occurrence thresholds may yield more relevant information to management than statistically-derived points of change in response values. Response values below and above change points may both be deemed high enough to indicate viable populations (also see Radford et al. 2005). In some cases, thresholds may even occur at habitat amounts that produce high responses. For example, Figure 5 of Radford et al. (2005) shows that the highest number of woodland dependent bird species was found in areas with only about 10-20% forest cover, which were areas with forest cover amounts just above the 'extinction threshold' amount they identified of 10%.

Confusion around what to do with 'thresholds' once they are quantified seems evident in the literature. Despite the statement in 67% (30 of 45) of studies that 'thresholds' are useful for conservation management, in only two studies did the authors provide a framework for setting quantitative goals for managers (Guénette and Villard

2005; Digiovinazzo et al. 2010). In all other studies, management targets either were not derived, were set arbitrarily at the threshold, or vaguely and generically set ‘above the threshold’. Other than by giving direction to maintaining habitat at some point ‘above the threshold,’ the most accurately and precisely quantified threshold will not tell managers where to set a management target. In addition, linear relationships may provide just as much or more information for management than non-linear relationships. For example, Homan et al. (2004) predicted a 50% probability of spotted salamander occurrence at 40-50% forest cover from a linear relationship, whereas the 'threshold' relationships they found at smaller spatial scales showed 50% probability of occurrence at about 20%-30% forest cover. The slope of the linear relationship was higher, indicating more rapid loss of salamanders with declines in forest cover. Thus, in this case the linear relationship may provide more useful empirical information in defining a target for forest protection in a risk-averse management strategy (also see Swift and Hannon 2010).

2.7. A General Framework For Using Species-Habitat Relationships to Guide Forest Management

I propose some general rules for the application of Island Biogeography Theory in tests for habitat thresholds which are intended to provide guidance for conservation targets: studies should be carried out with replication at the landscape scale, and the ‘matrix’ should truly be inhospitable to the study species (also see Haila 2002). Further, researchers should generate and test alternative hypotheses which could explain the responses of species across spatial gradients, given the ecology of the study species. If ‘patch’ selection is to be included as a variable, alternative explanations for less frequent selection at low cover of similar surrounding patches should be tested (rather than just simply assuming that inter-patch distance = demographic isolation). Possibilities include a decrease in the quality of patches as the amount of patch cover declines, and a clumped distribution of animals because they prefer breeding in communities (e.g. conspecific attraction in birds may occur for a variety of reasons, including opportunities for extra-pair copulation).

‘Threshold science’ has been applied in a wide array of disciplines other than conservation biology, including epidemiology (Ulm 1991), toxicology (Cox 1987), and climatology (Alley et al. 2003). The detection of thresholds is more generally and perhaps more accurately referred to as 'Change Point Analysis', and has become a well-developed area of study, particularly with respect to statistical methods to identify change points (Anderson et al. 2008). According to Anderson et al. (2008), even though the 'change point' problem is essentially the same regardless of the system under study, addressing the problem has not been cohesive across disciplines. For instance, they report that in one paper, the authors proposed a statistical technique which was a reinvention of a technique proposed about 50 years previously.

The same disconnect has occurred in 'habitat thresholds' studies. Despite the many theoretical and statistical applications in the wide field of change point analysis that may be helpful in efforts to derive management guidelines from species-habitat relationships, only six independent studies (no overlap in authorship) referenced relevant statistical methods applied in other disciplines, and only two referenced change point analysis (Homan et al. 2004, Denoël and Ficetola 2007).

Threshold analyses have typically focused on non-linearity. Segmented regression was the only statistical technique used in the majority of habitat thresholds studies that used statistical techniques to detect thresholds (10 of 17 studies, Table 2.1). The threshold identified from segmented regression is the value of the independent variable which joins two straight lines with statistically different slopes. Other, perhaps more relevant, change points are missed from such over-focus on non-linearity. The responses of some species may be linear across a habitat gradient but still contain a change in the relationship that is relevant to management. For instance, a change in the variability of the response variable might be more indicative of a relevant ecological process than the shape of the response (Carpenter and Brock 2006). Such a change was not considered in the any of the studies I reviewed. A statistical technique like maximally selected rank statistics (Muller and Hothorn 2004) divides the response into two sets at the value of the independent variable at which the difference between the two sets is largest. Thus, in many cases, maximally selected rank statistics or a similar technique may provide more relevant information to management than segmented regression, because the results can be more easily interpreted to identify sites representing the highest versus lowest species response.

I suggest it would be useful to shift the focus from non-linearity in species responses for defining 'thresholds', to using the theoretical and statistical framework available in the field of Change Point Analysis. In most cases, what many authors have referred to as 'thresholds' may be more accurately referred to as change points. The term 'threshold' could perhaps more usefully be reserved for the habitat value which elicits a shift from no response by the target species to some response. Change point analysis is a more general approach, which includes but is not limited to non-linearity. Thus, the types of change points of interest are best identified *a priori* in terms of their relevance to the study and to management. There are a number of important questions to ask, for example - what kinds of changes in the response are relevant to hypotheses being tested and to management? Is the point of largest response most relevant, the 'threshold' (between no response and response), or the point at which variability increases?

Habitat thresholds studies represent considerable intellectual and resource investment by researchers and the studies could provide valuable information for management. However, the information available in the species-habitat models is perhaps best mined outside of the habitat thresholds paradigm. It is essential that researchers interpret species-habitat models at the scale at which the input variables were measured. Presence-absence models probably quantify colonization rates of high quality habitat well, but offer little information on the key measures of the habitat thresholds paradigm - the fundamental population processes of birth and death which affect probability of persistence (Tyre et al. 2001). By limiting inferences at the appropriate scale, researchers will have a higher likelihood of identifying *what* vegetation characteristics to which species respond at local scales. This information can be used to set reliable management guidelines.

For the purposes of deriving management guidelines, I suggest that two kinds of 'biological reference points' be used to define the range of values that likely represent unsuitableand suitable habitat (also see Guénette and Villard 2005). The 'threshold' should be considered the habitat value at which the response changes from null, indicating unsuitable habitat, to a positive response (Figure 1). In contrast, 'change points' should refer to habitat values at which the relationship changes in magnitude, rate of change, or variability, which can be identified using various statistical methods. Biological reference points can then be used to divide the vegetation gradient into habitat zones which delineates 'good' habitat from unsuitable habitat. The range of habitat between unsuitable and good habitat may designated as marginal habitat, if researchers are confident that the response variable is well-correlated with habitat quality. If not, for example, when responses comprise measures of species distribution (Johnson 2007), then habitat ‘in between’ unsuitable and good should be considered to be of variable or uncertain quality.

2.8. But … How Much Is Enough?

More than a decade after its inception, there remains very little empirical support for the ‘extinction threshold’ hypothesis, primarily because few empirical studies have yet to test it effectively. Of the 45 studies I collated and analyzed, only three studies (Radford et al. 2005, Maron et al. 2012, Zuckerberg and Porter 2010) related population-level responses to the amount of habitat in the surrounding landscape, having measured both variables at several well-distributed points within multiple landscapes. I concur with other reviewers. The use of non-linearity in species-habitat relationships to define large-scale management targets, particularly for how much habitat to protect or restore, is fundamentally flawed because ‘thresholds’ vary by species and within species across space. Thresholds in community-level responses like species richness likely mask the loss of many species until too late, while species-level responses have limited usefulness for management across large spatial scales (Lindenmayer et al. 2005). Simply put, there is little if any empirical ecological evidence to support one common ‘threshold’ amount of habitat that will secure the persistence of all species that might be negatively affected by human disturbance (Mönkkönen and Reunanen 1999; Muradian 2001; Huggett 2005; Lindenmayer and Luck 2005; Swift and Hannon 2010). Furthermore, emphasis on habitat thresholds focuses attention on the ‘wrong’ end of the habitat loss gradient (Lindenmayer and Luck 2005). Shifting the focus to amounts of habitat that support species over the long-term (Lindenmayer and Luck 2005) is an analogous to shifting the ‘burden of proof’ for industry to show no harmful effects before resources are extracted (Dayton 1998).

Ecology does offer tools for identifying ‘thresholds’ useful for land management. Thresholds can be identified as amounts of landscape *disturbance* beyond which measures of ecological degradation increase in intensity (e.g. Riley et al. 2005; Scrimgeour et al. 2008). Similarly, thresholds can be identified as the levels of landscape disturbance predicted to result in population growth rates changing from positive to negative (e.g. Sorensen et al. 2008). Alternatively, the response variable can be broadened from species abundance, to using measures that represent ecosystem health and resilience (e.g. loss of trophic levels in response to harvest rates; Samhouri et al. 2010). Reviews suggest that conservation assessments like population viability analysis and site-selection algorithms may be more effective in setting conservation targets for how much land to protect and restore than the habitat thresholds paradigm (e.g. Svancara et al. 2005). Conservation assessments can include a wider set of measures that capture more of what conservation ecologists deem important, such as the concepts of resilience, redundancy, and representation. These concepts are related to habitat thresholds, but comprise a wider approach, because the the habitat thresholds paradigm focuses just on species and their relationship to ‘habitat’, which, in all of the studies I reviewed, was defined only in terms of vegetation.

‘Thresholds’, change points, conservation assessments, or any empirical ecological information can be used to inform target-setting, but ultimately the question ‘How much is enough?’ cannot be answered only from an ecological perspective (Wilhere 2008). ‘Biological reference points’ identified from threshold-like responses have been used for at least two decades in fisheries science to derive management targets (e.g. Mace and Sissenwine 1993). Interestingly, this literature was not referenced in the ‘habitat thresholds’ literature that I reviewed. The framework as it has been developed in fisheries science makes explicit the point that biologically derived thresholds are not equivalent to management targets, since targets need to be set using information on socio-economics and risk assessment (Sissenwine and Shepherd 1987; Mace 1994; Smith et al. 1993). Identifying socially-acceptable levels of ecological impact combined with cumulative impact assessment during regional planning processes may offer a more tractable solution than the search for ‘habitat thresholds’ (Hegmann and Yarranton 2011). Wilhere (2008) states the role for policy and economics succinctly, “…the question, how much is enough?, is really asking how much risk (to biodiversity) will society accept or tolerate?” and what is “… society’s willingness to pay for it.”

Table 2.1. Empirical studies testing for extinction, fragmentation, or habitat use thresholds.

Study	Taxon	Response	Scale	Number of landscapes sampled	Alternatives to patch and 'isolation' effects tested?	Alternatives	Habitat quality measured	Alternatives to IBT	Non-linear modeling	Method to detect thresholds
Population Threshold Studies – Testing for Fragmentation or Extinction Thresholds										
Andrén 1994	birds and mammals	yes or no effect of patch area or isolation on abundance	landscape	multiple	no, discussed	habitat quality (e.g. edge avoidance) confounded with habitat quantity, conspecific attraction	no		no	visual
Becker et al. 2011	birds	relative abundance, species richness and diversity, reproductive success	patch	1	no		no	high habitat diversity at intermediate levels of disturbance	no	segmented regression
Bergman et al. 2004	insects - butterflies	occupancy	patch	multiple	no		no		no	visual
Betts et al. 2006	birds - blackburnian warbler and ovenbird	occupancy	patch	2	no, discussed	conspecific attraction	no		no	visual
Betts et al. 2007	birds	occupancy	patch	2	no, discussed	habitat quality (e.g. opportunities for EPCs and alternative territories) confounded with habitat quantity	no		no	segmented regression
Betts et al. 2010	birds	occupancy	patch	3+	no, discussed	habitat quality confounded with habitat quantity	no		yes, GAM	segmented regression
Butcher et al. 2010	birds - golden-cheeked warbler and white-eyed vireo	abundance, reproductive success	patch	1	yes	habitat quality confounded with habitat quantity	yes, insect abundance		no	visual
Bütler et al. 2004	birds - three-toed woodpecker	occupancy	landscape	4	NA		no		no	visual

Study	Taxon	Response	Scale	Number of landscapes sampled	Alternatives to patch and 'isolation' effects tested?	Alternatives	Habitat quality measured	Alternatives to IBT	Non-linear modeling	Method to detect thresholds
Cushman and McGarigal 2003	birds	species richness, density, evenness,	landscape	3	yes	habitat quality (e.g. edge habitat) confounded with habitat quantity	no	high habitat diversity at intermediate levels of disturbance	no	visual
Denoël and Ficetola 2007	amphibians - newts	occupancy	patch	1	yes	habitat quality confounded with habitat quantity	yes, predator density and canopy cover		no	structural change analysis, segmented regression
Digiovinazzo et al. 2010	plants	species richness	patch	multiple	no		no		yes, GAM	visual
Dodd et al. 2006	mammals - tassle-eared squirrel	density, recruitment, survival	quasi-landscape	2	no		no, but higher recruitment found in habitat categorized as high quality		no	segmented regression
Drinnan 2005	birds, amphibians, fungi, plants	species richness	patch	1	no		no		yes, power and exponential	visual
Ecke et al. 2006	mammals - grey-sided vole	abundance	patch	4	no		no		yes, exponential	visual
Ellis and Betts 2011	birds	abundance, species richness, evenness	patch	2	NA		no		no	segmented regression
Gibbs 1998	amphibians	occupancy	quasi-landscape	1	no, discussed	habitat quality (e.g. predation and mortality rates, water quality) confounded with habitat quantity	no		no	visual
Homan et al. 2004	amphibians - spotted salamander and wood frog	occupancy	patch	1	no		no		no	visual, segmented regression, and binomial change point analysis
Imbeau and Desrochers 2002	birds - three-toed woodpecker	occupancy	patch	3	no		no		no	visual

Study	**Taxon**	**Response**	**Scale**	**Number of landscapes sampled**	**Alternatives to patch and 'isolation' effects tested?**	**Alternatives**	**Habitat quality measured**	**Alternatives to IBT**	**Non-linear modeling**	**Method to detect thresholds**
Jansson and Angelstam 1999	birds - long-tailed tit	occupancy	patch	1	no		no		no	visual
Jones et al. 2011	birds - orange-crowned warbler, MacGillivray's warbler, willow flycatcher	occupancy	patch	3	NA		no		no	Bayesian change point analysis
Lindenmayer et al. 2005	birds and lizards	species richness	patch	1	no		no		yes, GAM	segmented regression
Maron et al. 2012	birds	species richness	landscape	multiple	yes	habitat quality confounded with habitat quantity	yes, land productivity		yes, power and exponential	segmented regression
Mordecai et al. 2009	birds	occupancy and habitat use (proportion of time spent in the habitat)	patch	1	no		no		no	visual
Parker and MacNally 2002	insects - beetles	species richness, abundance	experimental landscape		no		no		no	visual
Radford and Bennett 2004	birds - white-browed tree creeper	occupancy	patch	multiple	yes	habitat quality confounded with habitat quantity	yes, presence of a competitor		no	visual
Radford et al. 2005	birds	species richness	landscape	multiple	no		no		yes, GAM, quadratic, cubic, inverse, exponential, S-curve, and power	segmented regression
Reunanen et al. 2004	mammals - Siberian flying squirrel	occupancy	quasi-landscape	1	no		no		no	visual
Rhodes et al. 2008	mammals - koalas	occupancy	patch	3	no, discussed	habitat quality (e.g. density of food resources) confounded with habitat quantity	no	Stochastic events (mortality from fire and disease), Allee effects	no	segmented regression

Study	Taxon	Response	Scale	Number of landscapes sampled	Alternatives to patch and 'isolation' effects tested?	Alternatives	Habitat quality measured	Alternatives to IBT	Non-linear modeling	Method to detect thresholds
Rodríguez and Andrén 1999	mammals - Eurasian red squirrels	occupancy	patch	6	no		no		no	visual
Schmidt and Roland 2006	insects - moths	species richness	patch	multiple	no		no	high habitat diversity at intermediate levels of disturbance	yes, quadratic	visual
Summerville and Crist 2001	insects - butterflies and skippers	habitat use, species richness	experimental landscape		yes	habitat quality confounded with habitat quantity	yes, amount of food	high habitat diversity at intermediate levels of disturbance	yes, quadratic and cubic	visual
Suorsa et al. 2005	birds - Eurasian treecreeper	occupancy	patch	1	no, discussed	habitat quality confounded with habitat quantity	no		no	visual
Villard et al. 1999	birds	occupancy	quasi-landscape	3	no		no		no	visual
Wiens et al. 1997	insects - a beetle	movement - distance, rate, and tortuosity	experimental landscape		no		no		no	visual
With et al. 1999	insects - a cricket	movement - distance, rate, and tortuosity	experimental landscape		no		no		no	visual
With et al. 2002	insects - two ladybird beetle species as predators and one aphid species as prey	occupancy	experimental landscape		no		no		no	visual
Zuckerberg and Porter 2010	birds	occupancy	landscape	multiple	no		no		yes, GAM	segmented regression
Habitat Use Thresholds										
Guénette and Villard 2005	birds	occupancy	patch		NA		no		no	ROC analysis
King et al. 2007	birds - red-headed woodpecker	occupancy	patch		NA		no		no	visual

Study	Taxon	Response	Scale	Number of landscapes sampled	Alternatives to patch and 'isolation' effects tested?	Alternatives	Habitat quality measured	Alternatives to IBT	Non-linear modeling	Method to detect thresholds
Maron 2007	birds	occupancy	patch		NA		no		no	visual
van der Ree et al. 2004	mammals - arboreal marsupials	occupancy	patch		NA		no		no	visual
Müller et al. 2009	birds - middle-spotted woodpecker	occupancy	patch		NA		no		no	maximally-selected rank statistics
Moning and Müller 2008	birds	abundance	patch		NA		no		no	maximally-selected rank statistics
Poulin et al. 2008	birds - brown creeper	occupancy	patch		NA		no		no	ROC analysis
Roberge et al. 2008	birds - three-toed woodpecker, lesser and middle spotted, and white-backed woodpeckers	occupancy, species richness	landscape		NA		no		no	visual

Table 2.2. Summary of area (ha) over which habitat variables were measured per sampling unit in habitat thresholds studies.

Objective	Scale	Mean (ha)	Range (ha)	Number of Studies
Population threshold				
	patch	1220	0.79-7850	22
	quasi-landscape	750	100-2000	4
	landscape	4580	100-10 000	6
Threshold in habitat use				
	patch	5	0.05-19.6	7
	landscape	100		1

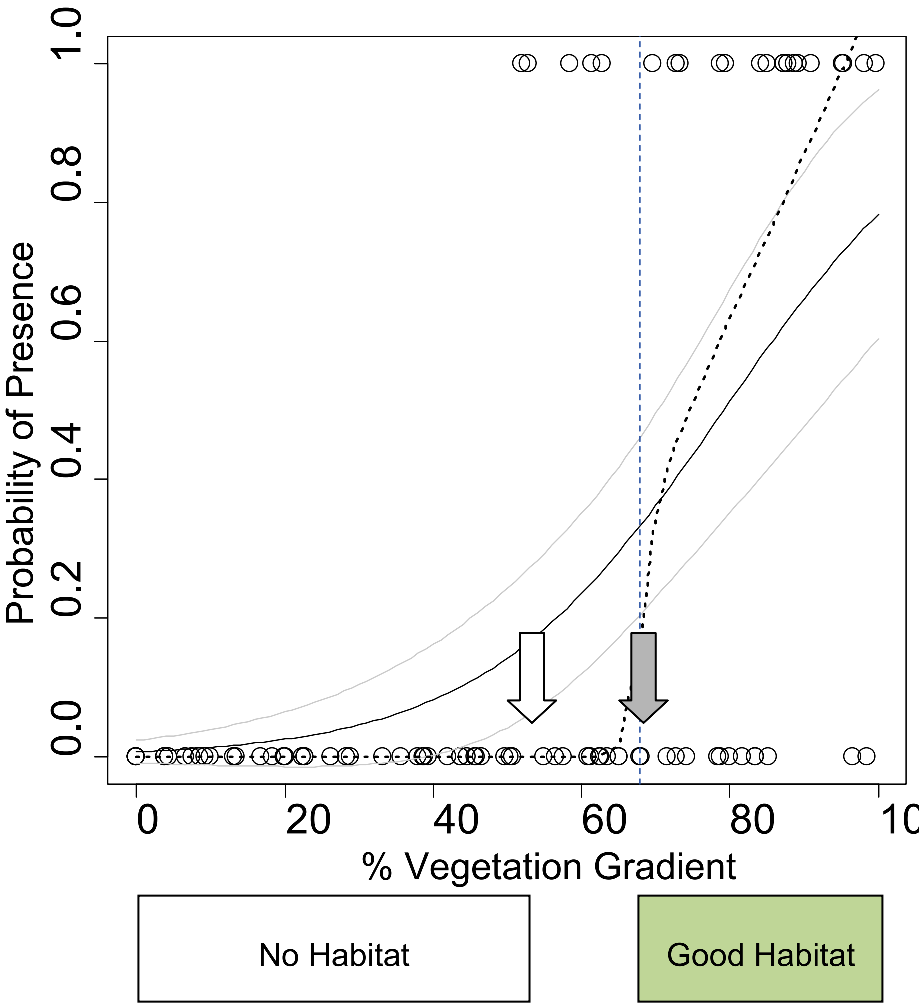


Figure 2.1. An example of using biological reference points (arrows) to delineate habitat quality. The unshaded arrow points to the 'threshold' – the value across the vegetation gradient below which the species does not occur. The shaded arrow points to the 'change point' – the point along the vegetation gradient at which the species response changes significantly. Vegetation in between the two zones may be marginal, variable, or of uncertain quality. The change point (dashed vertical line) was identified using maximally selected rank statistics.

3. CHAPTER 2

Management Implications of Songbird Abundance in Response to Forest Composition of the Mixedwood Boreal Forest of Northeastern British Columbia.

3.1. Abstract

The loss of mixedwood stands due to logging and other industrial activities in the boreal forest may be negatively impacting bird species that prefer mixedwood stands. One solution to minimize the effects of logging and to guide stand-level regeneration practices is to quantify ‘thresholds’ in forest composition beyond which the distinct mixedwood contribution to bird communities disappears. I related densities of songbird species derived from distance sampling (2007-2009) to the gradient in forest composition (% deciduous) and the amount of shrub cover in 90 old (> 100 years) forest stands in the mixedwood boreal forest of northeastern BC. Twelve of twenty commonly-detected species rarely occurred in stands with less than 20% deciduous content. The densities of three of nine tree generalists and two understory foragers were unimodal in response to forest composition suggesting preferences for mixedwood stands. A statistically significant change was detected from low to higher abundance above 33% deciduous trees for bird species that forage without preference from deciduous and coniferous trees. Stands that are managed to result in intimate mixes of coniferous and deciduous trees within with more than 30% deciduous will likely provide habitat for the majority of common songbirds.

3.2. INTRODUCTION

Mixedwood boreal forests in North America are comprised of intimate mixtures of both coniferous and deciduous trees at the stand scale. However, there are concerns that logging practices are causing an ‘unmixing’ of mixedwood boreal forests in North America (Hobson and Bayne 2000). In western North America, logging practices typically resulted in the replacement of mixedwood stands with either conifer-dominant or deciduous-dominant stands (Kabzems et al. 2007; Lieffers et al. 2008). The loss of mixedwood stands due to logging and other industrial activities may be negatively impacting bird species that prefer stands with a mixed species composition (Drapeau et al. 2000; Hobson and Bayne 2000). For example, the blackburnian warbler rarely chooses to breed in stands other than mixedwood stands where these are available (Girard et al. 2004; Young et al. 2005). One solution to minimize the effects of logging is to define an appropriate ‘mix’ of coniferous and deciduous trees in regenerating stands (Gauthier et al. 1996). However, significant uncertainties remain about how to implement such policies. For instance, it is unclear how low the proportion of either deciduous or coniferous trees can fall before the distinct mixedwood contribution to bird species richness and abundance disappears (Willson and Comet 1996; Knoke et al. 2008).

Quantities of coniferous and deciduous trees that birds use to choose whether or not forested sites are suitable as territories may be defined as ‘habitat thresholds’, which are represented by statistical discontinuities in the relationship of species richness and abundance to the gradient in forest composition. Because mixedwoods comprise a significant portion of the boreal forest in North America, knowledge of such thresholds in the relationship of birds to the gradient of forest composition - the relative proportions of coniferous and deciduous trees - would be useful to guide stand-level regeneration practices (Hobson and Bayne 2000).

Despite a long-standing literature on the relationships of birds to vegetation, bird responses to forest composition remain poorly understood (Enoksson et al. 1995; Young et al. 2005). Such paucity of studies is surprising, since forest composition is likely one of the most influential environmental gradients affecting the distribution of forest passerines and woodpeckers (James and Wamer 1982; Willson and Comet 1996; Hobson and Bayne 2000). But most studies relating birds to habitat have focused on relating birds to the diversity and structure of vegetation, and on describing landscape-scale patterns (Rotenberry 1985; Whelan 2001). Far fewer studies in temperate forests have been designed to understand the processes that result in patterned responses of birds to individual tree species, or to forest composition more generally. A parallel situation has existed in the literature on the relationships between insect communities and vegetation (Schaffers et al. 2008).

One of the most likely factors shaping bird distributions in response to forest composition is the preference of birds for certain tree species and tree type (i.e. either coniferous or deciduous) as substrates on which they nest, and as substrates from and on which they forage for arthropod prey (e.g. Hagar 2007). The forest passerine community is structured into distinct guilds based on where and how species forage (Holmes et al. 1979). Most species forage for insects primarily from one of three locations: the ground and understory, the bark of trees, or from the branches and foliage of trees (Holmes et al. 1979). Species that forage from tree branches and foliage can be further structured into guilds based on the primary use of one of three foraging techniques: ‘sallying’ from tree perches to catch insects mid-air, or foraging for insects found on tree branches or leaves by ‘gleaning’ while standing on tree branches or and leaves, or by ‘hovering’ in the air (Holmes et al. 1979). Most species of birds that forage from and on trees are generalist with respect to tree type, and spend equal amounts of time sallying from, or foraging within the foliage and branches of both deciduous and coniferous trees (Greenberg et al. 1999). However, some specialist species, such as golden-crowned kinglets, consistently forage more than 80%of the time from only one tree type (Greenberg et al. 1999; Mills 2007).

In this study, I related the density of songbirds to a gradient in forest composition in order to identify species occurring more abundantly in mixedwood stands in Northeastern British Columbia, Canada. Based on foraging preferences summarized from the literature (Table 3.1), I predicted that species that are generalist with respect to tree type will occur most abundantly in mixedwood stands, because stands with an abundance of both tree types likely provide a higher diversity of resources. I combined data for birds that are tree species generalists to identify statistical discontinuities or ‘change points’ in the relationship to forest composition, which I used to delineate mixedwood habitat. Because birds may also find resources for foraging and nesting in shrubs, I included the amount of shrub cover in predictive models. I quantified these relationships using three years of field data collected in the mixedwood boreal forest in the Peace River region of northeastern BC. I generate hypotheses to explain the relationships of birds to forest composition, and discuss implications of the results for forest management in the mixedwood boreal forest. .

3.3. METHODS

3.3.1. Study Area

The study was conducted within an area about 80 x 80 kilometers near the communities of West Moberly and Hudson's Hope (Figure 3.1). I examined three study sites which occur in the Boreal White and Black Spruce (BWBS) Biogeoclimatic (BEC) Zone, which is the most widely distributed terrestrial ecosystem type in Canada, stretching from Alaska across all provinces to Newfoundland (Meidinger and Pojar 1991). Comprising about 10% of BC's land area, this zone covers most of northeastern BC. Typical of boreal forest ecosystems, fire is the dominant natural disturbance in the mixedwood forest and occurs on average every 200-250 years (Cumming et al. 2000).

Two study sites (Site 2, ~32 000 ha and Site 3, ~12 000 ha) were in the northeast portion of Tree Farm License (TFL) 48, in the western half of the Dawson Creek Timber Supply Area (TSA, Figure 3.1). This area is the traditional land of the West Moberly and Saulteau First Nations. The third study site (Site 1) is approximately 35 000 ha within the southwestern portion of the Fort St. John (FSJ) TSA, within the traditional land of the Halfway River First Nations. In the region, precipitation is light (average was 56 mm for May-July 2007-2009), and temperatures cool (average was 13^0C for May-July 2007-2009) but with occasional hot days in July with temperatures above 30^0C (weather station data from Environment Canada).

The FSJ and Block 3 study sites are in forest that is typical of the flat, vast expanse of the mixedwood boreal plains, which extend beyond northeastern BC from Manitoba to Alaska (range of slope: Block 3 $0\text{-}12^0$, FSJ $0\text{-}5^0$; range of elevation: Block 3 700-920 m, FSJ ~600 m). These two study sites are found in the 'Moist Warm' subzone of the BWBS BEC Zone, which extends across the boreal plains of northeastern BC. At upland sites, the forest is characterized by: 1) deciduous stands dominated by trembling aspen (*Populus tremuloides*) with lesser amounts of balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera)* and Alaska birch (*Betula neoalaskana*); 2) mixedwood stands dominated by aspen and white spruce (*Picea glauca)*; and 3) coniferous stands dominated by white spruce and lodgepole pine (*Pinus contorta var. latifolia*). Black spruce (*Picea mariana*) and larch (*Larix laricina)* dominate in wet lowland 'muskeg' sites. In all forest types, willow (*Salix spp*), Sitka alder (*Alnus* sinuata), and green alder (*Alnus viridis*) are the only tall (> 1.3 m) shrub species present, though tall shrubs are infrequent in coniferous stands (Delong et al. 1991).

The Block 2 study site is found at the extreme western range extent of the mixedwood boreal forest, where the land rises in elevation in the foothills of the Rocky Mountains. Deciduous and mixedwood stands are less common as the land gains in elevation from east to west, such that these stand types are generally rare in Block 2 of TFL 48 and are mostly found in riparian valleys or as young stands regenerating from clearcut logging. The lower elevations where I sampled (slope 5-32^0, elevation 650-950 m) are found within the 'Wet Cool' subzone of the BWBS BEC Zone; forests at higher elevations are found within the Engelmann Spruce-Subalpine Fir (ESSF) BEC Zone. The dominant coniferous species in the wet cool BWBS subzone are white spruce, hybrid spruce (*Picea glauca x engelmannii*), lodgepole pine, and small amounts of subalpine fir (*Abies lasiocarpa*). Engelmann spruce (*Picea engelmannii*) and subalpine fir dominate at higher elevations in the ESSF Zone. The understory vegetation in coniferous-dominated stands in the Wet Cool BWBS Zone is similar to that of the Moist Warm BWBS Zone to the east, with the addition of black huckleberry (*Vaccinium membranaceum*) as a common species (Delong et al. 1991).

3.3.2. Sampling design and bird surveys

I used a stratified sampling design to sample birds and vegetation in 90 old (100-180 years; 70% were 110 to 150 years old) forest stands across a gradient in forest composition, varying in the proportion of deciduous versus coniferous trees (0%-100%). I selected forest stands delineated by age and tree species composition from satellite imager using a Geographic Information Systems (GIS) database in ArcGIS 9.1 (Environmental Systems Research Institute 1999-2005). The majority of accessible forest stands within Block 2 and 3 of TFL 48 were sampled, but stands were randomly selected from a pre-defined set of accessible stands in FSJ. To ensure relatively equal sampling across the gradient, I grouped stands into forest cover types based on the proportion of deciduous trees as follows: coniferous: 0-19% (n=20 stands), coniferous-dominated mixedwood: 20-39% (n=18), mixedwood: 40-59% (n=16), deciduous-dominated mixedwood: 60-79% (n=16), and deciduous: 80-100% (n=20).

I estimated the densities of songbirds using distance sampling (Buckland et al. 2001) at point count stations between 0415 and 0930 hours from 27 May to 4 July, 2007-2009. Point count stations were placed at the end of 200 m line transects that ran perpendicular to logging roads. Point count stations were spaced at least 200 m apart along the road to avoid multiple counts of individual birds, and were placed at least 100 m from stand edges. Most stands (75%) were sampled with one point count station (in proportion to stand size), but 22 larger stands (> 12 ha) were sampled with two point count stations. Most (60) stands were visited twice, once at the beginning (27th May-15th June) and once at end of the breeding season (16th June-4th July). Twenty of 25 stands visited twice in 2008 were visited a third time in 2009. Eighteen stands were surveyed once in 2007 and once in 2008. Twelve stands became inaccessible due to a road-washout so were surveyed only once in 2007.

I conducted surveys according to provincial standards (RIC 1999). All surveys were conducted by the same observer (K.Squires). I distributed survey effort approximately equally across each of the five forest types during each half of the breeding season, and during each daily interval (sunrise to 2 hours after sunrise; 2 hours after sunrise to 5 hours after sunrise). Birds flying over stations were recorded but not included in any analyses. Detections were noted by species code (Appendix B) and by detection type as ‘visual’, ‘song’, ‘call’, or ‘drum’. After a settling period of two minutes after arrival at point count stations, the distance and location with respect to the observer were recorded for all birds seen or heard during 5 minutes.

Distances were measured using a laser range finder (Bushnell Ltd. Yardage Pro Sport 450) to the nearest meter for birds detected within 30 m. I estimated distances to the nearest 5 m for most birds estimated to be 30-60 m away, and I made attempts to more accurately locate birds after the survey. For birds estimated to be 60-80 m away, I estimated distances to the nearest 10 m but only occasionally made attempts to find the birds after the survey. Thus, distances beyond 60 m were most often estimated using auditory cues only. I estimated distances to the nearest 10 m for birds that I estimated to be beyond 80 m. I derived detection functions using the program Distance (version 5.0, Thomas et al. 2010) to estimate the densities of species for each point count. Methods and results are summarized in Appendix C, E, and F.

3.3.3. Vegetation Sampling

I estimated forest composition and % shrub cover as the average of estimates within four 11.3 m radius (0.04 ha) circular plots centred on point count stations. These estimates were averaged for forest stands surveyed with more than one point count station. One vegetation plot was centred on point count stations; three other plots were centred on points 30 m away from the centre of stations along directions separated by 120^0 – the location of one of the three surrounding plots was chosen randomly (Martin et al. 1997). From the centre of each plot, I estimated forest composition by comparing the proportion of forest canopy and sub-canopy comprised of each tree species within my visual field, which usually extended to about 30 m. I also quantified stand composition from estimates of basal area derived from measurements of the diameter at breast height (DBH) of all trees (DBH > 15 cm) within vegetation plots. My visual estimates of stand composition at vegetation plots were highly correlated with estimates from basal area calculations (Figure 3.2). The estimates did not differ by more than 15 percentages at 85% (95 of 112) of point count stations – the mean difference was 5.67%. I used the average of the visual and basal area estimates to derive estimates of stand composition. From the centre of each plot, I visually estimated % cover of shrubs taller than 1.3 m (*Alnus* and *Salix* spp.) as the percent of ground area covered when the shrub crowns were projected vertically excluding any overlap.

To determine whether forest composition at larger spatial scales could be added as a predictor to GLM models, I quantified the proportion of deciduous within 150 m, 350 m and 650 m radii from point count stations using ArcGIS 9.1 (Environmental Systems Research Institute 1999-2005). The proportion of deciduous in old forest polygons (> 100 years) within each sampling plot was calculated by summing across each GIS polygon, weighting by polygon size, and then dividing by the total area sampled. Analysis via Spearman rank correlation revealed that the GIS-based estimate of the proportion of deciduous in old stands within 650 m from point count stations was highly correlated with my estimates of the proportion of deciduous within 60 m ($R_s = 0.77, 0.74, 0.65$; $P< 0.001$, for 15 0m, 350 m, and 650 m radii respectively). Thus, I did not use the additional measure of forest composition at larger spatial scales in GLM models.

3.3.4. Responses to Forest Composition and Shrubs

I compiled information from the literature to categorize bird species by preference for tree type for foraging (Table 3.1). To categorize species as tree type specialists, I used data from studies that measured preference at sites where both tree types were available (e.g. as more than 80% of time spent foraging in one tree type or the other, Greenberg et al. 1999). Categorization of species at tree type generalists was based on similar proportions of time spent foraging in both tree types (Greenberg et al. 1999), observations of typically coniferous-associated species foraging primarily from deciduous trees (e.g. ruby-crowned kinglet, Wilson and Comet 1996), and species accounts reporting no preferences for either tree type (e.g. Tennessee warbler, Rimmer and Mcfarland 2012). Categorization of ground-understory foragers was based frequently-cited guild assignments (Ehrlich et al. 1988; De Graaf et al. 1985). .

Within an information-theoretic approach (Burnham and Anderson 1998), I used second order AIC (AICc) to compare the strength of support for models relating bird species to forest composition with models relating species to shrubs, and to both variables together ($R_s = 0.47$). Of the three models, the model with the lowest AICc was chosen as the best model. The densities of individual species and of all tree generalist species (no foraging preference between deciduous and coniferous trees, Table 3.1) combined in relation to forest composition and shrubs were modeled using Poisson regression (GLM with log link). Counts were offset by effort x detection ability (Offset = Effort * [3.14 * (Effective Detection Radius)^2]). For Poisson models with over-dispersed data (>1.5), I used the negative binomial model if a likelihood ratio test showed a better fit than the Poisson (Pearce and Ferrier 2001). I chose the quadratic models as the final model if it resulted in an AICc of 2 or more units lower than the linear model.

Nagelkerke's Pseudo-R^2 was used to approximate the proportion of variability in the data explained by the Poisson regression models (Nagelkerke 1991).

In order to determine whether there was evidence of spatial auto-correlation across point count stations, I used correlograms of Moran's *I* coefficients to test for autocorrelation in the Pearson residuals of the best fitting GLM models (Diniz-Filho et al. 2003; 10 distances between 400 m to 10 km). The significance level for each correlogram was calculated using a Bonferroni correction ($\alpha = 0.05/k$ where k is the number of distances used in the correlogram; Diniz-Filho et al. 2003).

I used segmented regression ('Segmented' package, Muggeo 2003) and maximally selected rank statistics ('Maxstat' package, Müller and Hothorn 2004; Hothorn 2011) to statistically identify change points in the best models chosen using AICc. Segmented regression divides the data into two or more parametric models with different slopes by iteratively fitting linear models to each data set such that the 'gap' between the regression lines is minimized. The value of the independent variable at which the smallest gap occurs is the change point (Muggeo 2003). I considered change points to be statistically significant if segmented models resulted in an AICc of 2 or more units smaller than linear models. A maximally-selected rank statistic divides the data into two groups of 'high' and 'low' response using non-parametric two-sample linear rank statistics. The data are divided into two groups at values of the independent variable. The change point is the value at which the rank statistics (standardized by sample size) above and below the change point are maximized, and is thus the value at which the difference in response between the two groups is largest (Muller and Hothorn 2004).

I used occurrence thresholds and change points to delineate ranges of the gradient in forest composition representing unsuitable, marginal or uncertain, and suitable habitat (see “General Framework” and Figure 1 in Chapter 1). I then calculated mean densities across stands grouped according to habitat suitability.

Because GLM models appear non-linear on the probability scale, I checked the shape of GLM models using Locally Weighted Scatterplot Smoothing (LOESS), a form of Generalized Additive Modeling that fits a non-parametric line to the mean response within a ‘running window’ along the x axis. All statistical analyses were performed using R (R Development Core Team 2011).

3.4. RESULTS

A total of 61 forest bird species were detected during point counts in 90 stands across the 3 years of the study. Twenty species were each detected at least 30 times in more than 18 stands, and accounted for more than 85% of all 2182 detections (Appendix D). Evidence for spatial autocorrelation was not found in the Pearson residuals of the GLM models for the best-fitting models (American redstart, least flycatcher, warbling vireo, white-throated sparrow, yellow warbler, and golden-crowned kinglet).

3.5. Relationships to forest composition

The average abundance of male birds and of species richness was lowest in coniferous stands (Figure 3.3; mean of coniferous stands: 8.95 (±0.78) and 7.15 (±0.62) respectively, versus mean across all other stand types (14.4 (±0.54) and 11.5 (±0.44)). All five tree specialists (Table 3.1) had their highest density in stands dominated by the tree type I predicted would be preferred by them (Figure 3.4a and 3.4b). Forest composition explained relatively large portions of the variability in the data for tree specialists (33.1%-47.1%, 73.2% for AMRE and 69.5% for LEFL for models without shrubs, Table 3.3). Forest composition also explained a relatively high proportion of the variability in the model for the ground-foraging white-throated sparrow (Table 3.3, Figure 3.4e).

The densities of three of ten tree generalists (black-throated green warbler, Tennessee warbler, western tanager) and all tree generalists combined were quadratic in response to forest composition, indicating that density was lowest in stands that contained high proportions of either coniferous or deciduous trees (Figure 3.4c). Models were also quadratic for two ground foraging species – the dark-eyed junco and Swainson’s thrush. Models for tree generalists explained low to moderate amounts of variability (6.66%-27.4%, Table 3.3). There was no evidence for any species achieving its highest density in stands with approximately equal proportions of deciduous and coniferous trees (40%-60% deciduous). All species with quadratic relationships to forest composition had highest density in either coniferous-dominated or deciduous-dominated mixedwood stands, and similar but lower density in mixedwood (40-60% deciduous) stands (Figure 3.4).

3.6. Relationships to shrubs

Models relating the densities of the blue-headed vireo and magnolia warbler to shrubs had stronger support than models with forest composition (Table 3.2); but the model for the blue-headed vireo did not result in a statistically-significant slope and explained very little variability in the data (Table 3.3). The quadratic model for magnolia warblers had higher support; however, too few sites with 50% to 80% shrub cover were sampled to conclude whether the density of magnolia warblers was highest in stands with intermediate shrub cover or increased linearly with shrub cover (Figure 3.4d).

There was support for the addition of shrubs to models relating bird density to forest composition for the American redstart, least flycatcher, dark-eyed junco, Swainson's thrush, and for all tree generalists combined, but slopes were higher for the relationship to forest composition than to shrubs. For all other species, relationships to shrubs were not supported by the data (Table 3.3).

3.7. Using Change Point Analysis to Delineate Habitat Quality

Including the blue-headed vireo and magnolia warbler, twelve of twenty species did not occur or occurred rarely in stands with less than 20% deciduous trees (Figure 3.4, Table 3.4), reflecting the general pattern of low species richness and abundance in coniferous stands (Figure 3.3). The yellow-rumped warbler was the only generalist species found ubiquitously across the gradient in forest composition. Since it showed no change points, I excluded the yellow-rumped warbler to estimate change points in the relationship of the other tree generalists to forest composition. On average, the density of tree generalists was almost two times higher above a change point at 33% deciduous, identified using maximally-selected rank statistics (Table 3.4). The data of Figure 3.5 also show lower density in 'pure' deciduous stands (>90% deciduous), reflecting the lower occurrence and density in 'pure' deciduous stands for eight of ten tree generalists (all except the rose-breasted grosbeak and yellow-bellied sapsucker). No statistically significant change points were detected at high % deciduous, though segmented regression detected a non-significant change point at 95% deciduous.

The densities of three of five ground foragers (dark-eyed junco, Swainson's thrush, and ovenbird) were low in stands classed as 'pure' deciduous. Combined with the golden-crowned kinglet, a coniferous specialist that rarely occurred in 'pure' deciduous stands, a total of 12 of 20 species occurred less frequently in ‘pure’ deciduous stands than in the other stand types.

Using occurrence thresholds and change points, forest stands that represent suitable habitat were distinguished from stands representing unsuitable and marginal habitat for thirteen species (Table 3.3 and 3.4). Deciduous and deciduous-dominated mixedwood stands were identified as suitable habitat for the majority of commonly-detected species. Suitable habitat for four deciduous specialists was identified as stands with at least 50% deciduous, and stands with at least 40% deciduous for two species of ground foragers and four species of tree generalists (Table 3.3). Stands with about 50% to 70% deciduous were identified as suitable habitat for the western tanager. In contrast, coniferous and coniferous-dominated mixedwood stands were identified as suitable habitat for just two species – the coniferous specialist, golden-crowned kinglet, and a tree generalist, the red-breasted nuthatch.

The magnolia warbler showed the largest difference in density between suitable and marginal stands – density was about nine times higher in stands with more than 25% shrub cover than stands with less than this amount of shrubs (Table 3.3 and 3.4, Figure 3.4d). Reflecting strong relationships to forest composition, the densities of the white-throated sparrow and of all tree specialists except the yellow warbler were at least three times higher in suitable versus marginal habitat (Table 3.4). The densities of all other species for which change points were identified were at least one and a half times higher in suitable versus marginal habitat (range 1.7-2.6, Table 3.4).

3.8. DISCUSSION

3.8.1. Tree Generalists and Mixedwood Stands

Unimodal relationships between bird abundance and forest composition are expected for some species that forage without preference from both coniferous and deciduous trees, because ‘pure’ stands usually have less vegetation species and structures and thus likely provide fewer resources (Hobson and Bayne 2000). A key question is whether stands with similar proportions of both tree types (i.e. mixedwood stands ~40%-60% deciduous) provide additional, unique, or required resources for tree generalists (Girard et al. 2004). If so, then ‘mixedwood’ bird species can be identified as those with sharply unimodal relationships between abundance and forest composition, centered on approximately equal proportions of coniferous and deciduous trees. Alternatively, tree generalists may find equally adequate resources in mixedwood stands as coniferous- and deciduous-dominated mixedwood stands, or in more purely coniferous or deciduous stands (Willson and Comet 1996; Robichaud and Villard 1999; Young et al. 2005). Some species like the black-throated green warbler may only require a few coniferous trees for nesting, and are able to forage efficiently from coniferous trees, and deciduous trees and shrubs (Robichaud and Villard 1999). Unimodal relationships over a wide range of forest composition would be expected if mixedwood stands provide adequate but not additional or unique resources.

I did not find any true ‘mixedwood’ species as no species had highest abundance in mixedwood stands with approximately equal proportions of deciduous and coniferous trees (40%-60% deciduous). The majority of breeding males of tree generalists chose territories in either coniferous-dominated or deciduous-dominated mixedwood stands. Thus, there was no support for the hypothesis that mixedwood stands (40-60% deciduous) provide additional, unique, or required food for tree generalists that were not also available in coniferous- or deciduous-dominated mixedwood stands. However, the highest species richness and abundance was found in mixedwood stands combined with coniferous- and deciduous-dominated mixedwood stands, where tree specialists likely found adequate resources, and where most tree generalists, ground and understory foragers likely found additional resources compared to ‘pure’ stands.

3.8.2. Forest Specialists

Forest composition had a greater effect on the distributions of species that prefer to forage either in coniferous or deciduous trees, rather than ground foragers or tree generalists. This suggests that preference for tree types as a foraging substrate is likely a major factor affecting relationships to forest composition for tree specialists. Except for the ruby-crowned kinglet, most tree specialists selected territories in stands where the amount of their preferred tree type was above 50%, indicating that a relatively large number of trees may be required to meet foraging requirements. Similarly, Moning and Müller (2008) found that the abundance of 6 of 42 bird species was significantly related to forest composition in mixed montane forest in southeast Germany. Change points identified by Moning and Müller (2008) for four deciduous associates using maximally-selected rank statistics of 54% to 65% deciduous trees were very similar to those that I found (52%-81%).

The availability of arthropod prey to birds has been found to be spatially and temporally variable in both deciduous and coniferous stands, though to my knowledge no study has tested whether availability is more variable in one versus the other (Holmes and Schultz 1988; Schowalter and Ganio 1988; Marshall and Cooper 2004). Energy-rich lepidopteran larvae comprise a large portion of the diets of many forest passerines (Holmes and Shultz 1988; Marshall and Cooper 2004), and have been found to be more abundant in deciduous than coniferous trees (reviewed by Hagar 2007). Most arthropods, including lepidopteran larvae, are more abundant on the undersides than the upper sides of deciduous leaves. In contrast, with the exception of lepidopteran larvae, most arthropods are distributed across the upper surfaces of coniferous branches (Park et al. 2008; Holmes and Schultz 1986). To access leaf undersides, birds often need to use aerial techniques which are probably more energetically consumptive than gleaning (Remsen and Robinson 1990). Coniferous trees provide a substrate that may be easier to forage from, allowing efficient gleaning and other non-aerial foraging techniques (Franzreb 1978; Holmes and Robinson 1981). Arthropod availability may be equally variable in deciduous and coniferous trees, but foraging from deciduous trees may be less efficient than from coniferous trees if birds more often need to use aerial techniques to access prey on leaf undersides. Alternatively, individual prey items in coniferous trees may be less energy-rich, but more predictable across time and space than in deciduous trees. In either case, deciduous specialists may require more of their preferred tree species than the requirements for coniferous trees of coniferous specialists. I found evidence to support this hypothesis as all deciduous specialists occurred over a smaller gradient of forest composition than did the two coniferous tree specialists. One approach to test this hypothesis is to compare how foraging tactics vary between birds foraging from coniferous versus deciduous trees. If coniferous trees provide less variable and more predictable energy gains, coniferous specialists would be predicted to spend more time foraging per tree and visit less trees per foraging bout. An alternative experimental approach would be to test the effect of tree removal on the foraging efficiency of coniferous versus deciduous specialists. Tests of this hypothesis first require studies to address the dearth of information on how arthropod availability and energetic value differs for birds foraging from coniferous versus deciduous trees. ‘Maps’ of the spatial and temporal distribution of arthropod availability and energy value within individual coniferous and deciduous trees would be helpful to measure the relative stability and evenness of energy that the two tree types provide to bird predators.

3.8.3. Relationships to Shrubs

The magnolia warbler was the only species of the twenty that I studied for which adequate support was found for a stronger relationship to deciduous shrubs than to deciduous trees. This relationship was expected since this species is known to glean for insects from the undersides of shrub and sapling leaves by standing on branches and twigs below (Dunn and Hall 2010). Because shrubs generally provide denser branch and twig structure than trees, gleaning from the undersurface of shrub leaves may be more efficient energetically for the magnolia warbler, and perhaps for all species, than gleaning from the underside of tree leaves.

For all other bird species, the relationship between density and forest composition may be mediated by foraging from shrubs. Twelve of twenty species did not occur or occurred rarely in stands with less than 20% deciduous, which coincides with a point of change in the relationship of shrub cover to forest composition. On average, shrub cover was about twice as high in stands with more than 20% deciduous compared to coniferous stands (23% ± 2.0 versus 12% ± 4.4, respectively). Support for responses to shrubs in addition to forest composition was found for four of twenty commonly-detected species and for all tree generalists combined.

There is ample evidence in the literature that many bird species respond positively to the amount of shrub cover (Schmiegelow et al. 1997; Westworth and Telfer 1993), and some, like the Wilson’s warbler, have rarely been found in coniferous-dominated stands with less than 35% shrub cover (Hager 2004). But the contribution of shrubs versus trees as foraging substrate has rarely been studied. Five of the species that I studied - all four species of deciduous specialists and the rose-breasted grosbeak - have been found to be relatively abundant in young aspen stands with high shrub cover (Westworth and Telfer 1993), indicating that these species can efficiently forage from shrubs and may not even need trees as a prey source. While trees provide adults with foraging substrate, some studies suggest shrubs are also important for fledglings, because they provide cover from predators and perhaps easier foraging (Robichaud and Villard 1999). There may be a higher degree of competition among bird species for arthropods in shrubs versus trees. Shrub arthropods are available to members of all foraging guilds, including ground foragers like the Swainson's thrush and dark-eyed junco, for which I found support for shrubs as a predictor of density in addition to forest composition. My results suggest that shrubs also need to be managed across regenerating stands to provide habitat for species within multiple foraging guilds. But in order to fully understand the relationships of birds to forest composition and shrubs, and thus to guide regeneration practices for the mixedwood boreal forest, it may be necessary to quantify how the relationships of species to shrubs as foraging substrate varies temporally, across the gradient in forest cover types with the presence of competitors.

3.8.4. Using Change Point Analysis to Delineate Habitat Quality

Change points identified using segmented regression and MSRS are useful in predicting species response to habitat, but should be interpreted carefully. In this study, change points were identified in the relationship of density to forest composition and shrubs for just over half (12 of 20) of commonly-detected species. Using change point analysis I was able to distinguish forest stands representing suitable from marginal habitat for these twelve species. However, designation of forest stands where density was low as of 'marginal' quality is based on the assumption of a positive correlation between bird density and habitat quality. This assumption has been widely-applied, and is relatively well-supported by data, though Bock and Jones (2004) reported negative correlations between reproductive success and bird density in 36% of relationships in North American forests.

These results reveal a further key question needing attention prior to generating management guidelines from the results. What magnitude of difference in response is large enough to distinguish suitable from unsuitable habitat? For most species, I found that average density was at least two times higher in suitable habitat. If a benchmark value to distinguish suitable habitat is identified using differences in density for habitat specialists (i.e. > 3.2 fold difference in density), then habitat quality would be identified in this study for only two other species – the Tennessee warbler and white-throated sparrow. These results highlight the importance of considering whether the model accurately predicts species responses to habitat. A key question to ask is whether a high response (i.e. high density) measured in one study is high relative to the responses of populations elsewhere? Low responses below a change point may represent marginal habitat only relative to what was sampled.

Another key question is whether the magnitude of the difference in response above and below the change point is the only relevant distribution pattern for delimiting habitat quality, or whether the change point reveals additional patterns in bird distribution that may also be relevant. For example, suitable habitat would not be delimited for the yellow warbler using a three-fold difference in density below and above change points as a bench mark to distinguish suitable from marginal habitat. Inspection of the data (Figure 3.4a) reveals that, unlike the other habitat specialists, the yellow warbler was found relatively rarely but at high density below the change point, such that there was a relatively smaller difference in average densities below and above the change point.

Though yellow warbler density is on average higher above the change point, highest quality habitat may be represented by the few stands with high yellow warbler densities below the change point. Careful consideration of the meaning of the change point may lead researchers to investigate the processes leading to high density but low rates of colonization by the yellow warbler of mixedwood stands.

3.8.5. Management Guidelines for Mixedwood Stands

A major impact of the focus on regeneration of coniferous stands in the world's boreal forests has been a reduction in the amount of mixedwood stands, and the amount of shrub cover in younger stands (Niemi et al. 1998; Hagar 2007). In the boreal forest of western Canada, logging of mixedwood stands has resulted in an increase in stands dominated by either coniferous or deciduous species (Schieck and Hobson 2000). Though effort has been made to develop regeneration strategies that retain 'intimate' mixtures of coniferous and deciduous trees, such strategies have largely eluded researchers of boreal silviculture (Kabzems et al. 2007). Instead of naturally heterogenous mixtures of coniferous and deciduous trees, cutblocks in BC managed as a mixedwood stand continue to be planted as homogenous sub-blocks of either coniferous or deciduous trees (Martin 2005). Stand regeneration standards in Alberta and BC have led to large increases in the area over which deciduous species have been removed from regenerating stands by mechanical and chemical means. The standards largely focus on coniferous trees as crop trees that require the removal of competing taller deciduous tree and shrub species within a 1 to 2 m radius of coniferous saplings (Kabzems et al. 2007; Lieffers et al. 2008).

The results of my work suggest that while current practices will continue to provide habitat for coniferous tree specialists like the golden-crowned kinglet, they will reduce or eliminate habitat for the majority of common songbird species breeding in northeastern BC. Coniferous stands supported about five fewer bird territories per hectare of four fewer species than mixedwood and deciduous-dominated stands. With the exception of coniferous specialists, most other species did not occur or rarely occurred in stands with less than 20% deciduous content. Suitable habitat was identified using change point analysis for twelve species. For ten of these twelve species, suitable habitat was identified as deciduous and deciduous-dominated stands, in which densities were on average 2.9 (± 0.02) times higher than in coniferous-dominated stands.

As an example of the implications for bird conservation of continued forest practices that convert old growth mixedwood stands to >90% coniferous, in the Fort St. John TSA, 60% (12 of 20 species) of commonly detected species would experience loss of high quality habitat over 77% of the 46, 740 km^2 landbase if logged stands were planted to pure coniferous. Assuming that rarely-detected species (approximately 67 species – 44 detected in this study and 23 undetected) show similar patterns in relationships to forest composition as commonly-detected species, then 52 of 87 forest bird species would experience substantial loss of high quality habitat.

‘Thresholds’ delineating mixedwood from ‘pure’ forest habitats for songbirds occur at percentages of deciduous trees greater than 33% (9-44% 95% C.I.). However, the densities of coniferous specialists and most other species except deciduous specialists were lower in ‘pure’ deciduous stands (> 90% deciduous). Stands that are managed to result in intimate mixes of coniferous and deciduous trees will provide habitat for the majority of common songbirds, including deciduous specialists like the American redstart and least flycatcher.

Table 3.1. Foraging associations of commonly-detected forest birds around point counts in 90 old (>100 years) stands in the mixedwood boreal forest.

Foraging Associations			
Tree Specialist - Deciduous	**Tree Specialist - Coniferous**	**Tree Generalist**	**Ground/understory**
American redstart[1]	Golden-crowned kinglet[4]	Blue-headed vireo[5]	American robin[11]
Least flycatcher[2]		Rose-breasted grosbeak	Dark-eyed junco[1]
Warbling vireo[3]		Red-breasted nuthatch[6]	White-throated sparrow[11]
Yellow warbler[1]		Black-throated green warbler[1,7]	Ovenbird[11]
		Western tanager[1]	Swainson's thrush[12]
		Tennessee warbler[8]	
		Yellow-bellied sapsucker[9]	
		Yellow-rumped warbler[1]	
		Magnolia warbler[1]	
		Ruby-crowned kinglet[10]	

[1]Greenberg et al. 1999; [2]Sherry and Holmes 1985; [3]Airola and Barrett; [4]Mills 2007; [5]James 1998; [6]Ghalambor et al. 1999; [7]Robichaud and Villard 1999; [8]Rimmer and Mcfarland 2012; [9]Walters et al. 2002;; [10]Wilson and Comet 1996; Swanson et al. 2008; [11]Ehrlich et al. 1988; [12]De Graaf et al. 1985

Table 3.2. The relative strength of support using AICc of GLM models relating the density of forest birds to forest composition (% deciduous) in comparison to shrubs in old stands (n=90) in the mixedwood boreal forest.

Species	**Model**	**Forest Composition + Shrubs**	**Forest Composition**	**Shrubs**
AMRE	P	**208.4**	223.2	289.5
LEFL	P	**129.5**	133.8	173.6
WAVI	P	206.9	**205.9**	223.9
YWAR	P	121.8	**119.8**	143.5
GCKI	P	186.4	**184.5**	218.9
RCKI	P	179.8	**177.8**	181.5
BHVI	P	118.9	120.1	**118.2**
MAWA	P Q[a]	139.8	156.0	**135.0**
BTNW	NB Q	228.0	**225.9**	227.7
RBNU	P	170.1	**168.9**	170.6
RBGR	P	129.0	**127.5**	140.6
TEWA	P Q	183.2	**180.6**	196.6
WETA	P Q	167.1	**166.0**	173.8
YBSA	P	202.2	**201.0**	204.6
YRWA	P	317.8	**317.5**	317.6
AMRO	P	183.7	**183.4**	190.5
DEJU	NB Q	**168.3**	169.6	170.3
OVEN	NB	198.3	**198.0**	200.1
SWTH	P Q	**315.3**	319.3	318.8
WTSP	P	261.9	**259.9**	288.1
Tree Generalists[b]	NB Q	**1650.5**	1651.7	1669

Species names are given in Appendix B; parameters for the best models (bold) are shown in Table 3.3.
[a] Quadratic forms (Q) of Poisson (P) or Negative Binomial (NB) models resulted in AICc of 2 or more units for the relationship to forest composition (there was no support for quadratic relationships to shrubs by any species). [b] Excluding the yellow-rumped warbler.

Table 3.3. Results of GLM and change point analyses of relationships of birds to forest composition (% deciduous) and shrubs in the mixedwood boreal forest.

Species[a]	Slope	SE	OD [b]	R^2 [c]	AIC$_L$ [d]	AIC$_S$ [d]	SR (SE)[e]	Maxstat[e]	95% C.I.[e]
Tree Type Specialists									
AMRE FC	0.036****	4.56x10-3	1.05	87.2	208.4	193.4	81 (3.1)	73****	45-82
Shrubs	0.020****	4.87x10-3							
LEFL FC	0.048****	8.95x10-3	0.86	72.3				68***	51-86
Shrubs	0.021**	8.10x10-3							
WAVI	0.022****	4.62x10-3	1.19	33.1				52****	18-73
YWAR	0.039****	8.73x10-3	1.43	38.8				79***	50-87
GCKI	-0.024****	4.20x10-3	0.89	47.1	184.5	180.9	34 (8.9)	61***	9-64
Tree Type Generalists									
BHVI Shrubs	-0.016	0.011	0.89	4.41					
MAWA Shrubs^2	0.097***	0.031	1.01	38.5	138.3	131.5	25 (5.3)	24***	9-20
	7.95x10-4	4.04x10-4							
BTNW FC^2	0.041*	0.022	0.94	6.66					
	3.70x10-4	2.10x10-4							
RBNU	-0.011**	5.30x10-3	1.19	6.96	168.9	160.7	39 (15)		
RBGR	0.032****	8.58x10-3	1.31	27.4	127.5	125.1	69 (13)	78****	14-87
RCKI	-9.77x10-3**	4.76x10-3	1.08	6.81	177.8	170.8	78 (6.7)		
TEWA FC^2	0.065**	0.027	1.01	25.6	182.5	178.9	46 (8.9)	44***	7-79
	4.01x10-4	2.18x10-4							
WETA FC^2	0.080***	0.029	1.10	18.4	173.2	165.4	73 (6.9)	33***	9-52
	6.70x10-4	2.47x10-4							
YBSA	0.012***	4.44x10-3	1.02	9.84				42***	
YRWA	-4.19x10-3*	2.15x10-3	0.75	6.89					
Tree Gen[f] FC^2	0.040****	0.010	1.13	5.98				33****	9-44
	3.25x10-4	8.48x10-5							
Shrubs	6.24x10-3	3.37x10-3							
Ground and Understory Foragers									
AMRO	0.012***	4.71x10-3	0.99	11.7				79**	63-87
DEJU FC^2	-0.041**	0.025	0.99	19.0					
	0.022	2.31x10-4							
Shrubs	-0.021*	0.012							
OVEN	0.014*	7.60x10-3	0.84	6.03					
SWTH FC^2	0.014*	9.11x10-3	0.87	17.6					
	1.84x10-4	3.54x10-3							
Shrubs	8.86x10-3**	8.70x10-5							
WTSP	0.019****	3.43x10-3	1.19	38.7				61	9-68

Significance levels: *0.10 *<0.05 ***<0.01 ****<0.001. [a]Species names in Appendix B. [b]Overdispersion. [c] Nagelkerke's R-squared. [d]AICc of linear (AIC_{L}) and segmented (AIC_{S}) models. [e]Change points from segmented regression (SR ± standard error (SE)), and maximally-selected rank statistics (Maxstat) with 95% confidence intervals estimated from 1000 bootstrapped change points. [f] Tree generalists excluding the yellow-rumped warbler.

Table 3.4. Densities (+SE) of male birds averaged across forest stands grouped according to change points in the relationship of species to forest composition (% deciduous) and shrub cover.

Species[a]	Occurrence Threshold[b]	Low[c]	SE	Intermediate[c]	SE	High[c]	SE
Tree Type Specialists							
AMRE	20	1.11	0.23			2.52	0.55
LEFL	45	0.17	0.06			0.82	0.17
WAVI	20	0.32	0.09			1.02	0.15
YWAR	39	0.20	0.09			0.48	0.12
GCKI	None	2.00	0.25	1.60	0.03	0.32	0.11
Tree Type Generalists							
BHVI Shrubs			no change points				
MAWA Shrubs[2]		0.13	0.07			1.22	0.26
BTNW FC[2]			no change points				
RBNU		0.27	0.06			0.19	0.04
RBGR	18	0.10	0.03			0.28	0.08
RCKI	90	0.27	0.05			0.12	0.07
TEWA FC[2]		0.09	0.03			0.30	0.05
WETA FC[2]		0.29	0.15	0.50	0.08	0.37	0.10
YBSA		0.29	0.09			0.75	0.10
YRWA			no change points				
Tree Gen[c] FC[2]		0.26	0.05			0.44	0.03
Ground and Understory Foragers							
AMRO		0.20	0.04			0.42	0.08
DEJU FC[2]							
OVEN	13						
SWTH FC[2]							
WTSP		0.28	0.06			0.85	0.08

[a]Species names in Appendix B. [b]Lowest (or highest) % deciduous at which species occurred. [c]Average densities within stands with lower and higher % deciduous than change point values (see Table 3.3). Averages for low % deciduous did not include stands with % deciduous below occurrence thresholds. Intermediate refers to average densities in stands with intermediate % deciduous for species with two change points. [c]Averaged over nine tree generalist species (excluding the yellow-rumped warbler).

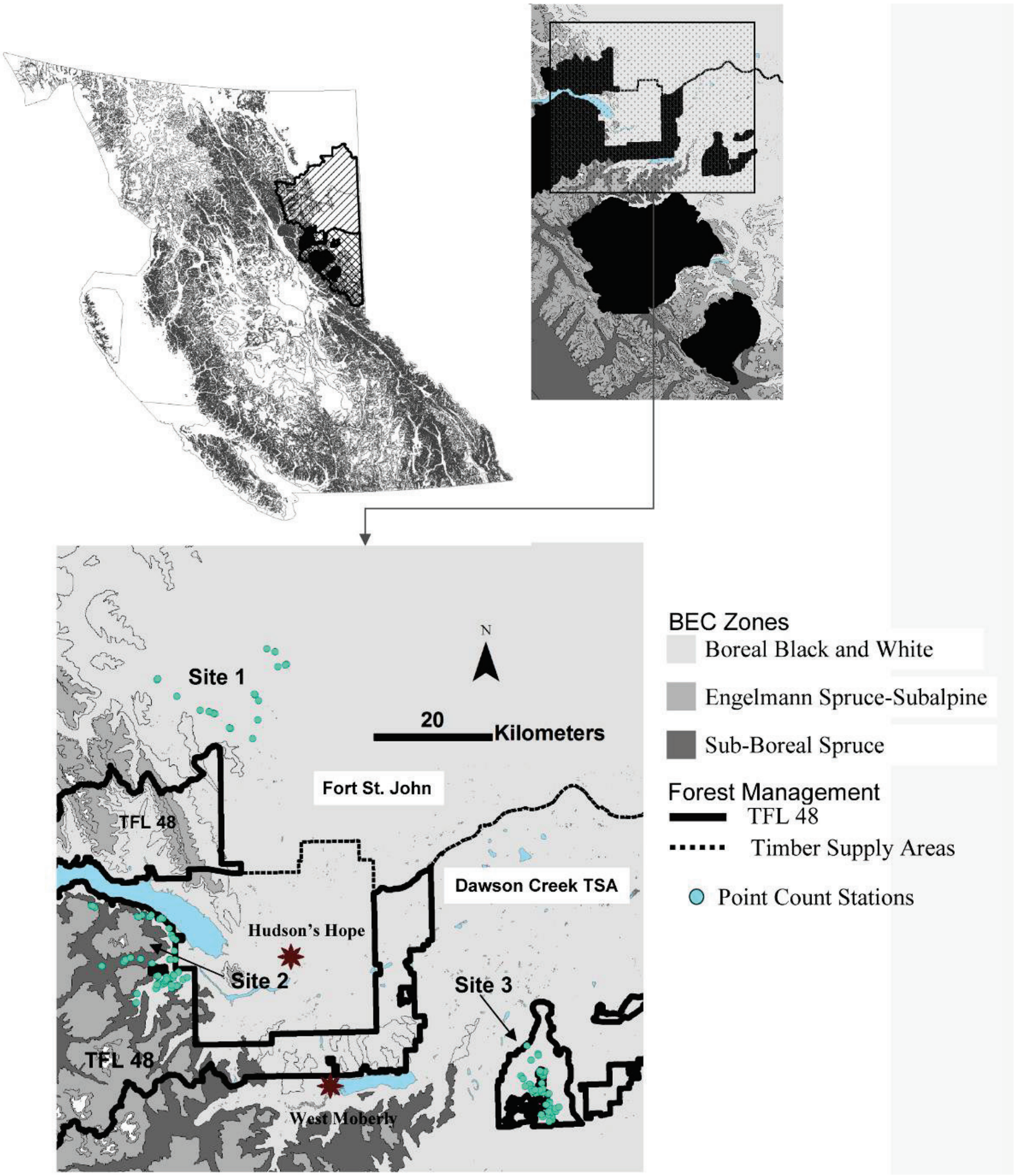


Figure 3.1. Map showing location of three study sites in northeastern BC.

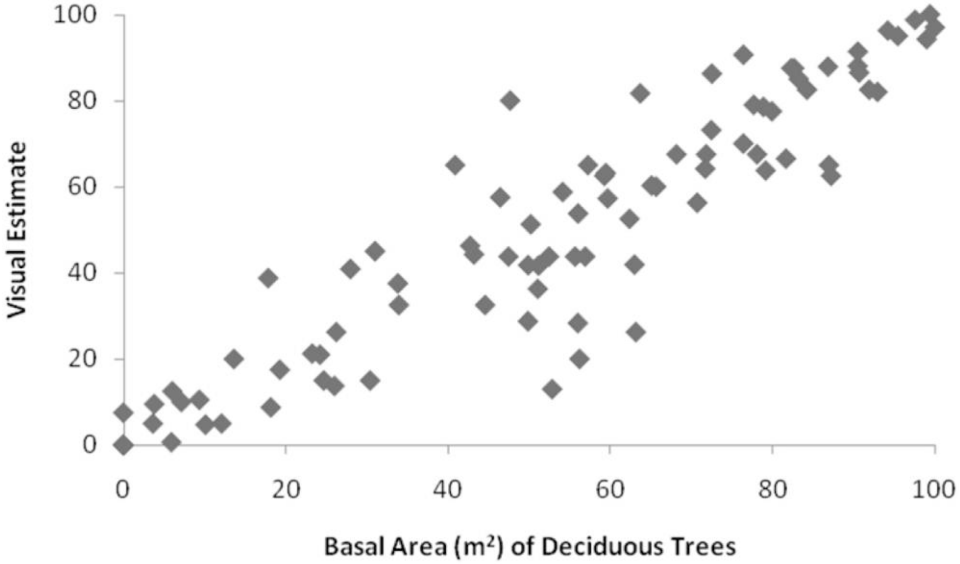


Figure 3.2. Spearman rank correlation (r_s = 0.92) between visual estimates and basal area measures of the proportion of deciduous trees around point count stations in 90 old (> 100 years) forest stands. Both measures were averaged over four 11.3 m radius (0.04 ha) circular vegetation plots centred on (one plot) and around (three plots) point count stations.

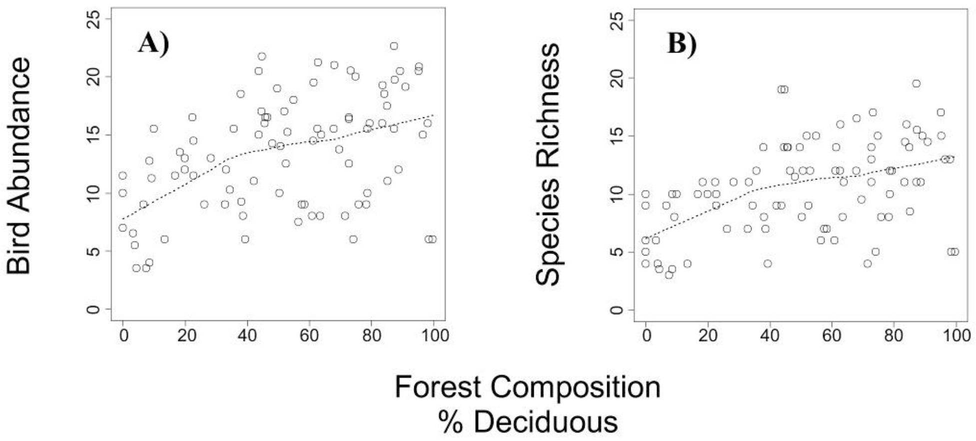


Figure 3.3. Average number of male birds detected (a) and species richness (b) during point counts within 90 old (>100 years) forest stands.

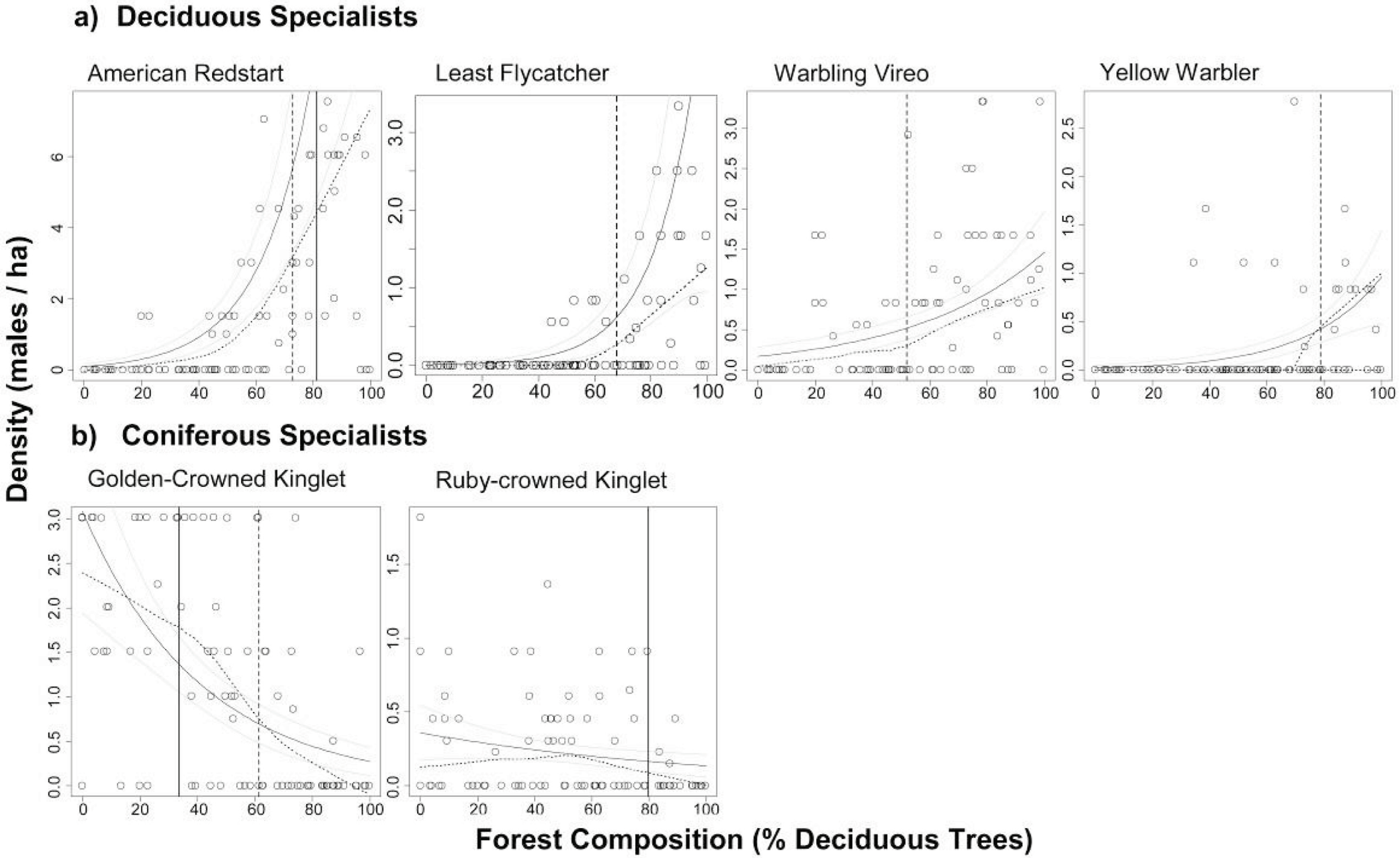
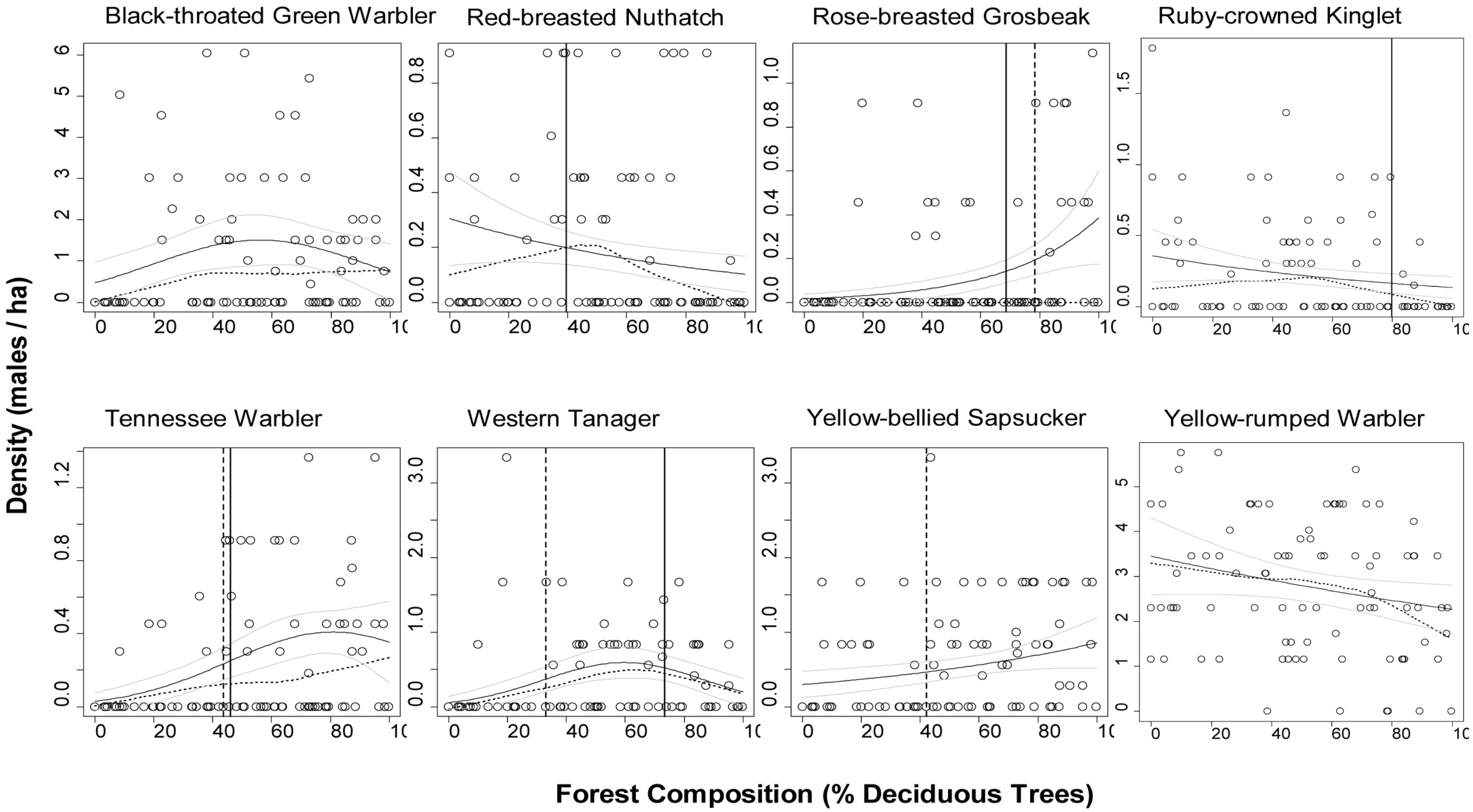
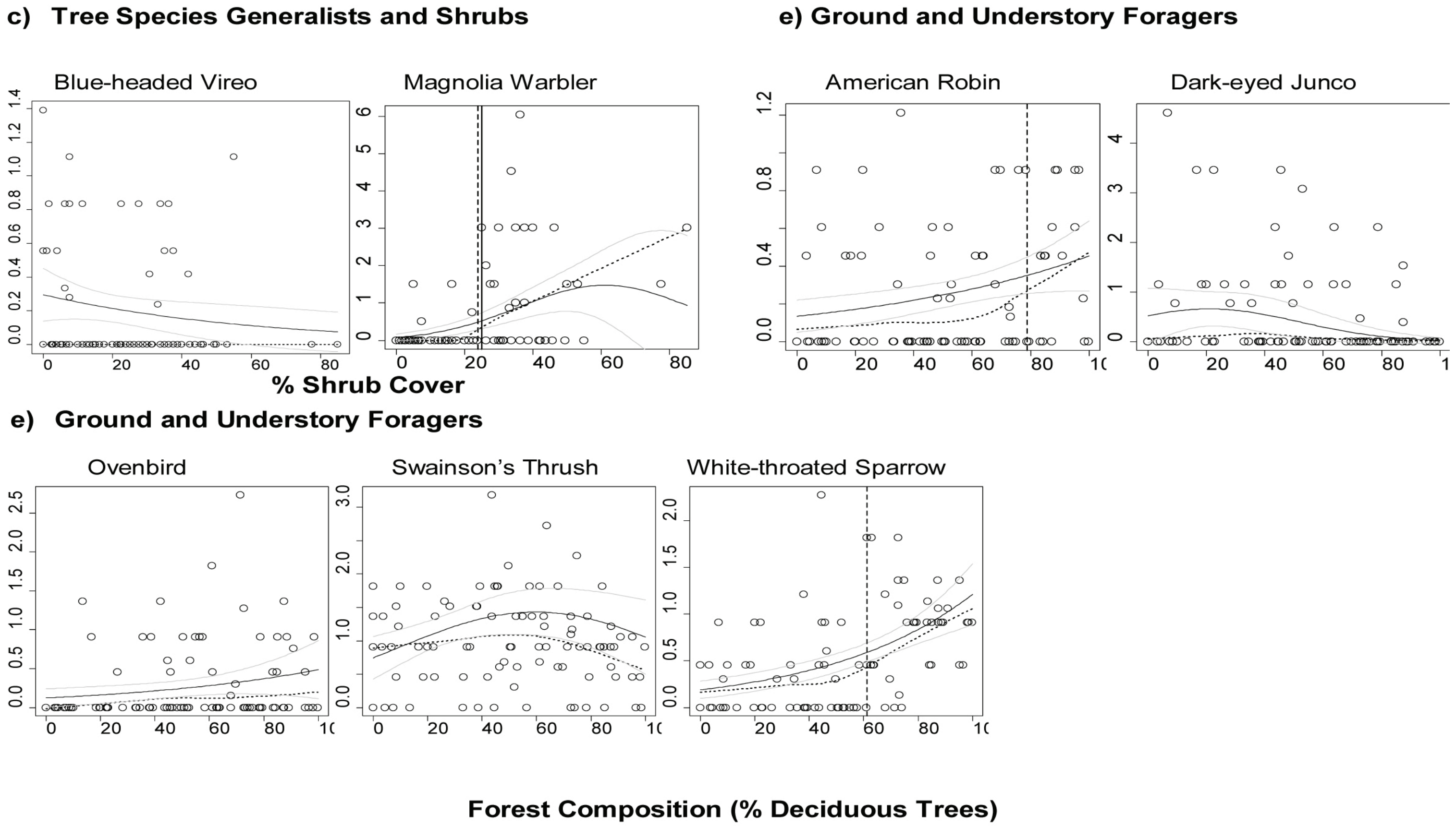

a) Deciduous Specialists
American Redstart
Least Flycatcher
Warbling Vireo
Yellow Warbler
b) Coniferous Specialists
Golden-Crowned Kinglet
Ruby-crowned Kinglet
Density (males / ha)
Forest Composition (% Deciduous Trees)
0
2
4
6
0.0
1.0
2.0
3.0
0.5
1.5
2.5
0
20
40
60
80
100

Figure 3.4. Predicted responses to forest composition (a-c, e) and shrubs (d) of the density with 95% confidence intervals of adult male birds in 90 old (> 100 years) forest stands using GLMs (log link). Change points are indicated by solid (segmented regression) and dashed (maximally-selected rank statistics) vertical lines. Dashed horizontal line is the LOESS line. Models shown are the most likely of models including forest composition and shrubs as predictors; predicted responses to forest composition are derived from models including shrubs for American redstart, least flycatcher, dark-eyed junco, and Swainson's thrush (Table 3.2). See Table 3.3 for parameter estimates.

c) Tree Species Generalists and Forest Composition




c) Tree Species Generalists and Shrubs
Blue-headed Vireo
Magnolia Warbler
% Shrub Cover
e) Ground and Understory Foragers
American Robin
Dark-eyed Junco
e) Ground and Understory Foragers
Ovenbird
Swainson's Thrush
White-throated Sparrow
Forest Composition (% Deciduous Trees)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0
1
2
3
4
5
6
0.5
1.5
2.0
2.5
3.0
0
20
40
60
80

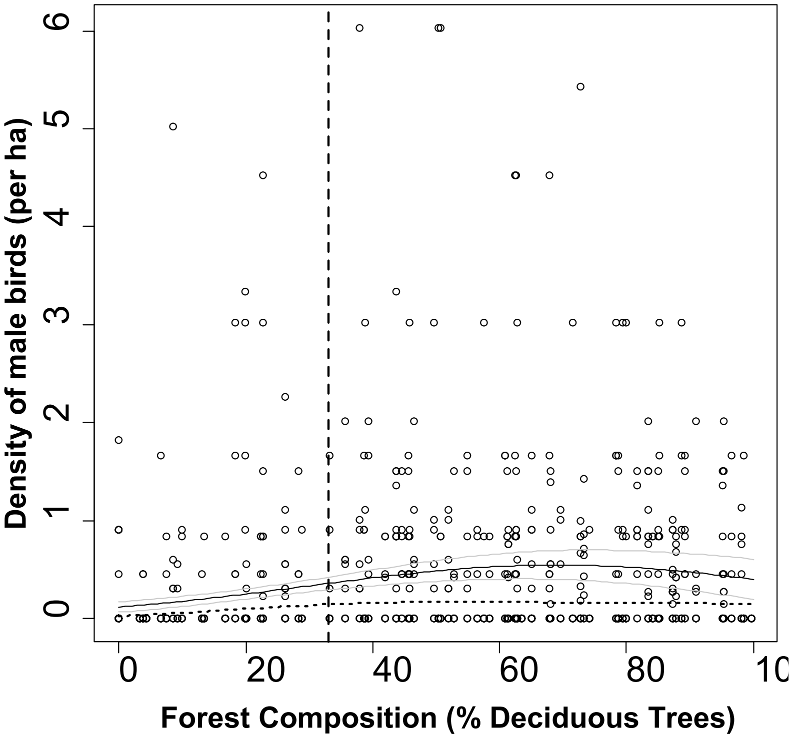


Figure 3.5. Density with 95% confidence intervals of adult male birds of species that are generalist with respect to foraging preference for deciduous and coniferous trees (excluding the yellow-rumped warbler, see Table 3.1 for species) in relation to the forest composition of old forest stands using Poisson GLM (log link). Predicted response is derived from a model that includes shrub cover (Table 3.2). Dashed vertical line is the location of a change point identified using maximally-selected rank statistics. Dashed horizontal line is the LOESS line. See Table 3.3 for parameter estimates.

4. Chapter 3

Quantifying High Quality Habitat for a Keystone Species in the Mixedwood Boreal Forest

4.1. Abstract

Studies of vegetation characteristics chosen for nest sites provide a relatively easily-quantified measure of bird habitat. Using three years of field data (2007-2009) collected in the Peace River region of northeastern BC, I related to vegetation the distribution and reproductive success of the yellow-bellied sapsucker - a keystone species of the mixedwood boreal forest. I quantified ‘change points’ in selectivity for fine scale vegetation for nest sites within territory cores using change point analysis and conditional logistic regression, and then quantified the relationship between territory density and forest composition (% deciduous) at the broader stand scale. To test whether broader scale distribution could be inferred from fine scale preferences, I related territory density to the availability of selected vegetation at the stand scale. I tested whether the vegetation structures selected in territory cores were related to reproductive success, measured as clutch size and fledgling counts. Yellow-bellied sapsuckers chose (n=58) live decaying aspen trees of intermediate size surrounded by on average twice the number of live decaying aspen trees than unused sites, indicating that the availability of other nest trees was important in territory selection. The density of yellow-bellied sapsucker territories was unimodally related to % deciduous of forest stands. Territory

density and the stand density of vegetation structures chosen for nesting were highly correlated. Similar to findings of other studies, none of the vegetation variables that were significant predictors of nest site selection were significantly related to reproductive success within the nestling stage. The results suggest that for species like woodpeckers with high nesting success, nest site preferences can be ‘scaled up’ to infer stand scale distribution, but measures of fledgling quality and survival may be required to more accurately quantify habitat quality.

4.2. INTRODUCTION

Within the context of sustainable forest management, the ultimate goal of the quantification of species-habitat relationships is to define management guidelines to ensure that enough ‘good’ habitat is retained to sustain species across logged landscapes. The quantification of habitat quality from species-habitat relationships has a somewhat confused history in the ecological literature, but in the past decade there has been agreement among researchers on an operational definition of high quality as habitat that confers the highest per capita contribution to population growth (Jones 2001; Tyre et al. 2001; Johnson 2007). Habitat preferences are assumed to be adaptive and inherited genetically (Jaenike and Holt 1991; Martin 1998) and perhaps socially. Thus, high quality habitat is defined as habitat preferred by sub-populations that are genetically or socially advantaged to select habitats that confer higher reproductive success and survival (Robertson and Hutto 2006; Arlt and Pärt 2007). Thus, it has become widely acknowledged that habitat quality should be quantified in terms of how the preferences of individuals affect their reproduction and survival (Jones 2001; Johnson 2007; Pärt et al. 2007).

Though species-habitat models based on *demographic* measures provide the best measures of high quality habitat from a theoretical perspective, models based on measures of *distribution* are often the most practical, especially when habitat quality needs to be quantified for large numbers of species. Indeed, most quantification of habitat quality has been limited to vegetation correlates of patterns of spatial or temporal distribution, measured by occurrence rates (presence or absence, percent occurrence), selection rates, and density or abundance (Tyre et al. 2001; Pearce and Ferrier 2001;

Nielsen et al. 2005). Distribution and demography must be positively correlated in order for distributional models to suffice as measures of habitat quality, but there are myriad reasons why this may at times not be so. Distribution and demography appear to be positively correlated in the majority of bird studies (Bock and Jones 2004), but a well-established literature finds empirical evidence that the relationship is variable across ecological conditions, scales, and life histories (see Jaenike and Holt 1991). For example, low fecundity in areas of high density can provide evidence for ‘ecological traps’ (reviewed in Battin 2004; Robertson and Hutto 2006), as well as support for the long-standing “ideal-despotic distribution” hypothesis (Fretwell and Lucas 1970).

The degree to which distribution and demographic measures are related remains unclear. Furthermore, various measures of either distribution or demography may be related to different environmental variables and at different scales (Johnson 2007). Vegetation characteristics that are correlated with reproductive productivity often differ from those that birds select at fine spatial scales from available vegetation (Misenhelter and Rotenberry 2000; references in Chalfoun and Martin 2007; Dalley et al. 2008; Hooge et al. 1999; Sadoti and Vierling 2010; Wightman et al. 2010). For example, productivity in wheatears is highest in short grasslands, but male wheatears show no selection for grassland height when selecting territory locations (Arlt and Pärt 2007). These studies suggest that the relationship between fine scale preferences and broader scale distribution, reproduction and survival should be assessed in order to determine the reliability of nest site selection as a measure of habitat quality.

Many studies have focused on quantifying habitat quality from species-habitat relationships, but considerably less attention has been concerned with how to use the relationships to guide management once they have been quantified. The concept of ‘habitat thresholds’ has been proposed as a quantitative and objective approach to determine how much habitat is necessary for species persistence. I argued the concept may be more usefully applied by using ‘change points’ in species-habitat relationships to delineate habitat quality rather than quantity (see Introduction, Chapter 1). My approach to delineating high quality habitat from species-habitat models is detailed in Chapter 1. In this chapter, I examine a ‘keystone’ woodpecker species and ask whether vegetation selected above change points in preferences for fine-scale vegetation features as nest sites can be used to predict broader-scale distribution, and whether nest site selectivity and productivity are correlated.

I related the distribution and reproductive success of yellow-bellied sapsuckers to vegetation using three years of field data collected in the mixedwood boreal forest in the Peace River region of northeastern BC. I tested for change points in selectivity for vegetation variables within territory cores at fine spatial scales, and then related the density of selected vegetation to the forest composition (% deciduous) of old stands (> 90 years). I tested whether fine scale preferences for nest sites could be used to predict broad scale distribution by correlating predicted values from models relating the density of preferred vegetation and nest territories to the forest composition of stands. I also examined whether the vegetation structures selected in territory cores were related to clutch size and fledgling counts to assess the reliability of nest site selection as a measure of habitat quality.

4.3. METHODS

4.3.1. Study Area

This research was conducted in three study sites within an area about 80 x 80 kilometers near the communities of West Moberly and Hudson's Hope (Figure 3.1) and within the Boreal White and Black Spruce (BWBS) Biogeoclimatic (BEC) Zone. Two study sites are found in the 'Moist Warm' subzone of the BWBS BEC Zone, which extends across the boreal plains of northeastern BC. At upland sites, the forest is characterized by deciduous stands dominated by trembling aspen (*Populus tremuloides*) with lesser amounts of balsam poplar (*Populus balsamifera*), paper birch (*Betula papyrifera)* and Alaska birch (*Betula neoalaskana*), mixedwood stands dominated by aspen and white spruce (*Picea glauca)*, and coniferous stands dominated by white spruce and lodgepole pine (*Pinus contorta var. latifolia*). Black spruce (*Picea mariana*) and larch (*Larix laricina)* dominate in wet lowland 'muskeg' sites. In all forest types, willow (*Salix spp*), Sitka alder (*Alnus* sinuata), and green alder (*Alnus viridis*) are the only tall (> 1.3 m) shrub species present, though tall shrubs are infrequent in coniferous stands. The third study site is found within the 'Wet Cool' subzone of the BWBS BEC Zone at the extreme western range extent of the mixedwood boreal forest, where the land rises in elevation in the foothills of the Rocky Mountains. Deciduous and mixedwood stands are less common as the land gains in elevation from east to west, such that these stand types are generally rare and are mostly found in riparian valleys or as young stands regenerating from clearcut logging. The dominant coniferous tree species are white spruce, hybrid spruce (*Picea glauca x engelmannii*), lodgepole pine, and small amounts of subalpine fir (*Abies lasiocarpa*); Engelmann spruce (*Picea engelmannii*) and subalpine fir dominate at higher elevations in the ESSF Zone. The understory vegetation in coniferous-dominated stands in the Wet Cool BWBS Zone is similar to that of the Moist Warm BWBS Zone to the east, with the addition of black huckleberry (*Vaccinium membranaceum*) as a common species (Delong et al. 1991).

4.3.2. Quantifying vegetation selected for nest sites

I quantified selection probabilities for vegetation variables measured within a ‘constrained’ study design (Keating and Cherry 2004; Battin and Lawler 2006). I chose available, unused trees by walking to a pre-selected coordinate using a handheld GPS, and selecting the randomly-chosen *n*th tree between 1 and 12 trees within a 30 m belt transect along a random direction from the coordinate. Inclusion criteria for available trees were: live, decaying aspen trees (Decay Class 2) with at least one fungal conk and no active woodpecker cavities. Decay Class was assessed using the Wildlife Tree Classification system in the provincial inventory standards for woodpeckers (RIC 1999). Coordinates were chosen in stands 100-180 years old using ArcGIS at a randomly-chosen direction and distance between 250 and 350 m (average 300 m) from the nest tree coordinate, based on the assumption that average territory size was less than 7 ha (data from this study). Since I found sapsucker nests at sites (< 30 m radius) with only a small (~2%) proportion of aspen trees in 2007, I selected coordinates in stands across the gradient in stand composition. I confirmed that available off-territory sites were not used by yellow-bellied sapsuckers by ensuring there were no nest cavities or sapwells, and by not eliciting responses to playback of sapsucker calls and drumming during one visit during the pre-fledging period in June.

I compared the following variables describing nest trees and available non-nest trees: diameter at breast height (dbh), decay state, tree height, height to live crown, tree top condition (broken or not), and the number of fungal conks. For nest trees, I recorded the height and orientation of the active cavity and the height, orientation, and age of unused cavities. I further assessed the decay of Decay Class 2 aspen trees which were nest or available trees (most nest trees and all available trees) by creating a ‘Decay

State' category as follows: Decay State 2a trees had some but few signs of decay and most branches were intact, Decay State 2b trees showed signs of decay and some branches were missing, Decay State 2c trees were almost dead, showed many signs of decay and had small live crowns.

I developed *a priori* models to determine which vegetation variables were important predictors of yellow-bellied sapsucker nest trees and sites. I chose variables that I hypothesized to be important from field observations, and from those that have been found to be statistically significant in published studies on yellow-bellied sapsuckers (Table 4.1). I quantified selection by comparing used sites with available unused sites at three spatial scales. The three scales were the tree, the tree site (<11.3 m radius), and the territory core (< 41.3 m, Figure 4.1). The tree scale was described by the characteristics of the focal tree itself. The 'tree site' scale was described within one 11.3 m radius circular vegetation plot centred on nest and available non-nest trees.

Selection at the territory core scale was measured within the tree site plot and within three additional plots positioned 30 m away along directions separated by 120^0. The location of the first outer plot was chosen randomly. In each plot, I measured the density of living birch stems > 15 cm DBH because other studies have found a greater incidence of sapwells in birch trees (Eberhardt 2000; Savignac and Machtans 2006). Shrub sap is also a food source for adults and young fledglings (Walters et al. 2002; my observations) and shrubs may also confer predator protection. I visually estimated the % cover of shrubs taller than 1.3 m (*Alnus* and *Salix* spp.) as the percent of ground area covered when the shrub crowns were projected vertically excluding any overlap. To quantify selection for nest trees with other potential nest trees nearby, the density of all aspen and live decaying aspen trees > 15 cm DBH were measured at the tree site and territory core scales.

Because yellow-bellied sapsuckers often re-pair with the same mate, and use the same territory in successive breeding seasons (Walters et al. 2002), I assumed that nests found within 70 m of nests used in previous seasons belonged to the same individuals. Most of the nest trees (85%) which I grouped into the same territory were within 50 m and on average 23.6 ± 2.48 m from each other. Nest trees of neighboring pairs of yellow-bellied sapsuckers within 250 m of one another were separated by at least 80 m and on average 135 ± 7.62 m apart. For territories for which I had multiple years of nest site data, I used the average of tree measurements across years in statistical analyses, and vegetation measurements around the first nest tree found per territory.

None of the variables used to build models were correlated ($R_s > 0.40$), except the density of aspen with decaying aspen, which I treated separately such that combinations of variables produced fifteen *a priori* models. To estimate the logit of selection probabilities for vegetation variables, I used conditional logistic regression because I used a case-control sampling design – nest trees and sites were paired with available unused trees and sites (Keating and Cherry 2004). Within an information-theoretic approach, the strength of support for models were compared using second order AIC (AICc). I tested quadratic relationships for variables showing non-linearity in univariate plots, and chose the quadratic model if it was two or more AICc units lower than the linear. Akaike weights (w_i) were computed as follows from the differences in AICc between R models from the *i*th model with the lowest AICc (ΔAIC): w_i = exp(-1/2$\Delta i / \sum_{r=1}^{R} \exp(-\frac{1}{2\Delta r})$, Burnham and Anderson 1998). The relative strength of support for models was assessed from evidence ratios, calculated as the ratio of model weights to the highest model weight. Models with evidence ratios less than two were considered to be equally likely. Goodness of fit of the best models was assessed using outputs from the ‘clogit’ function of the R ‘Survival’ package (Therneau and Lumley 2011).

4.3.3. Relating Territory Density to Forest Composition

I estimated the density of yellow-bellied sapsucker territories using a stratified sampling design. Yellow-bellied sapsuckers and vegetation were sampled in 90 old (100-180 years) forest stands across a gradient in stand composition. To ensure relatively equal sampling across the gradient in forest composition, I used a Geographic Information Systems (GIS) database in ArcGIS 9.1 (Environmental Systems Research Institute 1999-2005) to categorize stands by age and stand composition as follows: coniferous 0-19% (n=20 stands), coniferous-dominated mixedwood 20-39% (n=18 stands), mixedwood 40-59% (n=16 stands), deciduous-dominated mixedwood 60-79% (n=16 stands), deciduous 80-100% (n=20 stands).

I searched for sapsucker nests systematically along line transects that I had established to survey for songbirds (Chapter 2), though I also found sapsucker nests opportunistically while travelling between sampling points during songbird surveys. Nest sites were searched for, monitored, and quantified according to established protocols (Dudley and Saab 2003). I found nest trees by the sound of begging nestlings (59% of nests, 96 of 163 nest trees), by following adults back to the nest cavity or by observing wood chips at the base of nest trees and then later confirming the nest as active (67 nest trees). The latter two methods were used to find nests in the egg-laying (16 nests on 16 territories) and incubation (14 nests on 14 territories) stages. I quantified yellow-bellied sapsucker territory density as the number of nest territories per transect. I used the average territory density for stands surveyed with more than one transect. I included nests detected within 80 m of the start and end of transect lines in all directions, and within 80 m of the transect line. I chose this distance because 80 m was about the maximum distance from which I heard begging nestlings. The total area surveyed per transect was 5.2 ha (3.2 for the line and 2 x 1.0 ha for the half circles at the start and end of lines). Nest trees were at least 60 m from stand edges on 83 of 90 stands; territory cores likely overlapped adjacent stands for fifteen nest trees of eleven territories within seven stands.

In each stand sampled, I estimated stand composition in four 11.3 m radius circular plots centred on point count stations. One plot was centred on the station, and three plots were positioned 30 m away along directions separated by 120^0. The location of the first outer plot was chosen randomly. I quantified stand composition from estimates of basal area derived from measurements of the diameter at breast height (DBH) of all trees (DBH > 15 cm) within vegetation plots. I also estimated stand composition visually from the centre of vegetation plots to about 30 m as the relative proportion of deciduous trees that reached canopy. Because of the high ‘patchiness’ in tree species composition in mixedwood boreal forests, I used the average of the visual and basal area estimates of stand composition in statistical analyses. I found that vegetation plots were sometimes too small to accurately sample composition at the stand scale, but I also wanted to correct my visual assessments for any bias.

The density of yellow-bellied sapsucker territories in relation to forest composition was modeled using Generalized Linear Modeling (GLM). I used the negative binomial model with a log link because a likelihood ratio test showed a better fit than the Poisson (Pearce and Ferrier 2001). I chose the quadratic model as the final model because it resulted in an AICc of 2 or more units lower than the linear model. Nagelkerke’s Pseudo-R^2 was used to approximate the proportion of variability in the data explained by the model (Nagelkerke 1991). Because GLM models appear non-linear on the probability scale, I checked the shape of the GLM model using Locally Weighted Scatterplot Smoothing (LOESS), a form of Generalized Additive Modeling which fits a non-parametric line to the mean response within a ‘running window’ along the x axis.

4.3.4. Delineating high quality habitat

Using models relating yellow-bellied sapsucker territory density and nest site selection to vegetation, I delineated high quality habitat as the range of vegetation above statistically-significant change points over which these responses were higher. To find change points in the relationship between territory density and forest composition, I used segmented regression (‘Segmented’ package, Muggeo 2003) and maximally selected rank statistics (‘Maxstat’ package, Müller and Hothorn 2004; Hothorn 2011). Segmented regression divides the data into two or more parametric models with different slopes by iteratively fitting linear models to each data set such that the ‘gap’ between the regression lines is minimized. The value of the independent variable at which the smallest gap occurs represents the change point at which occurs the greatest change in the slopes of two partitions of the response variable (Muggeo 2003). I considered segmented models that differed from linear models by two or more AIC unit to be evidence of a statistically significant reference point. A maximally-selected rank statistic divides the data into two groups at values of the independent variable of ‘high’ and ‘low’ response using non-parametric two-sample linear rank statistics. The value at which the rank statistics (standardized by sample size) above and below are maximized represents the change point, and is the value at which the difference in response between the two groups is largest (Müller and Hothorn 2004). I derived confidence intervals for change points derived from maximally-selected ranks statistics from 1000 bootstrap samples of change points.

To quantify change points in nest tree and site selection, only maximally-selected rank statistics were used to identify change points, because the R ‘Segmented’ package does not function for the analysis of conditional logistic regression. I used univariate conditional logistic regression models of selection probabilities in relation to vegetation variables that were significant predictors in the multivariate models, and choose between the linear and quadratic models for each predictor variable using AIC.

4.3.5. Relating fine to broad scale vegetation relationships

A main objective of this study is to determine whether fine scale preferences for vegetation at nest sites are useful to infer broader scale distribution in relation to forest composition. Thus, I related the stand density of vegetation delineated as high quality habitat around nest sites (i.e. vegetation above change points in nest site selection models) to forest composition using Poisson GLM with a log link. I tested for change points in the relationship, and then correlated the predicted values with those from the model relating territory density to forest composition. Using Spearman rank correlation, I determined the relationship between average territory density within stands and the stand density of high quality nest habitat. Stand averages for territories and vegetation were then averaged over stands within each decile of percent deciduous. Vegetation densities and forest composition were estimated from vegetation plots around point count stations rather than around nests to ensure random sampling and sampling across the full gradient in forest composition. Finally, I used AIC to compare the relative strength of support for models predicting territory density from forest composition and the stand density of high quality nest habitat.

4.3.6. Relating nest productivity to vegetation selected for nest sites

I quantified reproductive success per yellow-bellied sapsucker pair as clutch size and the number of fledglings. I counted the number of fledglings per nest using a video camera mounted on an extendable pole (‘cavity peeper’, Sandpiper Technologies Inc.). I assumed that females did not produce more than one brood per season (Tozer et al. 2011), and that all monitored nests were the first and only nest attempt by each female. High cavities (> 14 m) and those with small entrance holes could not be monitored by the camera. On 60 territories, at least one nest was monitored by video camera (72 nests) and the rest were monitored without the camera (19 nests); 40 territories (54 nests) were monitored without the camera, and 33 nests on 20 territories were not monitored. I monitored nests every 3–4 days to record nest stage (egg-laying, incubating, nestling, fledgling), to count the number of eggs or chicks, to assess the age of nestlings, evidence of predation, and nest fate (success or failure).

Unlike eggs, fledglings were sometimes difficult to accurately count. Since incubating adults usually left the nest cavity in response to call-playback, clutch size was usually easy to assess using the camera. Fledgling counts for 8 nests on 7 territories may be under-estimates because counts were made during the last few days of the nestling stage, when one or two begging nestlings blocked views of the other nestlings in the cavity, or when at least one nestling may have fledged. Fledgling counts from nests found by the sound of begging nestlings (27 of 72 nests found June 24 to July 6) compared to those found earlier in the season (observations of parents: 13 nests found June 2 to June 29; 30 nests found in egg stage May 23 to June 13) may have been biased either because these nests found later represent a biased sampled of successful nests, or because these were nests of *less* successful pairs which initiated nests later in the season. I tested for bias in fledging counts by comparing results of statistical analyses using data from all nests to results from nests found earlier and with more accurate fledgling counts.

I used GLM with a log link to test whether the reproductive success of yellow-bellied sapsuckers during nesting was related to the vegetation variables that sapsuckers chose for nesting (n = 61 territories, 51 of 58 territories used in analyses of nest site selection). I used the maximum count of eggs and fledglings, and the average of vegetation variables selected for nesting for territories for which I had multiple years of data (11 of 61 territories). I also summarized the relationships by calculating means and standard errors of the vegetation selected by pairs with low (< 3 fledglings) and high productivity, and of the nest productivity of pairs that selected vegetation below and above points of change.

All statistical analyses were performed using R (R Development Core Team 2011).

4.4. RESULTS

4.4.1. Vegetation selected for nesting

I found 178 active nest cavities in 163 trees on 120 breeding territories during the three years of this study (Appendix G and H). Except for one cavity in a poplar snag, all nest trees were aspen trees with internal heart rot, as evidenced by the presence of fungal conks on 97% of trunks (Appendix H). Most nest trees (89.9%) were dying and showed signs of more advanced decay than randomly-selected trees; the rest were dead trees. Trees chosen for nesting by yellow-bellied sapsuckers had on average twice as many fungal conks, more often showed other signs of advanced decay (Decay States 2b and 2c), and the DBH was on average 6.70 cm smaller than available unused trees (Appendix H). Tree sites and territory cores had on average 3.8 and 2.4 more aspen trees per 0.04 ha, respectively, and about twice the number of live decaying aspen trees in comparison to unused sites adjacent to the nesting territory. Territory cores were in patches of forests (~60 m radius) with on average about 15% more deciduous trees than random sites adjacent to nesting territories (Appendix H).

There was overwhelming support for the model predicting nest site selection as a function of nest trees and the density of potential nest trees at the tree site scale (11.3 m versus 4 x 11.3 radius plots, Table 4.2). This model was almost 100 times more likely than the next best model (Table 4.2). Thus, there was no support for the models predicting site selection from the density of all aspen trees, from live decaying aspen measured at larger territory core scale, or from the availability of food resources (Table 4.2).

Goodness-of-fit tests showed that the diameter and decay stage of nest trees, and the presence of other potential nest trees around nest trees explained 74% of the variation in the data and the model including these variables fit the data well (Table 4.3). Maximally-selected rank statistics identified significant change points in univariate relationships between yellow-bellied sapsucker site selection and tree DBH, fungal conks, and the density of surrounding live decaying aspen (Table 4.3, Figure 4.2). Using these change points and the smallest diameter nest tree, I identified high quality nesting habitat for the yellow-bellied sapsucker as live decaying aspen trees 26 to 41 cm DBH with more than 4 fungal conks, surrounded within an 11.3 m radius by at least one other live decaying aspen tree.

4.4.2. Relating fine to broad scale vegetation relationships

Forest composition at the stand scale was a significant predictor of the density of yellow-bellied sapsucker territories and of preferred trees for nesting (live decaying aspen trees 25.5-41 cm DBH, fungal conks were not counted), and explained 27.3% and 43.8% of the variability in the data, respectively (Table 4.4; Figure 4.3a and b). The negative binomial with a quadratic term was the most likely model for each, and predicted lower densities in 'pure' deciduous stands (>90% deciduous). A significant change point resulted from segmented regression, but this occurred at around the occurrence threshold for nests – about 19% deciduous trees measured at the stand scale (Figure 4.3a). Thus, since segmented regression only distinguished used from unused stands but did not provide a change point that distinguished among the choices of nesting pairs, I used the change point identified using maximally selected rank statistics to delineate high quality habitat for yellow-bellied sapsuckers as stands with more than 41% deciduous trees (Table 4.4, Figure 4.3a). Average territory density was about 3.5 times higher in high versus low quality habitat (0.21 $\pm$ 0.03 pairs/ha versus 0.06 $\pm$ 0.02 pairs/ha).

The density of trees preferred for nesting was about three times higher in stands with forest compositions identified as high quality habitat (> 42% deciduous, 1.01 $\pm$ 0.13 versus 0.34 $\pm$ 0.13, average count within four 11.3 m radius plots within a 60 m radius of point count stations). A significant change point in the model relating the density of preferred trees to forest composition (Figure 4.3b) was similar in value to that found at 41% deciduous in the relationship of territories to forest composition (Figure 4.3a). Average territory density and the density of preferred trees within stands averaged among deciles of % deciduous were highly correlated (Figure 4.4, $r_s = 0.67$, $P = 0.04$, $n = 90$ stands). These results suggest the distribution of yellow-bellied sapsucker territories in relation to forest composition can be reliably predicted from the density of trees preferred for nesting. However, a model predicting territory density from forest composition alone is 2.4 times more likely than a model that includes the density of trees preferred for nesting (Table 4.5).

4.4.3. Relating nest productivity and vegetation selected for nesting

I counted the number of fledglings, measured as the number of old chicks in 72 nest cavities on 61 territories – I determined clutch size, measured as the number of eggs laid, for 30 of these nests on 30 territories (Appendix I). At least one young fledged from all monitored nests except two – therefore, nesting success was 97%. None of the vegetation variables that were significant predictors of nest site selection were significantly related to reproductive output in GLM models, measured either as clutch size or the number of fledglings (Nagelkerke's Pseudo r^2 =7.25 and 4.31 respectively, all p-values > 0.40). This result was not different when data were limited to nests found early in the breeding season or to nests with more accurate fledgling counts. However, the average DBH of trees containing pairs with fewer fledglings (< 3) was wider than those with more successful pairs (37.9 ($\pm$ 1.48) versus 34.9 ($\pm$ 0.89)), and pairs that selected trees of DBH above the change point fledged on average fewer young (3.46 ($\pm$ 0.42) versus 4.08 ($\pm$ 0.17)).

4.5. DISCUSSION

4.5.1. Selection for nest trees

Similar to other studies of the nest-site selection of yellow-bellied sapsuckers where aspen is abundant, I found that sapsuckers chose to nest almost exclusively in live decaying aspen trees within a specific size range rather than in the largest of the trees available, and more often in trees with more fungal conks than randomly-selected trees (Runde and Capen 1987; Giese and Cuthbert 2003; Savignac and Machtans 2006). With the exception of the white-headed woodpecker which eats coniferous seeds and thus prefers to nest in coniferous forests, preferential choice for nesting in aspen has been found for all woodpecker species breeding across the geographic range of aspen (Crocket and Hadow 1975; Harestad and Keisker 1989 – 88% of 243 nests; Li and Martin 1991 - 97% of 117 nests; Dobkin et al. 1995; Loose and Anderson 1995 - 30 of 33 nests; Steeger and Dulisse 2002 47% of 263 nests in a coniferous-dominated landscape; Bunnell et al. 2002; Martin et al. 2004 - 95% of 1692 nests in a coniferous-dominated landscape; Drapeau et al. 2009 - 98% of 278 nests). Even the conifer-associated black-backed woodpecker has been found to use aspen when it is available (e.g. Bonnot et al. 2008). Selection for live decaying aspen trees has been hypothesized to be related to two main factors – excavation ease and predator protection (Daily 1993; Losin et al. 2006; Tozer et al. 2009). Aspen probably also emerges as being so highly preferred because it is the most widely distributed native trees species in North America (Jones 1985), is among the few native trees with particularly soft bark and wood, and is one of the most prone to internal heart rot (Panshin and DeZeeuw 1980).

It is clear from this study and a review of other studies that sapsuckers and many other woodpecker species choose live decaying aspen trees with heart rot within a certain size range, rather than the largest trees. In this study, 85% of cavities were in trees of DBH between 28 and 42 cm, and nest trees were on average 6.7 cm smaller in diameter than randomly-chosen live aspen trees with heart rot. Mean DBH of nest trees across seven studies ranged between 30 and 35 cm for seven of the eight woodpecker species that commonly nest in aspen, while minimum and maximum DBH ranged from 24 to 32 cm and 27 to 45 cm respectively (Crocket and Hadow 1975; Harestad and

Keisker 1989; Li and Martin 1991; Dobkin et al. 1995; Walters 1996; Martin et al. 2004; Savignac and Machtans 2006).

Woodpeckers obviously must choose trees above some minimum diameter, because cavities need to be big enough to hold fledglings. Less obvious is the reason for an upper limit on tree diameter. Losin et al. (2006) showed that red-naped sapsuckers excavated cavities in trees with thinner sapwood than similarly-sized randomly-chosen live decaying aspen trees, and hypothesized that sapsuckers chose thinner sapwood because it was easier to excavate. I hypothesize that the dynamics of selection for live trees with heartrot is determined less by excavation ease *per se*, and more by an upper limit of sapwood thickness to ensure efficient movement through the cavity entrance. The diameters of cavity entrances appear to fit excavator’s bodies snugly. It is probable that birds are not able to move easily through a cavity entrance tunnel, the ‘sill’, longer than its body length, and it appears that average sill depth is about 4 to 6 cm - about a centimeter or two less than the body length of all aspen-nesting woodpecker species (e.g. Bull 1987; Wiebe 2001). The relationship between DBH, sapwood thickness, and extent of heartrot probably varies as the physiology of tree species interacts with the decay dynamics of fungal species across variations in climate, site conditions, and other factors (see review by Jackson and Jackson 2004). Thus, selection for tree size based on sapwood thickness undoubtedly varies across tree species, and may explain selection for moderately-sized aspen trees. In other tree species, woodpeckers may select trees of the largest diameters, but at high vertical positions where heartrot is extensive and the sapwood is thin enough (e.g. McClelland and McClelland 2000).

4.5.2. *Nest site selection at multiple scales*

I found support for nest site selection by yellow-bellied sapsuckers at a larger spatial scale than just the tree. Yellow-bellied sapsuckers more often chose nest sites with on average two more live decaying aspen trees immediately around the nest tree (within 11.3 m) than they did in otherwise suitable, but unused sites adjacent to nesting territories. Since sapsuckers return to territories in consecutive breeding seasons but more often choose a different but nearby tree for nesting (within about 24 m - data from this study), options for future nesting may be an important characteristic in choosing nest sites (Li and Martin 1991). Giese and Cuthbert (2003) also reported higher densities of aspen trees within an 11.3 m radius of nest site than randomly selected sites, which distinguished yellow-bellied sapsuckers from six other woodpecker species studied. However, they did not use a paired sampling design and so were not able to distinguish whether higher aspen densities around nests were simply an artifact of the commonly clumped distribution of aspen. More generally, other authors have found woodpecker nests in patches of forest with higher densities of potential nest trees (reviewed in Giese and Cuthbert 2003), but because paired designs were not used, it is unclear whether trees chosen for nesting occurred in clumps of similar trees. Bonnot et al. (2008) acknowledge this problem in their finding of higher aspen densities around the nests of black-backed woodpeckers in aspen trees.

The use of a paired design still does not eliminate the possibility that the finding of more aspen trees around nest trees simply reflects the frequent occurrence of preferred aspen trees within sparsely distributed clumps of aspen. If aspen clumps containing preferred trees are patchily-distributed, then randomly-chosen aspen trees would be surrounded by fewer aspen trees simply because of the sparse distribution of clumps in which preferred trees are found. Thus, to find evidence of selection for nest sites with other nest trees, it is necessary to first determine the spatial distribution of preferred aspen trees, to test whether randomly-chosen trees of the preferred size are less frequently surrounded by other aspen trees.

I found no support for the hypothesis that yellow-bellied sapsuckers chose nest sites with more food resources. Nest site selection was not related to the density of shrubs or birch trees measured within 40 m of nest trees. Similarly, Savignac and Machtans (2006) found no relation between nest tree density of yellow-bellied sapsuckers and the density of either all paper birch trees, or just those with sapwells. The use of birch for sapwells has been well documented in the literature (Walters et al. 2002). Several authors have suggested that birch sap is the preferred food resource of yellow-bellied sapsuckers (e.g. Savignac and Machtans 2006), or that their preference for sap from deciduous trees may be one of the main factors explaining their higher abundance in deciduous-dominated forests (e.g. Warren et al. 2005). I suggest that the relationship between yellow-bellied sapsuckers and birch or deciduous tree sap has been over-emphasized in the literature. So far, in no peer-reviewed study did researchers follow individual birds during breeding to measure time-forage budgets, thus it is not possible to conclude that birch sap is one of the most important food resources for sapsuckers. Savignac and Machtans (2006) found sapwells more often in birch than in green alder (65% versus 21%); however, sapwells on the boles of birch trees are more easily detected than those in alder or willow shrubs. Probably the least detectable are sapwells in coniferous trees, which are important food sources in early spring before deciduous sap rises (Walters et al. 2002). I observed a pair regularly feeding from sapwells in a white spruce tree, which were otherwise easily missed. Further, adults provision nestlings, and probably also themselves, with insects throughout the monthlong nestling period, and in the early fledgling period (Walters et al. 2002; personal observation).

I observed fledglings feeding from sapwells in alder and willow shrubs, but they also begged for insects from parents. I observed parents foraging for insects in shrubs, and shrubs may also provide concealment for juveniles from predators. I found no support for my hypothesis that nest-site selection is positively related to shrub density measured within 40 m of nests. I offer a caveat and encourage other researchers to test this relationship with better measures of shrub density. Though I measured shrub density at a small scale immediately around the nest, Eberhardt (2000) noted that yellow-bellied sapsuckers used sapwells on average 64 m from nest trees. Similarly, I frequently observed adults returning to provision nestlings from distances more than 40 m away. In order to more accurately test whether yellow-bellied sapsucker territory selection is related to shrub density, I suggest that researchers directly measure shrubs at the scale individuals are observed foraging, rather than immediately around the nest.

4.5.3. Predicting broader scale distribution from vegetation preferences for nesting

The results of this study show that the distribution of yellow-bellied sapsuckers can be adequately predicted at the stand scale by determining nest site preferences. Studies have commonly found that the proportion of deciduous trees in stands at the neighbourhood scale is a significant predictor of the probability of yellow-bellied sapsucker occurrence (Giese and Cuthbert 2003; Girard et al. 2004; Warren et al. 2005), with highest probabilities in mixedwood and deciduous stands (Girard et al. 2004). Here I provide evidence using estimates of territory density that mixedwood and deciduous-dominated mixedwood stands were chosen by the majority of breeding yellow-bellied sapsuckers, likely because these stands contained a higher density of the trees in which they prefer to nest.

Significant change points in models of nest site selection resulted in the delineation of preferred nest sites as mid-sized (25-41 cm DBH, 35-43 cm 95% C.I. for upper limit) live decaying aspen trees surrounded by more than one other live decaying aspen tree (0-1 95% C.I.) within an 11.3 m radius. Yellow-bellied sapsuckers did not nest in stands with less than 20% deciduous trees, and territory densities were lowest in 'pure' deciduous stands – both stand types had the lowest densities of preferred aspen trees. One reason for higher territory densities in stands with more patches of preferred aspen trees may be that yellow-bellied sapsuckers prefer nest sites with multiple trees suitable for nesting, perhaps to ensure an adequate supply of nest trees for future breeding.

4.5.4. Relationship of nest productivity and vegetation selected for nesting

I found no relation between reproductive success measured either as clutch size or the number of fledglings, and the trees and sites yellow-bellied sapsuckers chose for nesting using Generalized Linear Modeling. The majority of pairs (80%, 48 of 61) fledged 4 or 5 young such that none of the model relationship to nest tree diameter, fungal count, or the density of surrounding live decaying aspen trees were supported by the data. However, pairs that fledged three or fewer young (n=13 pairs) nested in larger aspen trees on average, which were less frequently selected across all pairs. Small sample sizes may have limited my ability to find stronger statistical relationships between reproductive success and preferred vegetation. Alternatively, for species with high nest success, accurate quantification of habitat quality using reproductive measures may require more direct measures, by quantifying for example, the vegetation preferences of older, dominate individuals in comparison to first time breeders (Robertson and Hutto 2006). Other more direct measures of preferences, such as vegetation structures or sites with high re-use rates (site fidelity) within a population might also provide better measures of habitat quality. Though much rarer, studies that use such direct measures of vegetation preferences, more often find relationships with reproductive success (e.g. Huhta et al. 1998; Chalfoun and Martin 2007), especially when reproduction is measured in ways other than fledgling counts, because preferred habitat may confer fewer but higher quality young (e.g. Chalfoun and Martin 2007).

Use-availability studies that relate selection rates to reproductive output are used to infer habitat preferences and thus to measure habitat quality. However, a growing number of studies are finding poor correlation between vegetation chosen more frequently for nesting and reproductive success (reviewed in Zhu et al. 2012). For populations that show high success during nesting for most pairs, reproductive output is less useful to quantify habitat quality. Woodpecker species usually show fine-scale preferences for trees that are easily excavated, which confer relatively high rates of nest success and nestling survival because nests in tree cavities are difficult for predators to access (Martin 1995). For populations with low variability in nest success and fledgling counts, other measures of reproductive productivity may be necessary to quantify habitat quality, such as fledgling quality and survival. However, these measures are usually difficult to get, and fledgling survival may be poorly related to vegetation selected by adults for nesting because of the multitude of factors affecting young birds after they fledge.

It is possible that more experienced pairs of yellow-bellied sapsuckers are more selective for nest trees and sites, and that their narrower selectivity confers higher reproductive success. I did not measure the experience of breeding pairs, and so my analyses probably measured the selections for nest trees and sites made by both experienced and inexperienced breeders. By measuring for example nest tree and territory re-use rates, it would be possible to quantify whether preferred vegetation (i.e. higher re-use) confers higher reproductive success.

Table 4.1. Vegetation variables used in model building to quantify habitat features important in nest site selection by yellow-bellied sapsuckers at three spatial scales (nest tree, tree site < 11.3 m radius, territory core < 41.3 m radius).

Habitat Feature	**Variable**	**Scale**
Large diameter decaying aspen trees	DBH (cm), number of fungal conks	Nest Tree
Food	Stem density of live birch % Shrub cover	Tree Site
Additional trees for nesting	Stem density of aspen	Tree Site and Territory Core
	Stem density of live decaying aspen	Tree Site and Territory Core

Table 4.2. Model selection statistics for conditional logistic regression models of the probability of presence of yellow-bellied sapsucker nest sites paired to unused available sites adjacent (250-350 m, n=58 pairs of sites) to nesting territories. The best model is shown in bold.

Model	Variables	AICc	∆AIC	w_i	ER
Nest Tree and Tree Site (within 11.3 m)					
Tree	DBH + Conks	44.8	11.4	<0.01	
Density of Potential Nest Trees	Aspen	69.4	36.0		
	Decaying aspen	54.7	21.3		
Tree + Density of Potential Nest Trees	DBH + Conks + Aspen	46.7	13.3	<0.01	
	DBH + Conks + Decaying Aspen	33.4	0.00	0.99	1.00
Territory Core (within 41.3 m)					
Food	Birch + Shrub Cover	82.5	49.14		
Density of Potential Nest Trees	Aspen	63.1	29.7		
	Decaying aspen	64.8	31.4		
Tree + Food	DBH + Conks + Birch + Shrub Cover	46.0	12.6	<0.01	
Tree + Density of Potential Nest Trees	DBH + Conks + Aspen	47.1	13.7	<0.01	
	DBH + Conks + Decaying Aspen	46.8	13.4	<0.01	
Food + Density of Potential Nest Trees	Birch + Shrub Cover + Aspen	72.8	39.4		
	Birch + Shrub Cover + Decaying Aspen	69.4	35.9		
Tree + Food + Density of Potential Nest Trees	DBH + Conks + Birch + Shrub Cover + Aspen	48.2	14.9	<0.01	
	DBH + Conks + Birch + Shrub density + Decaying Aspen				
	DBH + Conks + Birch + Shrub Cover + Decaying Aspen	44.0	10.7	<0.01	
Null		80.5	47.1		

Table 4.3. Parameter estimates (± SE), odds ratios and 95% confidence intervals from the most likely conditional logistic regression model explaining yellow-bellied sapsucker nest site selection in comparison to sites adjacent to nesting territories (n=58 pairs of sites).

Variable	**β_j**	**SE**	**Odds ratio**	**Odds ratio CI**	**MSRS[1]**
Pseudo $r^2 = 0.74$; Likelihood ratio test=43.3, df=3, $P<0.001$; Wald test=16.2, df=3, $P<0.01$					
Conks	0.25	0.09	1.28	1.08-1.52	4 (0-5)
DBH (cm)	-0.11	0.04	0.89	0.83-0.96	41 (35-43)
Density of Live Decaying Aspen within 11.3 m radius	0.67	0.27	1.95	1.14-3.34	1 (0-1)

[1] Change points estimated using maximally selected rank statistics; 95% confidence interval from 1000 bootstrapped samples of change points.

Table 4.4. Parameter estimates (± SE), relative rates or odds ratios, and 95% confidence intervals of GLMs relating the density of yellow-bellied sapsucker territories and of high quality nest sites to the proportion of deciduous trees in old forest stands.

Variable	**β_j**	**SE**	**Relative rate**	**Relative rate CI**	**Segmented[b]**	**MSRS[b]**
Territory Density: Negative Binomial Quadratic GLM, AIC = 208.1; Nagelkerke's Pseudo r^2 = 27.3; AIC Linear = 213.3 Segmented AIC = 201.3 Poisson Quadratic: AIC = 214.1, Overdispersion = 1.51						
[a]Proportion Deciduous	0.087***	0.030	1.09	1.03-1.16	22 (14-30)	41** (26-41)
Proportion Deciduous^2	-6.07×10^{-4}	2.59×10^{-4}				
Density of mid-sized live decaying aspen trees: Negative Binomial Quadratic GLM, AIC = 387.1; Nagelkerke's Pseudo r^2 = 43.8; AIC Linear = 400.8 Segmented AIC = 386.9 Poisson Quadratic: AIC = 558.7, Overdispersion = 3.92						
[1]Proportion Deciduous	0.104****	0.022	1.11	1.06-1.16	36 (23-48)	33** (8.6-33)
Proportion Deciduous^2	-7.71×10^{-4}	1.92×10^{-4}				

[a] Average of visual and basal area estimates at four 11.3 m radius vegetation plots around point count stations. [b] Change points (and 95% confidence interval) estimated using segmented regression and maximally selected rank statistics. **P<0.05 ***P<0.001

Table 4.5. Model selection statistics for GLMs relating the territory density of yellow-bellied sapsuckers to the density of high quality nests sites and the forest composition (% deciduous) of old (> 100 years) forest stands (n=90). The best model is shown in bold.

Model	AICc	∆AIC	w_i	ER
Forest composition	208.1	0	0.70	
Density of high quality nest sites	217.0	8.9	0.01	0.01
Forest composition + Density of high quality nest sites	209.9	1.8	0.29	0.41

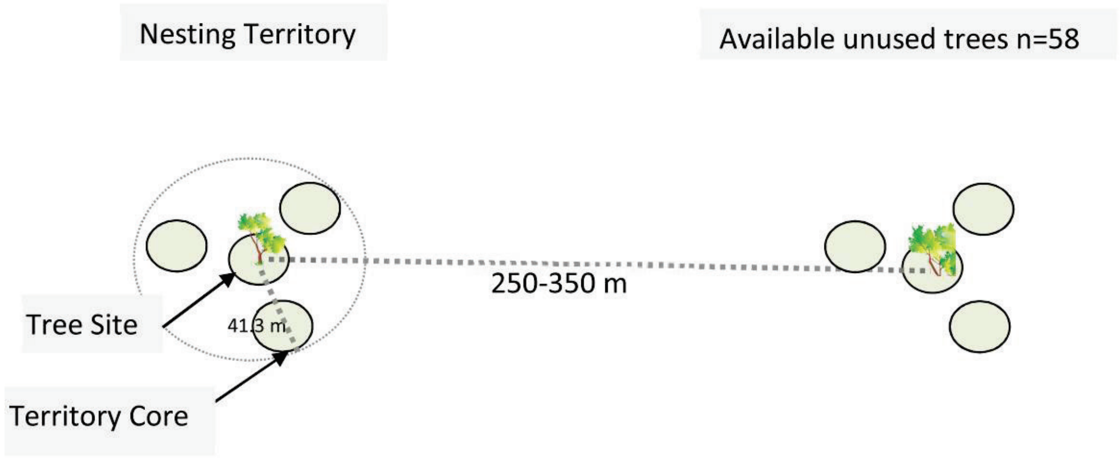


Figure 4.1. Schematic of study design for quantifying nest site selection at the scale of the nest tree, tree site, and territory core.

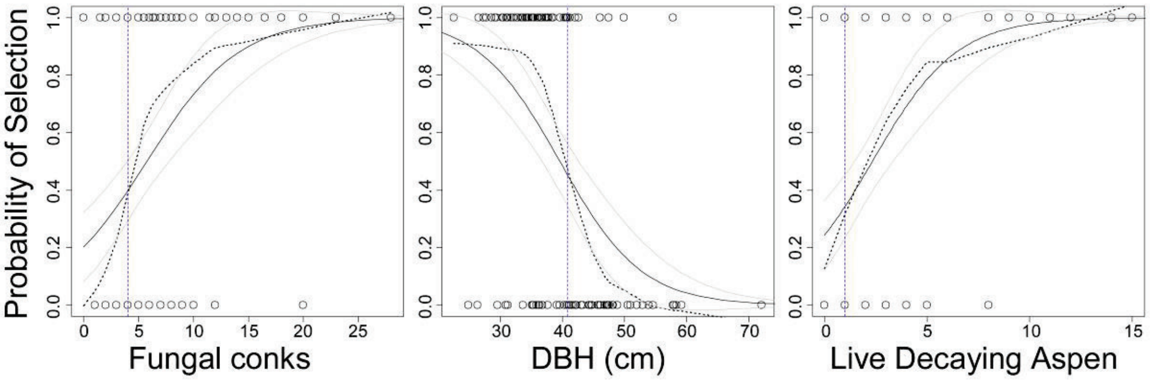


Figure 4.2. Predicted probability of selection using univariate conditional logistic regression of yellow-bellied sapsucker nest trees and sites as a function of the differences between nesting trees and available unused trees at sites adjacent to nesting territories. All variables are significant predictors of nest site selection in a multivariate conditional logistic regression model (Table 4.3). Dashed vertical lines are change points identified using maximally-selected rank statistics. Dashed curved line is the LOESS line.

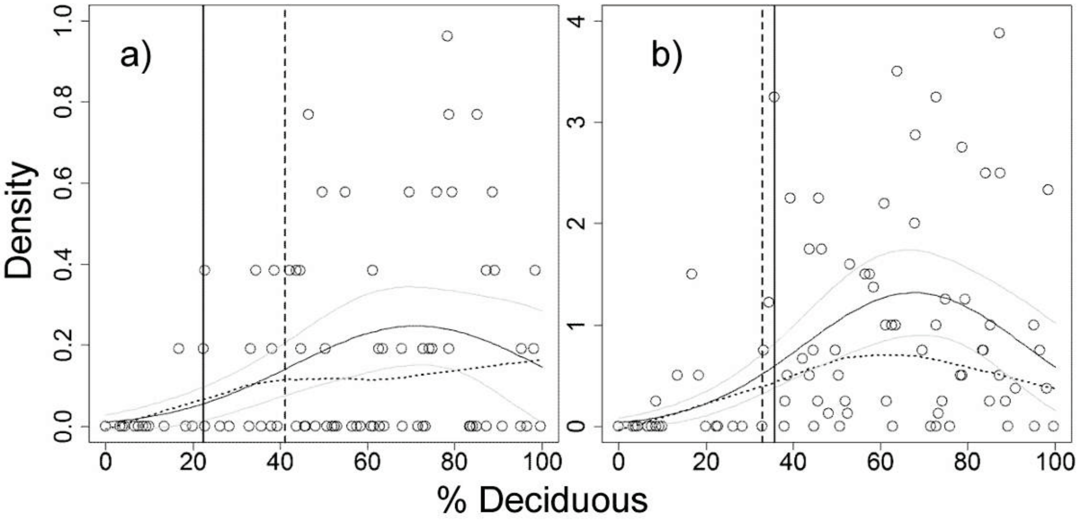


Figure 4.3. Predicted density with 95% confidence intervals of yellow-bellied sapsucker a) territories per ha and of b) high quality nest sites (number of mid-sized live decaying aspen trees per 0.04 ha) in relation to the proportion of deciduous trees in old forest stands (> 100 years) using GLM with log link (see Table 4.4 for parameter estimates). The proportion of deciduous was estimated as the average of visual estimates and basal area measures within four 11.3 m radius plots centred on point counts. Dashed and solid vertical lines are statistically significant change points identified using maximally-selected rank statistics and segmented regression respectively. Dashed curved line is the LOESS line.

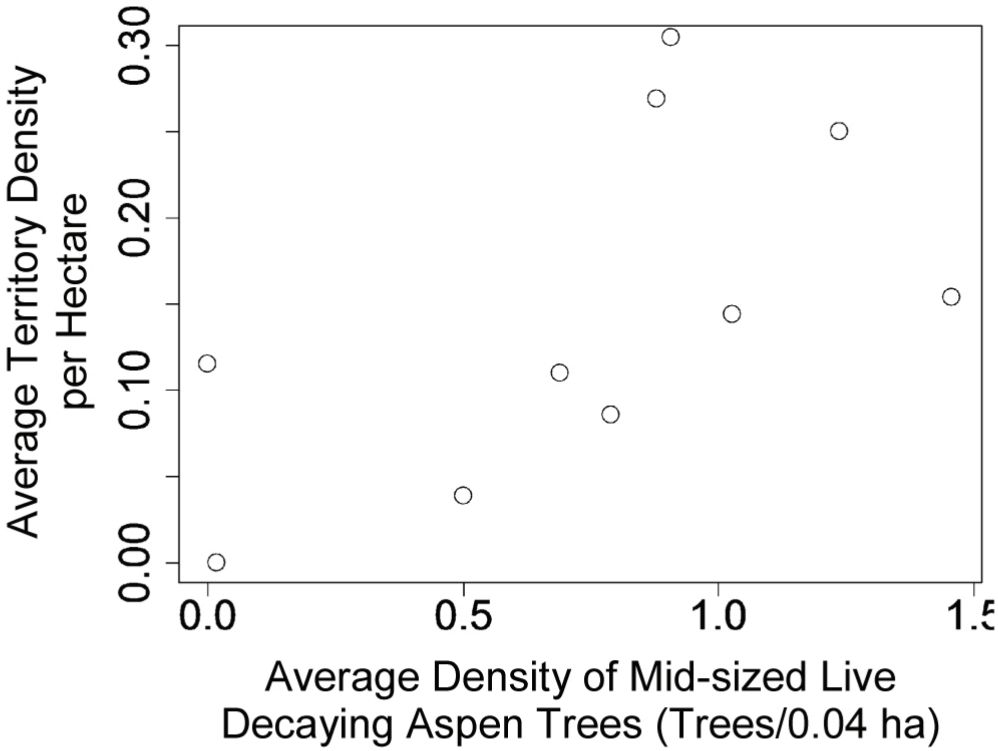


Figure 4.4. Relationship between average territory density of yellow-bellied sapsuckers and average count of live decaying aspen trees 25.5-41.0 cm DBH in 0.04 ha vegetation plots in stands grouped into deciles of % deciduous (r_s = 0.67, P=0.04, n=90 stands).

5. CHAPTER 4

Comparing the roadside Breeding Bird Survey with forest interior surveys using Cost-Effectiveness Analysis

5.1. Abstract

The roadside Breeding Bird Survey (BBS) is one of the most widely applied conservation data sets in North America. The data have been used in many ways, including predictions of the responses of bird species to forest habitat. However habitat models generated from bird surveys along roads may be biased due to roadside habitat structures and processes that differ from the forest interior. Using data generated from roadside and forest interior surveys, I compared the shapes of predicted responses using logistic regression of birds to forest composition by comparing regression slopes and support for non-linearity. I assessed the cost-effectiveness of the roadside survey by assessing the incremental cost to improve the discrimination ability (Area Under the Curve (AUC)) of roadside models using forest interior data. Roadside detections were too infrequent to create models for two species that were commonly-detected in the forest interior (blue-headed vireo, black-throated green warbler). For species for which models could be created, useable models resulted from roadside data for only six of ten species for which usable models were generated from forest interior data. These included five species that are specialists with respect to forest composition, because they forage primarily from either deciduous or coniferous trees, and the white-throated

sparrow, for which models were similarly-shaped and of similar quality. Cost-effectiveness analysis revealed that a roadside BBS survey using remotely-sensed data on forest composition is more cost-effective than a forest interior survey for tree type specialists. However, forest interior surveys using field data are necessary to maximize the number of useable habitat models, and cost about $2,000 per unit of discrimination ability (AUC).

INTRODUCTION

Despite wide recognition that roadside data may be biased, very few studies have adequately measured bias (Kadmon et al. 2004). Biases associated with surveying along roads include differences in detectability, habitat gains or losses associated with roadside habitat structures and processes, and differences in the amount of some habitat types sampled along roads compared to habitat available in surrounding landscapes (Hutto et al. 1995; O’Connor et al. 2000; Betts et al. 2007). Despite these limitations, population trend estimates generated from the roadside North American Breeding Bird Survey (BBS) are one of the most widely applied conservation data sets in North America (Sauer and Link 2011). The estimates have been used to list bird species as endangered, to prioritize species for conservation efforts, and to predict the impacts of land use and climate change (Thomas and Martin 1996; Keller and Scallan 1999; Sauer and Link 2011). But the question of roadside bias remains a key factor in determining the efficacy of the BBS decades after the survey began in 1966, and tests are necessary of the ability of the BSS survey to produce reliable data (O’Connor et al. 2000; Francis et al. 2005).

An ability to relate changes in wildlife populations to land use pressures is arguably the most important feature of a monitoring program, but the BBS is not designed to infer causal factors in population trends (Sauer et al. 2003; 2005). Despite this, species-habitat models have been created using BBS data in relation to habitat measured from vegetation data collected on the ground and aerially (Fearer et al. 2007; Twedt et al. 2010), and these have been used to infer the effects of habitat loss on population size (e.g. Thogmartin et al. 2004). But continued used of BBS data to create habitat models requires testing whether roadside habitat models are as reliable as those derived from surveys away from the road in the forest interior. Reliability can be assessed by comparing predicted responses and quality of habitat models generated from road and forest interior survey data.

Ultimately, surveys conducted in the forest interior may need to be incorporated into the BBS design to improve its efficacy and its credibility to land use managers as a reliable tool (Sauer et al. 2003; 2005). Decisions regarding how much effort to allocate to surveys in the forest interior may be more easily made by considering the costs of such efforts in order to assess the extent to which forest interior surveying is justified. Decisions are clear in circumstances when forest interior surveying is costly but does not result in many gains in the reliability of data, or where cost is minimal and the benefits are great. However, where roadside bias is significant, but mitigating it is costly, decision-making can be facilitated using measures of the costs associated with improving habitat models.

Formal decision analysis processes like Cost-Effectiveness Analysis (CEA) can help simplify the process of examining trade-offs between data quality and costs. CEA is a good alternative to Cost Benefit Analysis because it allows comparisons between alternative strategies for which ‘benefits’ or outcomes are better captured in non-monetary units (Hughey et al. 2003). CEA is widely used in medical science to compare new health care strategies that are more effective and expensive with a default strategy (Russell et al. 1996). The outcome of CEA analysis is the Incremental Cost Effectiveness (ICE) - the ratio of incremental cost to incremental effectiveness for each new strategy in comparison to the default (Hughey et al. 2003). To my knowledge, CEA has never been applied to investigate cost effectiveness associated with improved bird surveys over default methods. In the context of monitoring, CEA could allow decision makers to compare multiple survey methods with a baseline method such as the BBS to determine which new method is the most cost effective. In this chapter, I use CEA to compare two alternative choices that result in the same total survey cost - one choice is to use only roadside data, the second choice is to replace half the roadside data with forest interior data of the same cost.

I generated habitat models and used CEA to compare the Breeding Bird Survey method with a forest interior survey in the mixedwood boreal forest of northeastern BC. My research questions were:

1) Are roadside surveys biased in terms of the frequency with which some species are detected relative to surveys in the forest interior?

2) For species that are frequently detected along roadsides and in the forest interior, how do predicted responses and the quality of species-habitat models compare for models derived from roadside versus forest interior data?

3) How cost-effective is a roadside compared to forest interior survey; is it more cost effective to replace a portion of roadside with forest interior surveying?

5.2. METHODS

5.2.1. Forest Interior Survey

I conducted forest interior surveys stratified by forest type and consisting of five minute counts at 112 point count stations in 90 old (100-180 years) forest stands varying in the proportion of deciduous versus coniferous trees (Table 5.1). Point count stations were spaced at least 200 m apart and 100 m from stand edges at the end of 200 m line transects that ran perpendicular to logging roads. Most stands (75%) were sampled with one point count station (in proportion to stand size), but 22 larger stands were sampled with two point count stations. Most (60) stands were visited twice in the same year, 20 of 25 stands visited twice in 2008 were visited a third time in 2009, and eighteen stands were surveyed once in 2007 and once in 2008. Twelve stands were no longer accessible due to a road-washout so were surveyed only once in 2007. A total of 232 point counts were conducted (19.3 survey hours). All forest interior surveys were conducted by the same observer (K. Squires). Forest composition was estimated as the average of visual estimates and basal area calculations of trees (> 15 cm diameter at breast height) in 11.3 m radius (0.04 ha) vegetation plots. Vegetation plots were centred on point count stations and on three points 30 m away from the centre of stations along directions separated by 120^0. These are the same data used in Chapter 2 - more detailed methods are given in that chapter.

5.2.2. Roadside Survey

Roadside and forest interior surveys were conducted in the northern portion of TFL 48 and the southwestern portion of the Fort St. John Timber Supply Area (TSA; see Figure 3.1). Point count surveys were conducted according to provincial standards (RIC 1999) between 0415 and 0930 hours from the end of May to the beginning of July, 2002-2008. The roadside survey was conducted by other researchers as part of a separate study according to the BBS method (Preston et al. 2006). Point count stations were spaced 800 m apart on logging roads along 40 km survey routes (50 stations per route). Birds were recorded as occurring either on the right or left side of the road during 3 minute counts. Stations were surveyed once per season by the same two observers across all years. Five survey routes overlapped the area I surveyed in the forest interior, but only six roadside stations occurred in the same forest stand as forest interior stations so paired analyses were not possible. Birds were surveyed between 2002 and 2008 in

TFL 48, and between 2005 and 2008 in the Fort St. John TSA. The number of routes surveyed differed each year. All five routes were surveyed in 2005 and 2006, four in 2003 and 2004, three in 2007 and 2008, and two in 2002, resulting in 1300 point count surveys over the seven years of the study. The roadside survey was not stratified by forest type so analyses were restricted to data from 85 of the 250 stations (448 point count surveys; 22.4 survey hours) in which detections were made in one forest stand on one or both sides of the road (Table 5.1). Bird presence and absence was related to GIS estimates of forest composition (% deciduous).

5.2.3. Habitat Modeling

The presence-absence of species in relation to forest composition was modeled using binomial regression (GLM with logit link). Models were generated for frequently detected species, defined as those with at least 25 detections at more than 20% of sample units. I evaluated the discrimination ability of logistic models using results generated from Receiver Operating Characteristics (ROC) graph analysis. The discrimination ability of models can be categorized according to the AUC value (reasonable: AUC 0.70-0.79, good 0.80-0.89, excellent 0.90-1.0, Swets 1988). I considered 'useable' models those with AUC $\geq$ 0.70 (Boyce et al. 2002). Species models from the forest interior survey with AUC values greater than 0.70 were compared to models generated from the roadside and roadside-forest interior combined surveys. I chose the quadratic model as the final model if it resulted in an AIC of 2 or more units lower than the linear model. Statistical significance of logistic regression models was determined using the Hosmer-Lemeshow-Cressie test (Hosmer et al. 1997). I compared the shapes of predicted responses to habitat in models derived from each survey method by comparing the slopes, and whether the best models were linear or quadratic. I used AUC as measures of model quality in cost-effectiveness analyses.

5.2.4. Cost Estimation

I estimated costs for both surveys using consultant rates for wages, and for all other expenses from actual costs incurred for the forest interior survey in 2007-2009. Each survey was conducted by a principal and an assistant researcher. Project logistics involved accommodation at motels, and daily travel by vehicle to survey sites. I calculated weekly operational expenses by dividing the total costs by the total number of weeks spent in the field over the three years of the study (Table 5.2). I then calculated yearly operational costs assuming project durations of six weeks for the roadside survey and eight weeks for the forest interior survey (Table 5.3). The additional two weeks for the forest interior survey were necessary for vegetation sampling in July.

The total survey cost equaled the cost of the habitat models for the forest interior survey, but not for the roadside survey. Data from only 85 of 250 stands along five of fifteen routes were used to generate habitat models, which required calculating the cost of each point count to determine the total survey cost for five routes and the cost of the data used to generate models. I assumed that 625 roadside stations could be surveyed per year, resulting in an annual cost per point count of $79.20. I estimated the cost of the habitat models from the cost of surveying all 250 stations for one year in addition to the cost of surveying the 85 stands in subsequent years (Table 5.3). Stations were randomly located with respect to forest type, and thus the cost of ‘finding’ 85 stations which sampled one forest type on at least one side of the road was the cost of surveying all 250 stations of the five routes.

5.2.5. *Cost Effectiveness Analysis*

I evaluated the decision to replace half the roadside effort with forest interior surveys of the same cost by generating models from a combined roadside and forest interior survey (50% roadside stands combined with 12% of forest interior stands). To assess cost-effectiveness of these alternative decisions, I used the quality and number of useable habitat models generated from the data. I measured model quality using AUC, and used the difference in AUC values summed over all species as the measure of effectiveness in calculating the Incremental Cost Effectiveness (ICE) according to the following formula:

$$\text{ICE AUC} = \frac{\Delta\,\text{Cost}}{\sum_{i=1}^{n} \Delta\text{AUC} \times 100}$$

where n = number of species.

5.3. RESULTS

5.3.1. *Detection Rates of Species in Forest Interior and Roadside Surveys*

Over the three years of the forest interior survey, I made 2182 detections of 62 species (Table 5.4). Totals for the seven years of roadside surveying were very similar - 2033 detections of 63 species were made at 85 stations along five routes. Though total survey hours were similar, almost twice as many point counts were conducted for the roadside survey (Table 5.1). Thus, the detection rate along roadsides was lower compared to the forest interior (1.51 detections versus 1.88 detections per minute, average of 4.16 ± 0.25 versus 9.34 ± 0.26 detections per point count station).

Seventeen species were detected frequently during both the forest interior and roadside surveys – four of these species (Swainson's thrush, warbling vireo, white-throated sparrow, yellow-rumped warbler) accounted for 36% and 40% of all detections in the forest interior and roadside surveys, respectively (Table 5.4). The blue-headed vireo and black-throated green warbler were relatively common in the forest but were rarely detected along roadsides. The rose-breasted grosbeak was frequently detected in the forest interior, but was detected about 2.5 times less frequently along roadsides. Three species (orange-crowned warbler, pine siskin, white-winged crossbill) frequently detected along roadsides were rarely observed in the forest and two species (chipping sparrow, Wilson's warbler) frequently detected along roadsides were seen there at more than twice the rate as in the forest, where the detection rate was too low to categorize the species as frequently detected.

5.3.2. Habitat Modeling

Habitat models were generated for the 17 species frequently detected during both the forest interior and roadside surveys. Useable models (AUC ≥ 0.70) were generated for ten of the 17 species from the forest interior data, and these were compared to models for the same species generated using roadside data (Table 5.5, Figure 5.1). Five of the ten species are tree type specialists, defined as species that prefer to forage primarily from deciduous or from coniferous trees (Chapter 2). The other five species are tree type generalists, and show no preference for foraging from either coniferous or deciduous trees (Chapter 2).

With the exception of the magnolia warbler, slopes for all regression models using forest interior data were larger than models generated from roadside data. Regression models generated from the two survey methods were similarly-shaped for the five species of tree specialists, plus the magnolia warbler and white-throated sparrow. For the golden-crowned kinglet and warbling vireo, regression slopes were similar between models of the two surveys, but y-intercepts differed because of the difference in detection rates of these two species on roads compared to the forest interior (Table 5.4). The non-linear model fit the forest interior data better than the linear model for western tanager – for this species and two others (Tennessee warbler and yellow-rumped warbler), the roadside data did not generate models with statistically significant slopes.

5.3.3. Cost-Effectiveness Analysis

The roadside survey generated useable models for only six of the ten species for which useable models were generated from the forest interior survey – all five tree specialists and the white-throated sparrow (Table 5.6). Generating these six models from the roadside survey cost $151,623 less than it cost to generate them from the forest interior survey. Improvements in the quality of models for just three species (Tennessee warbler, yellow-rumped warbler, western tanager) contributed 65% of the ICE of $2,197 for each increase of one AUC unit in model quality. Model improvements for the tree specialists, white-throated sparrow, and magnolia warbler were relatively small.

The combined survey (50% roadside + 12% forest interior data) resulted in data which generated half the number of useable habitat models as the forest interior survey alone (Table 5.6). The ICE values for improvements in model quality reveal that conducting a roadside survey rather than an equally-expensive roadside and forest interior combined survey is about 3.5 times more cost effective. There were no gains in the number of useable habitat models when roadside was combined with some forest interior surveying, whereas an additional model was generated when the same effort was expended along the road (Table 5.6).

5.4. DISCUSSION

The BBS has become a long-term and continent-wide monitoring effort for landbirds because it requires less effort and expense than forest interior surveying, and is easy to implement over large areas. However, the results of this study corroborate experimental studies showing different detection rates along roadsides for a small portion of the bird community. Some species prefer roadside habitat, while others avoid roads; some differences may be due to lower detectability along roads versus the forest interior. For species that are specialist with respect to tree type in old forests, reliable and cost-effective models can be generated using roadside data, except for specialist species with different detection rates along roads. For these specialist species and for generalist species, surveys in the forest interior are necessary to reliably predict habitat relationships to forest composition of old forests.

5.4.1. Roadside Bias

Results of this study suggest surveys along roads will be biased for some bird species, supporting recommendations to strengthen the BBS survey by integrating forest interior surveying into the design (O’Connor et al. 2000; Sauer et al. 2003). I cannot conclude, however, whether differences in detections were due to roadside bias since the roadside and forest interior point counts were not paired. Some differences may have simply been because of the placement of count stations in high density ‘patches’ of some species.

But my results are consistent with those from other studies that have used an experimental approach to quantify detection rates along roads versus forest interior (Hanowski and Niemi 1995; Hutto et al. 1995; Keller and Fuller 1995; see review in Harris and Haskell 2007). These studies have found that the largest difference was a higher detection rate on roads of species associated with open, edge, or shrub habitat. In my study, the white-winged crossbill, pine siskin, chipping sparrow, orange-crowned warbler, and Wilson’s warbler were recorded more than twice as much along roadsides than in the forest. The difference for the white-winged crossbill may simply reflect different protocol between the two surveys for nomadic species like crossbills. I frequently observed white-winged crossbills during forest interior point counts but excluded most of the detections as flyovers. The other species were likely attracted to roads because of the habitat resources roads provide. I frequently observed flocks of pine siskins foraging on road surfaces, but I rarely observed them in the forest interior. The two warbler species and the chipping sparrow show strong relationships to shrubs, and open, grassy habitat, respectively, which were dense along roadsides. The pine siskin, chipping sparrow, and Wilson’s warbler were also detected more often on roads in paired designs testing for roadside bias (Hanowski and Niemi 1995; Hutto et al. 1995; Keller and Fuller 1995).

I detected the blue-headed vireo, black-throated green warbler, and golden-crowned kinglet much more frequently in the forest interior. Other researchers have also detected more golden-crowned kinglets at forest interior stations than along roadsides (Hanowski and Niemi 1995; Hutto et al. 1995). These species may avoid edges, but it’s also possible that detectability was lower along roadsides than in the forest interior.

When walking to forest interior stations, I noticed that I could hear birds once I was ‘in’ the forest that I was not able to hear while on the road, especially if there was a slight breeze. In an experiment to quantify variation in detectability by observers, Simons et al. (2007) found that almost a third less birds were recorded by observers during breezy conditions. It is possible that for an observer on roads, trees create a barrier which mutes bird songs, particularly of quieter species and that wind, funnelled down road corridors may obscure bird sounds that would be audible in the forest. I found that the golden-crowned kinglet and black-throated green warbler were the quietest species, which was reflected by a shorter truncation distance of the detections used to estimate detectability functions (Chapter 2, Appendix C and E). These results suggest that studies are needed to test for roadside bias due to variable detectability and habitat availability along roads versus the forest interior.

5.4.2. Habitat Modeling

Habitat models of the responses of tree type specialists and the white-throated sparrow to forest composition were reliably derived from roadside data. Regression slopes and model quality were very similar to those of forest interior models. However, due to a higher detection rate of the golden-crowned kinglet in the forest interior and the warbling vireo on the roadside, the predicted probability of presence for each species was larger, especially in coniferous-dominated stands. As discussed in the previous section, the golden-crowned kinglet may have been less frequently detected along roadsides due to the difficulty in hearing their songs. Higher detections may have represented high abundance of the warbling vireo on roadsides because it uses shrubs for foraging and nesting, which are abundant along roadsides (Hutto et al. 1995; Sallabanks et al. 2006).

The results highlight how the prevalence of a species affects the probability of presence predicted from logistic regression – probabilities are always biased to the more prevalent state (i.e. presence or absence) within a sample and do not necessarily measure the species' selection for habitat (Real et al. 2006). For example, if 50% probability of presence is used as a rule of thumb to delimit 'good' habitat, then stands of all forest types would be managed for the warbling vireo using roadside data. Along roadsides the warbling vireo was detected frequently enough to result in 50% probability of presence across all stand types. In contrast, only deciduous stands (>60%) would be managed using forest interior data, where the warbling vireo was less frequently detected. Different management actions would arise, but these decisions would not necessarily reflect the habitat preferences of the warbling vireo, but rather the detection frequency on roadsides versus the forest interior. Differences in species prevalence can also result in poor predictive accuracy of models developed in one region when applied in another (Vernier et al. 2008).

Similarly, AUC is a measure of the ability of a model to correctly discriminate sites that support species presence from sites that do not, but is not a measure of how well the model quantifies species habitat preferences. Low AUC values result from models in which species increase in presence but are generalist in response to the predictor variable, even though the model may accurately predict species distribution. Specialist species with restricted ranges with respect to the predictor variable will always have high AUC values, even though models may measure habitat preferences poorly (Lobo et al. 2007). In this study, models for specialist species and the white-throated sparrow had highest AUC values, consistent across habitat data collected from remote-sensing and in the field. Similarly, habitat models for woodpeckers based on remotely-sensed data had poor discrimination ability compared to models using data collected in the field, except for habitat specialists (Russell et al. 2007).

Unlike forest interior models, those generated from roadside data for the Tennessee warbler, yellow-rumped warbler, and western tanager predicted no relationship between probability of presence and forest composition. Because it was estimated using aerial imagery within a GIS database, less accurate measurements of forest composition along roadsides may have contributed to higher variability in the relationships.

5.4.3. Cost-Effectiveness

Cost-effectiveness remains one of the key study parameters needed in future research aimed at providing managers with guidelines to match monitoring objectives with sampling design (Elphick 2008). Choosing a survey design that maximizes data quality while minimizing costs requires cost and data quality estimates for each method under consideration. Data quality has been measured in several ways, but most often as the statistical power to detect population trends (e.g. Carlson and Schmiegelow 2002; Field et al. 2005). Seavy and Reynolds (2007) suggested that in some cases, other measures like precision and area coverage may be more informative as measures. This study provides an example of the use of Cost Effectiveness Analysis to quantify the incremental cost of improving the discrimination ability of habitat models using forest interior data compared to data collected using the roadside BBS method.

Comparing incremental costs between alternative forest interior surveys – for example, comparing a point count with a spot-mapping survey - would allow managers to choose the most cost-effective method, or to choose a combination of methods that maximize data quality given a fixed budget. If the goal of surveying is to generate useable habitat models for a small portion of bird species, then the results of this study show that a roadside BBS survey is more cost-effective than a forest interior survey. If prior knowledge suggests strong relationships of focal species to the habitat gradient of interest, in this case, tree type specialists to forest composition, then a roadside survey using remotely-sensed habitat data will the most cost-effective approach. Forest interior surveys are a cost-effective way to increase the number of useable habitat models, but are not a cost-effective strategy to improve on already useable models. The roadside survey was a more cost effective way to improve habitat models than a survey of equal cost that used a combination of roadside and forest interior data. However, if the goal is to maximize the number of species for which to make reliable predictions of their relationship to forest habitat, then forest interior surveying will be necessary and will cost about $2,000 per AUC unit increase in discrimination ability of predictive models.

Though the roadside BBS survey was not designed to quantify habitat relationships, this study shows that habitat models can be reliably and cost-effectively generated using BBS surveys and remotely-sensed data on forest composition - but only for species that are specialists with respect to forest composition. However, care must be taken when using roadside models for habitat specialists to inform management decisions, as the models, though statistically reliable and affordable, may not accurately reflect forest habitat preferences. For example, warbling vireos that nested along roadsides were frequently found across the gradient in forest composition, but rarely nested in interior coniferous-dominated forest. This pattern was likely due to abundant shrubs along roads that cut through coniferous-dominated stands, where shrubs were otherwise relatively scarce in the forest interior. Thus, for species like the warbling vireo for which detection rates differed along roadsides, forest interior surveys may be required even when roadside data produces statistically reliable models. Thus, though this study shows that roadside data can generate reliable habitat models, two caveats are necessary to place limits on generalising results. First, the study was conducted in a forested landscape, where differences between roadsides and the forest interior are less than in agricultural- or urban-dominated landscapes. It is likely that roadside data in landscapes with more disturbed forest would provide less reliable habitat models. Second, this study does not include measures of the 'costs' of failing to generate habitat models from roadside data for two species (blue-headed vireo, black-throated green warbler) that were rarely detected along roadsides, but common in the forest interior. A more thorough assessment of the value of roadside surveys to predict species distributions should include to include other measures of costs. Further, a broader range of measures used to deem models as 'useable', such as measures of predictive accuracy using external data, would ensure a broader range of species were used to compare the reliability of roadside data.

An important caveat regarding the use of AUC in cost-effectiveness analysis is that it is not useful to determine the reliability of habitat models used for conservation problems for which the costs of incorrect absences need to be tallied separately from the cost of incorrect presences. For example, incorrect predictions of species absence of an endangered species would result in important habitat sites left unprotected, whereas incorrect predictions of species presence may result in costly site protection that does not provide habitat. The AUC value for a model provides no indication of misclassification rates for absences versus presences (Lobo et al. 2007).

Table 5.1. Sampling design for forest interior and roadside bird surveys in northeastern BC.

Sampling Design	**Forest interior**	**Roadside**
Number of survey years	3	7
Total number of stations surveyed	112	250
Total number of point counts	232	1300
Number of point counts used for habitat modeling	232	448
Count duration (minutes)	5	3
Survey hours	19.3	22.4
Sample size for habitat modeling (number of forest stands)	90	85

Table 5.2. Project budget for forest interior and roadside bird surveys in northeastern BC.

Operational Costs	**Details**	**Per week cost**
Food	$30 per person/day	$420
Gas		$250
Accommodation	$80 per person/day	$1120
Salary - principal researcher	$450 per day	$3150
Salary - assistant researcher	$350 per day	$2450
Truck rental		$415
Research consumables		$325
Total operational costs per week		**$8130**

Capital Costs		
Research equipment		
	2 x Binoculars	$850
	2 x Handheld Global Positioning Systems	$480
	2 x Laptop computers, hardware, software	$3015
Camp equipment		
	VHF radio	$708
Total capital costs		**$5053**

Table 5.3. Cost calculations for forest interior and roadside bird surveys in northeastern BC.

	Forest interior	**Roadside**
Time spent in the field per year	8 weeks	6 weeks
Operational costs per year	\$65,040	\$48,780
Number of survey years	3	7
Total annual cost of survey[1]	\$66,724	\$49,502
Number of stands surveyed per year	30	625
Cost per point count	\$863.80	\$79.20
Cost per stand	\$2224.14	\$571.18
Total cost of survey	\$200,173	\$102,960[2]
Cost of data used in statistical models	\$200,173	\$48,550[3]

[1] Operational costs per year + total capital costs/number of survey years.
[2] Cost per stand x 1300 point counts (Table 5.1).
[3] Cost per stand x total number of stations surveyed in one year + Cost per stand x (number of point counts in habitat modeling data – sample size for habitat modeling). See Methods and Table 5.1.

Table 5.4. Effort-adjusted counts and frequency of occurrence of birds detected at point count stations in roadside and forest interior stands. Bold font shows species frequently detected during both surveys (>25 detections at >20% of stations).

	Forest Interior						Roadside					
Species Code[1]	**Count**	**Frequency**	**Adjusted Count**	**SE**	**Adjusted Frequency**	**SE**	**Count**	**Frequency**	**Adjusted Count**	**SE**	**Adjusted Frequency**	**SE**
ALFL	3	2	0.01	0.01	0.01	0.01	11	8	0.03	0.01	0.03	0.01
AMRE	176	41	0.62	0.09	0.34	0.04	58	30	0.14	0.03	0.12	0.02
AMRO	74	41	0.28	0.04	0.23	0.03	83	45	0.20	0.02	0.17	0.02
ATTW	16	14	0.09	0.03	0.08	0.02	3	3	0.01	0.00	0.01	0.00
BAWW	3	3	0.01	0.01	0.01	0.01	2	2	0.01	0.00	0.01	0.00
BBWO	2	2	0.02	0.01	0.02	0.01						
BCCH	18	15	0.07	0.02	0.07	0.02	15	12	0.04	0.01	0.03	0.01
BHCO	11	7	0.04	0.01	0.04	0.01	3	3	0.01	0.00	0.01	0.00
BHVI	32	24	0.12	0.03	0.11	0.02	4	4	0.01	0.01	0.01	0.01
BLPW	1	1	0.00	0.00	0.00	0.00						
BOCH	13	12	0.08	0.02	0.08	0.02	3	3	0.01	0.00	0.01	0.00
BRCR	4	3	0.03	0.02	0.03	0.02	4	4	0.01	0.01	0.01	0.01
BTNW	102	41	0.39	0.06	0.31	0.04	3	3	0.01	0.01	0.01	0.01
CAFI	1	1	0.00	0.00	0.00	0.00						
CAWA	8	7	0.03	0.01	0.03	0.01	2	1	0.00	0.00	0.00	0.00
CHSP	24	16	0.08	0.02	0.08	0.02	65	41	0.17	0.02	0.15	0.02
CEDW	2	1	0.01	0.01	0.01	0.01	8	2	0.03	0.03	0.01	0.00
CONW	1	1	0.00	0.00	0.00	0.00						
CORA	8	8	0.03	0.01	0.03	0.01	9	7	0.02	0.01	0.02	0.01
COYE							1	1	0.00	0.00	0.00	0.00
DEJU	48	27	0.19	0.04	0.15	0.03	65	42	0.16	0.02	0.14	0.02
DOWO	2	2	0.01	0.01	0.01	0.01						
DUFL	3	2	0.01	0.01	0.00	0.00	6	5	0.02	0.01	0.02	0.01
EVGR	2	2	0.01	0.01	0.01	0.01	6	5	0.01	0.01	0.01	0.00
FOSP	1	1	0.01	0.01	0.01	0.01						
GCKI	84	51	0.42	0.05	0.38	0.04	30	25	0.08	0.02	0.08	0.02
GRAJ	17	15	0.08	0.02	0.08	0.02	40	23	0.10	0.02	0.08	0.02

HAFL	1	1					14	11	0.03	0.01	0.03	0.01
HAWO	7	6	0.03	0.01	0.03	0.01	9	8	0.02	0.01	0.02	0.01
HETH	5	5	0.02	0.01	0.02	0.01	7	7	0.02	0.01	0.02	0.01
HOWR							1	1	0.00	0.00	0.00	0.00
LISP	10	7	0.04	0.02	0.03	0.01	15	10	0.04	0.01	0.04	0.01
LEFL	59	24	0.21	0.05	0.16	0.03	46	21	0.11	0.03	0.09	0.02
MAWA	41	23	0.18	0.04	0.15	0.03	25	17	0.06	0.01	0.05	0.01
MGWA	3	2	0.02	0.01	0.02	0.01	11	8	0.03	0.01	0.03	0.01
MOWA	20	11	0.08	0.02	0.07	0.02	14	12	0.03	0.01	0.03	0.01
NOFL	1	1	0.00	0.00	0.00	0.00	5	5	0.01	0.01	0.01	0.01
NOWA	14	12	0.06	0.02	0.06	0.02	7	5	0.02	0.01	0.01	0.01
OCWA	9	7	0.04	0.02	0.04	0.02	39	26	0.10	0.02	0.10	0.02
OSFL	5	3	0.02	0.01	0.02	0.01	6	4	0.01	0.01	0.01	0.01
OVEN	76	31	0.35	0.06	0.25	0.04	49	23	0.13	0.03	0.12	0.02
PHVI							2	2	0.00	0.00	0.00	0.00
PIGR							3	2	0.01	0.01	0.01	0.01
PISI	7	5	0.04	0.02	0.04	0.02	51	29	0.12	0.02	0.08	0.01
PIWO	1	1	0.01	0.01	0.01	0.01	5	5	0.01	0.01	0.01	0.01
PSFL							9	6	0.03	0.01	0.03	0.01
RBGR	37	24	0.17	0.03	0.16	0.03	22	15	0.06	0.01	0.05	0.01
RBNU	47	36	0.25	0.04	0.24	0.04	35	21	0.08	0.02	0.07	0.02
RCKI	55	37	0.25	0.04	0.23	0.03	57	30	0.14	0.03	0.13	0.02
RECR							5	1	0.01	0.01	0.00	0.00
REVI	13	8	0.06	0.03	0.05	0.02	23	14	0.06	0.02	0.05	0.02
RUBL							1	1	0.00	0.00	0.00	0.00
RUGR	1	1	0.01	0.01	0.01	0.01	11	10	0.03	0.01	0.03	0.01
RUHU	2	1	0.01	0.01	0.01	0.01	1	1	0.00	0.00	0.00	0.00
SWSP	1	1	0.00	0.00	0.00	0.00						
SWTH	261	76	1.10	0.08	0.69	0.04	336	79	0.80	0.06	0.58	0.03
TEWA	70	33	0.29	0.05	0.19	0.03	88	44	0.22	0.03	0.19	0.03
TOWA	9	8	0.07	0.03	0.05	0.02	7	7	0.01	0.01	0.03	0.01
VATH	23	13	0.10	0.03	0.06	0.02	20	15	0.04	0.01	0.04	0.01
WAVI	99	42	0.41	0.06	0.31	0.04	177	67	0.45	0.04	0.36	0.03
WETA	58	42	0.26	0.04	0.23	0.03	37	23	0.09	0.02	0.08	0.02

WIWA	17	15	0.07	0.02	0.07	0.02	56	33	0.13	0.02	0.12	0.02
WIWR	9	8	0.04	0.01	0.04	0.01	8	7	0.02	0.01	0.02	0.01
WTSP	158	58	0.62	0.07	0.48	0.04	126	46	0.31	0.05	0.25	0.03
WWCR	4	4	0.02	0.01	0.02	0.01	40	25	0.11	0.02	0.08	0.02
WEWP	8	7	0.04	0.01	0.04	0.01	11	8	0.02	0.01	0.02	0.01
YBFL							13	9	0.03	0.01	0.02	0.01
YBSA	80	48	0.36	0.04	0.34	0.04	59	35	0.14	0.02	0.13	0.02
YRWA	278	84	1.23	0.07	0.75	0.04	120	59	0.30	0.03	0.28	0.03
YWAR	37	18	0.12	0.03	0.10	0.02	41	24	0.10	0.02	0.08	0.02

Table 5.5. Results of logistic regressions of the presence-absence of bird species in response to the forest composition (% deciduous) of old forest (> 100 years) at forest interior and roadside point count stations in the mixedwood boreal forest.

	Forest Interior			**50% Roadside**			**100% Roadside**			**50% Roadside + 12% Forest Interior**		
Species	**Slope**	**SE**	**HLC**^{a}	**Slope**	**SE**	**HLC**	**Slope**	**SE**	**HLC**	**Slope**	**SE**	**HLC**
Tree Specialists												
AMRE	0.060****	0.013	0.12	0.031***	0.011	0.33	0.039****	0.009	0.95	0.034****	0.010	0.21
LEFL	0.066****	0.016	0.55	0.030**	0.012	0.87	0.044****	0.011	0.56	0.037***	0.012	0.66
WAVI	0.035****	0.009	0.75	0.193** -1.86 x10^{-3}	0.091 9.25 x10^{-4}	0.30	0.022***	0.007	0.73	0.016	8.98 x10^{-3}	0.20
YWAR	0.063****	0.018	0.96	0.037***	0.014	0.72	0.027****	0.007	0.87	0.044***	0.014	0.76
GCKI	-0.039****	0.010	0.36	-0.022**	0.010	0.52	-0.028****	0.009	0.85	-0.024***	0.009	0.85
Tree Generalists												
MAWA	0.105** -8.19x10^{-4}	0.048 4.12x10^{-4}	0.21	0.013	0.011	0.10	-0.107** 8.14x10^{-4}	0.050 4.26x10^{-4}	0.18	0.025 -1.28 x10^{-4}	0.047 4.58 x10^{-4}	0.44
TEWA	0.026***	0.008	0.27	4.49 x10^{-3}	8.50 x10^{-3}	0.08	-0.002	0.006	0.37	3.11 x10^{-3}	7.64 x10^{-3}	0.23
YRWA	-0.040**	0.019	0.65	9.32 x10^{-3}	9.11 x10^{-3}	0.69	0.005	0.007	0.68	0.011	0.008	0.73
WETA	0.151*** -9.48x10^{-4}	0.045 3.93x10^{-4}	0.38	2.10 x10^{-3}	9.03 x10^{-3}	0.91	0.008	0.007	0.87	3.20 x10^{-3}	8.07 x10^{-3}	0.88
WTSP	0.037****	0.009	0.23	0.037***	0.011	0.75	0.032****	0.008	0.41	0.038****	0.010	0.79

Significance levels: *0.10*<0.05 ***<0.01****<0.001. ^{a}Goodness of fit test: Hosmer-Lemeshow-Cressie (HLC).

Table 5.6. Incremental cost effectiveness of habitat modeling derived from roadside (RS) and forest interior (FI) bird surveys.

	AUC				**Δ AUC**		
Species	**100% FI**	**50% RS**	**100% RS**	**50% RS+ 12% FI**	**A**	**B**	**C**
Tree Specialists							
AMRE	0.86	0.8	0.84	0.81	0.02	0.04	0.01
LEFL	0.86	0.77	0.84	0.82	0.02	0.07	0.05
WAVI	0.75	0.71	0.72	0.67	0.03	0.01	-0.04
YWAR	0.83	0.76	0.75	0.80	0.08	-0.01	0.04
GCKI	0.78	0.68	0.73	0.70	0.05	0.05	0.02
Tree Generalists							
MAWA	0.71	0.58	0.68	0.63	0.03	0.1	0.05
TEWA	0.70	0.53	0.51	0.46	0.19	-0.02	-0.07
YRWA	0.72	0.57	0.59	0.58	0.13	0.02	0.01
WETA	0.72	0.52	0.59	0.53	0.13	0.07	0.01
WTSP	0.79	0.82	0.78	0.82	0.01	-0.04	0
				SUM	**0.69**	**0.29**	**0.08**
ICE AUC					**$2,197**	**$837**	**$3,034**

A: 100% forest interior vs 100% roadside B: 100% vs 50% roadside C: 50% roadside + 12% forest interior vs 50% roadside

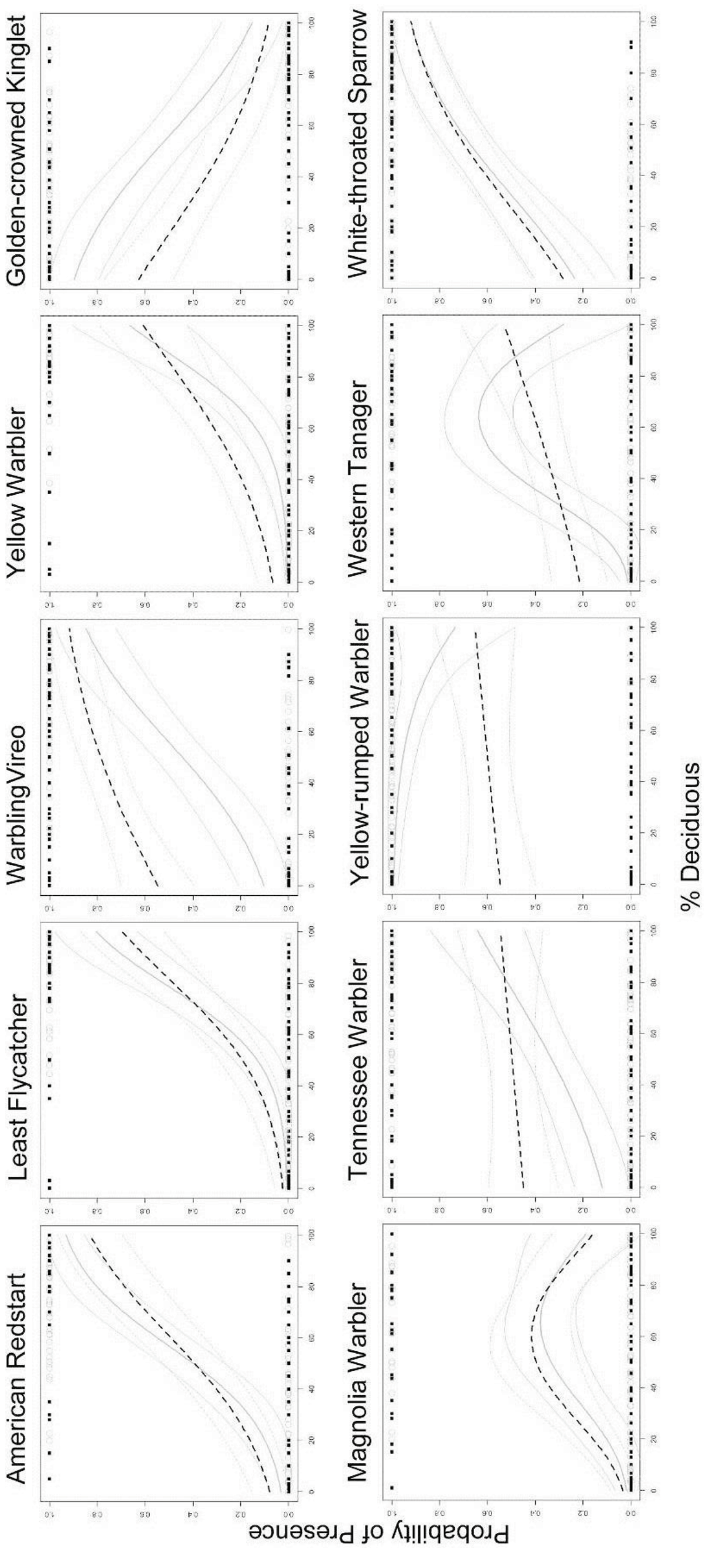

American Redstart
Least Flycatcher
WarblingVireo
Yellow Warbler
Golden-crowned Kinglet
Magnolia Warbler
Tennessee Warbler
Yellow-rumped Warbler
Western Tanager
White-throated Sparrow
Probability of Presence
% Deciduous
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
100

Figure 5.1 Probability of presence with 95% confidence intervals predicted from binomial GLM (logit link) of adult male birds in relation to the forest composition of old stands at forest interior (solid) and roadside (dashed) point count stations. See Table 5 for parameter estimates.

6. Conclusions

A considerable body of empirical literature has documented the response of forest species to changes in habitat structure and composition, more recently at multiple scales. These studies can be divided into two groups. In one group, researchers have used linear regression to model species responses. More recently other researchers have tested for non-linear relationships, especially in studies testing for habitat thresholds. Rather than an assumption of linearity on the one hand, or a focus on non-linearity on the other, applied research relating species to habitat may be more broadly relevant with a more comprehensive approach. Such an approach would include testing alternative hypotheses explaining the responses of species to habitat gradients, including linear and non-linear responses, and tests for change points to delineate suitable from marginal habitat along gradients. Management targets can be derived both from non-linear relationships without abrupt changes in responses and from linear relationships.

I showed that empirical tests of the habitat thresholds paradigm have not provided reliable estimates of the amount of habitat needed for species persistence. Rather than focusing on habitat *quantity*, I argue that these empirical tests can provide managers with guidelines for managing habitat *quality*. Change point analysis of species responses to habitat gradients can be used to identify suitable from marginal habitat, assuming that the response variable is well correlated with habitat quality. A key component of this framework is correct interpretation - models need to be interpreted at the scale at which data were measured. For birds, most models have been generated from measurements made at the territory scale.

I applied the framework of Chapter 1 to delineate suitable from marginal compositions of forest stands for commonly-detected songbirds in the mixedwood boreal forest. I found that forest stands with more than 30% deciduous trees supported on average twice as many territories of tree generalists. Tree specialists selected territories in stands where the amount of their preferred tree type was above 50%. These results suggest that forest composition is a major factor affecting bird distribution in mixedwood boreal forests. Generalist species likely find more resources in mixedwood stands, while tree specialists nest where their preferred foraging substrates – either coniferous or deciduous trees - grow abundantly. To conserve the majority of bird species in logged landscapes, regenerating stands should have more than 30% deciduous trees.

I also applied the framework I developed in Chapter 1 to delineate suitable from marginal nest sites of the yellow-bellied sapsucker. Management for this keystone species of the mixedwood boreal forest will require strategies other than snag retention guidelines, which usually consist of minimum stand densities for standing dead trees. Yellow-bellied sapsuckers nested only in live decaying aspen trees, and I found that sites with groups of suitable trees were chosen, perhaps to ensure future options for nesting. I found that the density of suitable nest sites can be ‘scaled up’ to infer stand scale distribution of yellow-bellied sapsuckers. However, similar to other studies of nest site selection, I found that vegetation selected by most pairs as nest sites did not produce higher nest productivity. Because nest productivity was similar among pairs, it was not a reliable indicator of habitat quality. Measures of fledgling quality and survival may be required to more accurately quantify habitat quality for yellow-bellied sapsuckers.

Finally, Cost-effectiveness Analysis revealed that generating habitat models from a roadside survey for birds using remotely-sensed habitat data is more cost-effective than a relatively intensive forest interior survey, but only for tree specialists in relation to forest composition. Forest interior surveys using field data are necessary to maximize the number of useable habitat models, and cost about $2,000 per unit increase in model quality. One of the main ‘costs’ of a cheaper survey along roadsides is simply that habitat models cannot be generated for some species. Roadside detections were too infrequent for models of two species that were commonly-detected in the forest interior – the blue-headed vireo and black-throated green warbler. Infrequent detections may have resulted from bird avoidance of roadsides, or because birds were less detectable along roadsides. Roadside models for commonly-detected species were less reliable than forest interior models, perhaps because of the inaccuracy of remotely-sensed habitat data.

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Appendices

Appendix A.

Empirical studies of habitat thresholds.

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Appendix B.

American Ornithologist's Union species codes for all birds observed.

Code	Common Name	Scientific Name
ALFL	Alder Flycatcher	*Empidonax alnorum*
AMRE	American Redstart	*Setophaga ruticilla*
AMRO	American Robin	*Turdus migratorius*
ATTW	American Three-toed Woodpecker	*Picoides dorsalis*
BAWW	Black and White Warbler	*Mniotilta varia*
BBWO	Black-backed Woodpecker	*Picoides arcticus*
BCCH	Black-capped Chickadee	*Poecile atricapillus*
BHCO	Brown-headed Cowbird	*Molothrus ater*
BHVI	Blue-headed Vireo	*Vireo solitarius*
BLPW	Blackpoll Warbler	*Setophaga striata*
BOCH	Boreal Chickadee	*Poecile hudsonicus*
BRCR	Brown Creeper	*Certhia americana*
BTNW	Black-Throated Green Warbler	*Setophaga virens*
CAFI	Cassin's Finch	*Carpodacus cassinii*
CAWA	Canada Warbler	*Cardellina canadensis*
CEDW	Cedar Waxwing	*Bombycilla cedrorum*
CHSP	Chipping Sparrow	*Spizella passerina*
CORA	Common Raven	*Corvus corax*
CONW	Connecticut Warbler	*Oporornis agilis*
COYE	Common Yellowthroat	*Geothlypis trichas*
DOWO	Downy Woodpecker	*Picoides pubescens*
DEJU	Dark-eyed Junco	*Junco hyemalis*
DUFL	Dusky Flycatcher	*Empidonax oberholseri*
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*
FOSP	Fox Sparrow	*Passerella iliaca*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
GRAJ	Gray Jay	*Perisoreus canadensis*

HAFL	Hammond's Flycatcher	*Empidonax hammondii*
HAWO	Hairy Woodpecker	*Picoides villosus*
HETH	Hermit Thrush	*Catharus guttatus*
HOWR	House Wren	*Troglodytes aedon*
LEFL	Least Flycatcher	*Empidonax minimus*
LISP	Lincoln's Sparrow	*Melospiza lincolnii*
MAWA	Magnolia Warbler	*Setophaga magnolia*
MGWA	MacGillivray's Warbler	*Geothlypis tolmiei*
MOWA	Mourning Warbler	*Geothlypis philadelphia*
NOFL	Northern Flicker	*Colaptes auratus*
NOWA	Northern Waterthrush	*Parkesia noveboracensis*
OCWA	Orange-crowned Warbler	*Oreothlypis celata*
OSFL	Olive-sided Flycatcher	*Contopus cooperi*
OVEN	Ovenbird	*Seiurus aurocapilla*
PHVI	Philadelphia Vireo	*Vireo philadelphicus*
PIGR	Pine Grosbeak	*Pinicola enucleator*
PISI	Pine Siskin	*Spinus* pinus
PIWO	Pileated Woodpecker	*Dryocopus pileatus*
PSFL	Pacific slope flycatcher	*Empidonax difficilis*
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*
RBNU	Red-breasted Nuthatch	*Sitta canadensis*
RCKI	Ruby-crowned Kinglet	*Regulus calendula*
RECR	Red Crossbill	*Loxia curvirostra*
REVI	Red-eyed Vireo	*Vireo olivaceus*
RUBL	Rusty Blackbird	*Euphagus carolinus*
RUGR	Ruffed Grouse	*Bonasa umbellus*
RUHU	Rufous Hummingbird	*Selasphorus rufus*
SWSP	Swamp Sparrow	*Melospiza georgiana*
SWTH	Swainson's Thrush	*Catharus ustulatus*
TOWA	Townsend's Warbler	*Setophaga townsendi*
TEWA	Tennessee Warbler	*Oreothlypis peregrina*
VATH	Varied Thrush	*Ixoreus naevius*
WAVI	Warbling Vireo	*Vireo gilvus*
WBNU	White-breasted Nuthatch	*Sitta carolinensis*

WETA	Western Tanager	*Piranga ludoviciana*
WIWA	Wilson's Warbler	*Cardellina pusilla*
WIWR	Winter Wren	*Troglodytes hiemalis*
WTSP	White-throated Sparrow	*Zonotrichia albicollis*
WWCR	White-winged Crossbill	*Loxia leucoptera*
WEWP	Western Wood-pewee	*Contopus sordidulus*
YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*
YRWA	Yellow-rumped Warbler	*Setophaga coronata*
YWAR	Yellow Warbler	*Setophaga petechia*

Appendix C.

Methods for Density Estimation from Distance Sampling

I derived detection functions using the program Distance (version 5.0, Thomas et al. 2010). Data were truncated to exclude 5-10% of observations to improve goodness of fit tests. Replicate point counts within stands were treated independently to model the detection functions. Detection functions were only fit to species with more than 60 detections (the minimum sample size necessary for coefficients of variation of 0.15 or less), as suggested by Buckland et al. (2001).

Based on the shape of histograms, species were divided into four species groupings and detection functions were fit to those species with more than 60 detections each within each grouping (Appendix E). The detection function was then used to derive density estimates for all other species in the group with less than 60 detections. I grouped the American redstart, black-throated green warbler, golden-crowned kinglet, and magnolia warbler because the histograms for each species showed the need for shorter truncation distances relative to all other species. I fit the detection function only to the data for the American redstart and black-throated green warbler. There were less than 60 detections of the magnolia warbler. I did not use the golden-crowned kinglet detections because the data appeared to be biased by the tendency for kinglets to move toward us as we walked through stands and during point counts (85% of observations were within 20 m of the station).

I combined the data for the dark-eyed junco and yellow-rumped warbler into a second species grouping because the histograms for each showed evidence of the movement of individuals away from the point, which I also noticed while in the field. Thus, I used wide grouping intervals for the first few distance groups to improve the fit of the model and the reliability of the estimates. The remaining species were separated into two species groupings based on the mode of the detection distances, which seemed to correspond with song loudness. Species were grouped into those with data showing shoulders around 30-40 m, and into those showing wide shoulders to 50-60 m within which detection probabilities were about equal. These latter species were all relatively louder species. The warbling vireo and yellow-bellied sapsucker data were used to model a detection function to derive density estimates for those two species and for the blue-headed vireo, least flycatcher, western tanager, and yellow warbler. Data for five relatively louder species – the American robin, ovenbird, Swainson's thrush, Tennessee warbler, and white-throated sparrow - were used to model a detection function for three other relatively loud or easily-detected species with insufficient detections – the red-breasted nuthatch, rose-breasted grosbeak, and ruby-crowned kinglet.

Models with the lowest AIC and highest p-values from goodness of fit tests were chosen as the best fit model. Selection of adjustment terms was sequential and as suggested by Buckland et al. (2001), the following six models were tested: uniform with cosine and simple polnomial, half-normal with cosine and hermite polynomial, hazard-rate with cosine and simple polynomial. When AIC values differed only slightly (less than 1), I chose the best model as the one with higher *p*-values in goodness of fit tests and upon visual assessment of Q-Q plots.

Once I chose the best model, I compared the pooled model with models fit to data stratified by forest cover type coniferous (coniferous: 0-20%, coniferous-dominated mixedwood: 21-40%, mixedwood: 41-60%, deciduous-dominated mixedwood: 61-80%, deciduous 81-100%), species, and year to determine whether detection functions fit to strata would give better density estimates. The AIC values from models fit to strata were summed, and then deemed better if the sum was 1 or more AIC units lower than the AIC of the pooled model. I found that even very slight breezes created noise from the movement of deciduous leaves. Thus, I hypothesized that detectability was higher in coniferous versus deciduous forests with mixedwoods being intermediate. Lower detectability in deciduous forests has been found elsewhere (e.g. Matsuoka et al. 2010). The AIC sums for forest cover strata were not lower than the AIC of pooled models for each species group (Appendix F); however, I had too few detections in coniferous forests to fit detection functions for two species groups. Thus, while my data showed no evidence that detectability differed across forest types for my data, a higher number of observations from coniferous forests in future studies may show different detectability. There was also no evidence that detectability differed across species within a species group (Appendix F). However, there was evidence that detectability differed across years for each species group - the sum of the AIC for the data fit by year were lower than the pooled model. However, the differences in the Effective Detection Radius (EDR) were not consistent across species groups. Detection distances were smaller in 2008 for three of the four species groups, but the difference was only on average 5 m for the warbling vireo-yellow-bellied sapsucker group. Thus, I fit detection functions to the pooled data for each of the four species grouping to estimate the EDR, which I then used to estimate the density of each species per point count (density estimate = total count/(number of visits x 3.14 x EDR^2). Variances were calculated by Distance using the delta method. Estimates per point count were averaged for stands with two stations.

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Appendix D.

Frequency of occurrence (number of stands) and average abundance of birds detected in the forest interior.

Species names are given in Appendix B

Species Code	Frequency	Average	Species Code	Frequency	Average
YRWA	84	1.23	REVI	8	0.06
SWTH	76	1.10	TOWA	8	0.07
WTSP	58	0.62	CAWA	7	0.03
GCKI	51	0.42	BHCO	7	0.04
YBSA	48	0.36	WWPE	7	0.04
WETA	42	0.26	LISP	7	0.04
WAVI	42	0.41	OCWA	7	0.04
AMRO	41	0.28	HAWO	6	0.03
BTNW	41	0.39	HETH	5	0.02
AMRE	41	0.62	PISI	5	0.04
RCKI	37	0.25	WWCR	4	0.02
RBNU	36	0.25	BAWW	3	0.01
TEWA	33	0.29	OSFL	3	0.02
OVEN	31	0.35	BRCR	3	0.03
DEJU	27	0.19	DOWO	2	0.01
BHVI	24	0.12	DUFL	2	0.01
RBGR	24	0.17	EVGR	2	0.01
LEFL	24	0.21	ALFL	2	0.01
MAWA	23	0.18	BBWO	2	0.02
YWAR	18	0.12	MGWA	2	0.02
CHSP	16	0.08	CONW	1	0.00
BCCH	15	0.07	BLPW	1	0.00
WIWA	15	0.07	CAFI	1	0.00
GRAJ	15	0.08	NOFL	1	0.00

ATTW	14	0.09	SWSP	1	0.00
VATH	13	0.10	CEDW	1	0.01
NOWA	12	0.06	FOSP	1	0.01
BOCH	12	0.08	PIWO	1	0.01
MOWA	11	0.08	RUGR	1	0.01
CORA	8	0.03	RUHU	1	0.01
WIWR	8	0.04			

Appendix E.

Distance Sampling: Model selection statistics for detection functions of pooled data.

Key function	Adjustment term	Number of parameters	*p*-value[1,2]	AIC	Density Estimate	CV[3]
American Redstart and Black-throated Green Warbler (56 m)						
Half-normal	Cosine	2	0.71, 0.73	2086.7	3.22	0.21
Half-normal	Hermite	2	0.80, 0.76	2086.7	2.68	0.14
Hazard-rate	Simple polynomial	3	0.94, 0.81	2087.0	3.71	0.39
Dark-eyed Junco and Yellow-rumped Warbler (Grouped, 64 m)						
Half-normal	Cosine	1	0.97	847.3	2.69	0.09
Hazard-rate	Cosine	2	0.86	851.3	2.70	0.13
Hazard-rate	Simple polynomial	2	0.86	851.3	2.70	0.13
Warbling Vireo and Yellow-bellied Sapsucker (73 m)						
Uniform	Cosine	1	0.75, 0.79	1415.8	1.20	0.11
Uniform	Simple polynomial	3	0.99, 0.70	1416.6	1.31	0.15
Half-normal	Hermite polynomial	1	0.93, 0.84	1429.9	1.28	0.13
American Robin, Ovenbird, Swainson's Thrush, Tennessee Warbler, White-throated Sparrow (84 m)						
Hazard-rate	Cosine	2	0.34, 0.35	5013.4	1.89	0.08
Hazard-rate	Simple polynomial	2	0.34, 0.35	5013.4	1.89	0.08
Half-normal	Cosine	1	<0.01, <0.01	5024.9	2.71	0.09

Data analyzed by grouping of the detections into distance intervals are indicated in brackets as are distances at which the data were truncated. Density estimates are shown for comparison among models. The best models are shown in bold. Goodness of fit tests: [1] Kolmogorov-Smirnov [2] Chi-squared - only the chi-squared is given for data analyzed in groups. [3] Coefficient of variation of the density estimate.

Appendix F.

Distance Sampling: Model selection statistics and estimates fit to stratified data of best fitting model using pooled data (shown in brackets).

Data structure	*p*-value[1,2]	AIC	EDR[3]	% CV[4]	CI[5]
American Redstart and Black-throated Green Warbler (Half-normal Cosine, truncation 56 m)					
Pooled	0.71, 0.25	2086.7	32.5	9.31	27.0-39.1
Year					
2007	0.38, 0.08	131.1	40.9	27.0	23.3-71.8
2008	0.06, 0.02	906.3	23.9	5.11	21.6-26.5
2009	0.92, 0.10	1016.9	38.2	6.09	33.8-43.0
	Total	2054.3			
Species					
AMRE	0.67, 0.01	1364.7	29.8	4.55	27.2-32.6
BTNW	0.91, 0.53	723.9	35.0	6.57	30.7-39.9
	Total	2088.6			
Forest Cover					
Coniferous	Too few detections				
Coniferous-dominated mixedwood	0.66, 0.66	177.4	28.8	15.1	21.0-39.5
Mixedwood	0.83, 0.14	559.7	33.0	7.17	28.6-38.1
Deciduous-dominated mixedwood	0.44, 0.72	371.3	28.4	10.1	23.2-34.8
Deciduous	0.89, 0.89	988.1	32.3	5.53	28.9-36.1
	Total	2096.5			
Dark-eyed Junco and Yellow-rumped Warbler (Half-normal Cosine, truncation 64 m)					
Pooled	0.97	847.3	37.2	3.56	34.7-39.9
Year					
2007	Too few detections				
2008	0.47	401.1	36.1	4.50	31.4-39.1
2009	0.37	384.4	44.7	6.20	39.6-50.6
	Total	833.3			

Data structure	*p*-value[1,2]	AIC	EDR[3]	% CV[4]	CI[5]
Species					
DEJU	0.41	152.5	46.7	10.4	37.8-57.6
YRWA	0.80	697.6	35.7	3.77	33.1-38.4
	Total	850.1			
Forest Cover					
Coniferous	0.70	195.5	44.1	8.63	37.1-52.4
Coniferous-dominated mixedwood	0.29	162.2	41.4	9.03	34.6-49.7
Mixedwood	0.68	303.0	35.1	5.67	31.4-39.3
Deciduous-dominated mixedwood	Too few detections				
Deciduous	0.91	187.5	33.1	7.50	28.5-38.5
	Total	848.2			
Warbling Vireo and Yellow-bellied Sapsucker (Uniform Cosine, truncation 73 m)					
Pooled	0.75, 0.79	1415.8	43.7	2.92	41.3-46.3
Year					
2007	0.78, 0.79	180.5	47.7	11.4	37.6-60.4
2008	0.46, 0.54	610.4	42.8	3.12	37.4-45.3
2009	0.77, 0.72	623.0	47.4	11.7	42.2-53.3
	Total	1413.9			
Species					
WAVI	0.93, 0.78	725.1	44.0	4.11	40.6-47.8
YBSA	0.68, 0.92	692.6	43.4	4.12	39.9-47.1
	Total	1417.7			
Forest Cover					
Coniferous	Too few detections				
Coniferous-dominated mixedwood	Too few detections				
Mixedwood	0.57, 0.75	605.0	45.6	5.57	40.8-50.9
Deciduous-dominated mixedwood	0.87, 0.54	249.5	41.5	5.81	36.8-46.7
Deciduous	0.65, 0.61	386.4	41.4	3.52	38.5-44.4
	Total	1418.3			
American Robin, Ovenbird, Swainson's Thrush, Tennessee Warbler, White-throated Sparrow (Hazard-rate Cosine, truncation 84 m)					
Pooled	0.17, 0.19	5013.4	68.4	2.09	65.6-71.3

Data structure	*p*-value[1,2]	AIC	EDR[3]	% CV[4]	CI[5]
Year					
2007	0.95, 0.68	458.2	49.7	24.7	30.5-80.9
2008	0.47, 0.23	2194.6	60.4	2.37	57.6-63.3
2009	0.07,<0.01	2293.3	76.9	2.59	73.1-80.9
	Total	4946.11			
Species					
AMRO	0.83, 0.85	568.6	67.6	4.58	61.7-74.1
OVEN	0.59, 0.49	557.4	72.3	7.08	62.8-83.3
SWTH	0.75, 0.11	2101.8	64.0	4.72	58.3-70.2
TEWA	0.69, 0.95	579.6	71.4	4.14	65.8-77.5
WTSP	0.58, 0.42	1218.1	65.1	6.38	57.4-73.9
	Total	5025.5			
Forest Cover					
Coniferous	0.80, 0.31	571.0	75.2	7.47	64.8-87.3
Coniferous-dominated mixedwood	0.20, 0.22	692.0	61.1	7.35	52.8-70.7
Mixedwood	0.86, 0.48	1759.5	69.8	3.39	65.2-74.6
Deciduous-dominated mixedwood	0.99, 0.60	455.2	70.9	8.32	60.0-83.8
Deciduous	0.73, 0.62	1540.4	66.6	3.11	62.6-70.8
	Total	5018.1			

Goodness of fit tests: [1] Kolmogorov-Smirnov [2] Chi-squared – only the chi-squared is shown for data analyzed in groups [3] Effective Detection Radius [4]Coefficient of variation of the EDR estimate [5]95% confidence interval of EDR estimate.

Appendix G.

Yellow-bellied sapsucker breeding territories found during 2007-2009 in northeastern BC

	Survey Year			
Number of years surveyed	**2006**	**2007**	**2008**	**2009**
1	6	6	5	35
2	2 (2)	8 (7)	19 (12)	
3	0	36 (30)*		
4	3 (2)			
Total	**11**	**50**	**24**	**35**

The number of territories re-used in subsequent years is shown in brackets. *17% (6) not re-used, 17% (6) used over 2 years, 19% (7) used in two non-consecutive years, 47% (17) used over 3 years.

Appendix H.

Vegetation characteristics of yellow-bellied sapsucker nest sites compared to available unused sites.

	Nesting Territory				Adjacent to Territory			
TREE								
	Mean	**SE**	**n**	**Range**	**Mean**	**SE**	**n**	**Range**
DBH (cm)	37.0	0.49	119	25.5-57.9	43.7	1.20	58	24.8-60.5
Tree Height (m)	24.9	0.42	120	9-38.4	24.9	0.51	58	8.00-34.0
Crown Height (m)	19.9	0.36	112	9.2-31.9	17.2	0.34	58	10.9-21.9
Fungal Conks	7.68	0.49	104	1-30	4.01	0.50	58	1-20
Decay State	2.16	0.05	120		1.31	0.10	58	
Cavity Height (m)	10.7	0.38	120	3.2-21.2				
	Count	**%**	**n**		**Count**	**%**	**n**	
Broken Tree Top	26	24	108		0			
Decay State 2a[1]	28	25	114		42	72	58	
Decay State 2b[1]	40	35	114		12	21	58	
Decay State 2c[1]	32	28	114		4	7	58	
Decay Class 3	8	7	114					
Decay Class 4	3	3	114					
Decay Class 5	3	3	114					
Cavity Age – Old	20	17	120					
Southerly Aspect[2]	78	65	120					
No other cavities	64	53	120					
1 other cavity	50	42	120					
2 other cavities	3	2.5	120					
3 other cavities	2	1.6	120					
TREE SITE	**Mean**	**SE**	**n**	**Range**	**Mean**	**SE**	**n**	**Range**
Live Birch[3]	0.60	0.21	58	0-8	0.83	0.18	58	0-5
% Shrub Cover	13.9	2.47	58	0-70	17.5	2.61	58	0-90
Aspen[3]	10.3	0.84	58	0-26	6.53	0.79	58	0-26
Live Decaying Aspen[3]	3.74	0.43	58	0-15	1.74	0.34	58	0-17

	Nesting Territory				Adjacent to Territory			
TERRITORY CORE	**Mean**	**SE**	**n**	**Range**	**Mean**	**SE**	**N**	**Range**
Live Birch[4]	0.77	0.16	58	0-6	0.95	0.17	58	0-6
% Shrub Cover	16.0	1.90	58	0-54	18.5	1.93	58	0-63
Aspen[4]	6.82	0.52	58	0.25-19	4.40	0.51	58	0-18
Live Decaying Aspen[4]	2.05	1.51	58	0-8	1.31	0.22	58	0-12
Stand composition[5]	67.6	3.19	58	22-100	51.5	2.81	58	5-99

[1]Decay Class 2 - Live decaying trees. [2]Cavity. [3]Density of tree stems > 15 cm DBH in one 11.3 m radius plot. [4] Density of shrub clumps and tree stems > 15 cm DBH in four 11.3 m radius plots. [5]Percent deciduous within ~60 m radius - average of visual estimates and basal area measures.

Appendix I.

Averages for reproductive data for yellow-bellied sapsuckers.

	Clutch Size (Eggs)	Number of Old Chicks[1]	Number of Old Chicks[2]	Hatching Date	Nestling Period (days)	Fledging Date
Mean	5	4	4	June 17	25	July 8
Mode	6	4	4		27	
SE	0.20	0.21	0.14		0.45	
Min	3	1	0	June 10	21	June 30
Max	7	6	6	July 3	31	July 24
n	30	30	61	39	28	94

[1] Nests for which clutch size was counted. [2] All territories