

**EFFECTS OF RIPARIAN BUFFER WIDTH ON SONGBIRDS
AND FOREST STRUCTURE IN THE SOUTHERN INTERIOR OF
BRITISH COLUMBIA**

by

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ABSTRACT

In harvested landscapes, the retention of riparian buffers along streams may mitigate the effects of habitat loss and fragmentation by providing usable habitat for songbirds. To explore this hypothesis, I studied the influence of riparian buffer width on breeding songbirds and forest structure in a high elevation forest of south-central British Columbia.

I studied four different buffer widths, consisting of very narrow (2-3 m), narrow (11-15 m), medium (30-34 m) and wide buffers (57-69 m). Buffer and control (unharvested forest) sites were each replicated twice for a total of ten study sites. I conducted spot map surveys and habitat sampling to measure width effects on songbird density and vegetation, and to assess the influence of forest structure on songbird density. To examine habitat use by forest birds, I observed the foraging behaviours and movements of four songbird species: winter wren, yellow-rumped warbler, golden-crowned kinglet and Townsend's warbler.

Riparian buffer width had several effects on the songbirds breeding within the study area. First, buffer width influenced songbird community structure and composition. The juxtaposition of clearcut and forest in the study grids containing medium and wide buffers maximized species richness and diversity. As buffer width decreased, generalist and open-habitat species replaced forest species within the study grids; very narrow and narrow buffers provided little habitat for forest songbirds. Second, although changes in forest structure occurred across buffers, width was the most important factor determining the richness and density of forest songbird species. Third, buffer width influenced the movement patterns of foraging songbirds. Individuals in buffers moved greater distances upstream and downstream than they did towards and away from the stream; individuals in unharvested stands moved almost equally in all directions.

Overall, there did not appear to be a threshold buffer width beyond which there was a disproportionate loss of species and individuals. Although several common forest species were present to a certain extent in all riparian buffers, forest songbirds would benefit most from buffers ≥ 30 m in width.

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INTRODUCTION

In North America, songbirds face habitat loss and fragmentation through a variety of human activities, namely deforestation, land conversion and urbanization (Terborgh 1989). Habitat loss and fragmentation can have several deleterious consequences, including an overall reduction in habitat area, increased isolation of habitat patches, greater edge to interior ratio and decreased habitat quality (Askins et al. 1987, Wiens 1994, Faaborg et al. 1995). Area and isolation effects can result in the loss of particular species, lowered species diversity and fewer recolonization events following local extinctions (Ambuel and Temple 1983, Freemark and Collins 1992). Edge effects, while traditionally viewed as beneficial to game species (Harris 1984, Hunter 1990), can have negative effects on non-game species in the form of increased predation, parasitism and competition (Gates and Gysel 1978, Brittingham and Temple 1983, Simberloff 1994, Vander Haegen and Degraaf 1996, Brand and George 2000; but see Haskell 1995, Zarette 2000, Davidson and Knight 2001). As forested areas become increasingly fragmented, the number and abundance of forest-associated songbird species is reduced in patches (Faaborg et al. 1995, Austen et al. 2001) and along edges (Brand and George 2001). As well, forest birds in smaller fragments may be negatively affected by increased competition with edge and open-habitat species.

In British Columbia (B.C.), forest harvesting comprises a major segment of the provincial economy and occurs in much of the province. In south-central B.C., many lower elevation forests have been logged and harvesting is now focusing on montane and subalpine forests. Songbirds breeding in these high-elevation

environments face harsh climates and limited resources (Sabo 1980, Sabo and Holmes 1983), and may not respond well to reduced habitat and resource availability. Conversely, high-elevation forests in the B.C. interior have been historically disturbed by natural forces, including stand-initiating fire and insect outbreaks (Province of B.C. 1995a). The songbird species inhabiting these forests have adapted to natural disturbance and thus may be able to adjust to forest harvesting effects (Bunnell 1995).

In high-elevation forests, stream riparian ecosystems are productive areas for tree growth and are frequently subject to timber extraction. The Riparian Area Management Guidelines are used to regulate harvesting in these ecosystems within B.C. (Province of B.C. 1995b). Streams have been classified on the basis of average channel width, fish presence and use as a community watershed. The retention of Riparian Management Areas (RMAs) is required along streams in harvested sites. These areas are composed of two sections: the *riparian reserve zone* and the *riparian management zone*. The reserve zone acts as a buffer, within which harvesting is prohibited. Harvesting is permitted in the management zone, but may be modified to meet specific objectives. The width of the RMA is specific to the stream class; all streams are assigned a management zone, but only those possessing fish or community watershed values are assigned a reserve zone.

Headwater streams, generally small and rarely fish-bearing, receive little or no protection under the current guidelines and may be at particular risk of riparian habitat degradation. In high-elevation forests, these riparian areas are used by bird species associated with both riparian and mature forest (Kinley and Newhouse 1997,

Wiebe and Martin 1998). Riparian buffers along streams at high elevations may not possess the same degree of avian richness and diversity as found along lower elevation streams, but they are important habitat in their own right (Wiens 1994) and can provide additional mature forest to songbirds breeding in a fragmented landscape. However, the retention of buffers along these small streams poses a trade-off between economics and conservation. Maintaining buffers on every headwater stream would provide abundant habitat to songbirds and other vertebrates, but the harvesting constraints would be excessive. Therefore, it is important to determine the value of streamside riparian buffers to songbirds, and in particular, to which species.

This thesis examines the influence of riparian management strategies on songbirds breeding in a montane forest within south-central B.C. The primary goal of this project was to determine if riparian buffers provide habitat for forest songbirds in general, and specifically, whether or not wide riparian buffers provide habitat to a disproportionately greater number of species and individuals than do narrow buffers. The project objectives were twofold: (1) measure the effects of riparian buffer width on the community composition and density of breeding songbirds, and (2) describe the habitat use and associations of particular forest-associated songbird species. The first objective is addressed in Chapter 1, "The effect of riparian buffer width on breeding songbirds". The second objective is addressed in Chapter 2, "Vegetation characteristics of riparian buffers and the use of riparian buffers by foraging forest songbirds".

CHAPTER 1. The effect of riparian buffer width on breeding songbirds.

INTRODUCTION

Some songbird species avoid small forest patches and are present only within large tracts of forest. Other species, although present in small forest patches, occur at greater density in large patches. In a study of songbird habitat associations, Whitcomb et al. (1981) classified forest songbirds as (1) forest-interior specialists, (2) interior-edge generalists, (3) edge species, and (4) field-edge species. The term 'forest-interior specialist' has since been linked to 'edge avoidance' and 'area-sensitivity' in songbirds. Edge avoidance describes forest birds that nest only within forest interiors and tend to avoid edge habitats (Whitcomb et al. 1981); area-sensitivity refers to those forest species that are uncommon or absent in smaller forest fragments (Freemark and Collins 1992).

A number of habitat fragmentation studies have demonstrated that forest area is a principal determinant of songbird community composition (Askins et al. 1987, Freemark and Collins 1992, Austen et al. 2001). Freemark and Merriam (1986) concluded that forest size was the most important variable influencing the presence of forest-interior birds, and that interior species were found infrequently in small forest patches. Villard et al. (1999) determined that forest cover was a significant predictor of species presence, and Trzcinski et al. (1999) found that forest cover had a greater effect than forest fragmentation on species presence. Forest fragments do not possess a random assemblage of species, but rather contain a subset of those species found in continuous forests (Ambuel and Temple 1983, Blake and Karr 1987, Hobson and Bayne 2000).

Although forest area is a strong predictor of species presence in forest fragments, the actual mechanisms causing the disappearance of certain species remain uncertain. The fact that Neotropical migrants are absent from forest patches much larger than their average territory size points to some qualitative change in the habitat (Faaborg et al. 1995). Area-dependent changes in the forest environment, such as edge effects, have been hypothesized as a key cause. Edge effects are those ecological characteristics associated with habitat edges that influence the species living there (Harris 1988). Forest edges are prone to altered microclimates and wind regimes, leading to changes in habitat features like vegetation species composition and structure (Chen et al. 1992). Because anthropogenic forest edges are generally an abrupt junction of forested and open habitats, they may also experience a greater level of biotic interaction. For forest songbirds, interactions include an increased number of open-habitat and/or edge species (Schieck et al. 1995, Hobson and Bayne 2000, Pearson and Manuwal 2001), increased rates of nest predation (Gates and Gysel 1978, Donovan et al. 1997, Burke and Nol 2000) and nest parasitism (Brittingham and Temple 1983, Robinson 1992, Robinson et al. 1995), and lowered food supply in small fragments (Zanette and Jenkins 2000)

Stream riparian buffers (i.e., forest retained along a stream after harvesting or other land use activity) essentially represent long fragments of forest, particularly when harvesting has occurred on both sides of a stream. Riparian buffers are primarily retained for the preservation of water quality and other aquatic values, but they also provide habitat for terrestrial vertebrates confronted by an increasingly fragmented landscape. Research has indicated that riparian buffers can provide

habitat to a segment of the songbird community, but that long and narrow buffers may exclude certain edge avoiding and area sensitive species.

Studies of mixed-wood forests in the east and northeastern United States have found that wide riparian buffers are required to maintain songbird assemblages similar to those of undisturbed forests. Croonquist and Brooks (1993) examined bird communities in stream riparian corridors in central Pennsylvania and found that buffers greater than 25 m in width were necessary to maintain disturbance-sensitive species. In Maryland and Delaware, Keller et al. (1993) discovered that Neotropical migrants were primarily present only in buffers wider than 100 m. Both Thurmond et al. (1995) in Georgia and Meiklejohn and Hughes (1999) in Vermont determined that while forest-interior specialists were abundant (# individuals/transect) in undisturbed forests, they were significantly less abundant in riparian buffers ranging from 50 -164 m in width.

Research has yielded similar results in the conifer-dominated forests of eastern Canada and the Pacific Northwest. In Newfoundland, Whitaker and Montevecchi (1999) found that interior forest species were rare even in the widest lakeside buffers (40-50 m) when compared with local interior forest habitat. In Quebec, a study of streamside riparian buffers by Darveau et al. (1995) determined that 60-m wide strips were required to prevent the loss of most forest songbirds. Hagar (1999), comparing riparian buffer widths in western Oregon, found that buffers >40 m wide were likely to provide the most benefit for forest songbirds. Within B.C., two studies in mid to high-elevation forests indicated that songbird density (detections/ha) increased with buffer width (Kinley and Newhouse 1997), and that

forest strips <38 m wide were unsuitable for five forest songbird species (boreal chickadee (*Poecile hudsonica*), brown creeper (*Certhia Americana*), Swainson's thrush (*Catharus ustulatus*), Townsend's warbler (*Dendroica townsendi*), winter wren(*Troglodytes troglodytes*)) (Gyug 1996).

This chapter examines how the width of riparian buffers, retained after harvesting, affects songbirds breeding in a high-elevation coniferous forest. My objectives were to: (1) measure changes in the songbird community (richness, diversity, similarity) across a range of buffer widths, and (2) quantify variation in songbird territory density as a function of buffer width. I hypothesized that as buffer width increased, the resulting increase in the amount of forest habitat and the number of niches available would effect changes in the songbird community. I predicted that the number of forest songbird species would increase with buffer width while the number of open-habitat and generalist species would decrease. Species classifications are given in Table 1.2 and Appendix 2. I also predicted that wide buffers would possess a songbird assemblage most similar to that of the unharvested forest, and that the similarity between treatments and unharvested forest would decrease with decreasing buffer width. Finally, I predicted that increases in buffer width would result in higher densities (# territories/ha) of forest songbirds and lower densities of open-habitat and generalist songbirds.

METHODS

Study Area and Experimental Design

The study was conducted within Tree Farm License (TFL) #35, a 30,000 ha area of forested land currently licensed to Weyerhaeuser Canada Ltd. TFL #35 is located in the Kamloops Forest Region and is approximately 30 km north of Kamloops, British Columbia (Figure 1.1). It occurs in the Thompson-Okanagan Plateau Ecoregion, an area of the South Interior Ecoprovince that consists of a broad plateau with low elevation basins. This region has mean annual temperatures and precipitation ranging from 1.8°C and 1900 mm in high elevations to 10°C and 330 mm in low elevations, making it one of the driest and warmest climates in B.C. (Meidinger and Pojar 1991).

Experimental units ranged in elevation from 1100 m to 1600 m and were characterized by east-southeast facing aspects (Table 1.1). The matrix surrounding each unit was composed of coniferous forest interspersed with clearcut patches of various ages. Forest stands contained subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), hybrid white spruce (*Picea engelmannii* Parry *x glauca* Voss) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), with lesser amounts of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco). The average age of the stands surrounding the experimental units ranged from 101 to 250 years.

The study focused on two biogeoclimatic zones: the mid-elevation Montane Spruce (MS) zone and the high-elevation Engelmann Spruce-Subalpine Fir (ESSF) zone. Specifically, experimental units were located in the Montane Spruce, dry mild variant 2 (MSdm2) and the Engelmann Spruce-Subalpine Fir, dry cold variant 2

(ESSFdc2). The MSdm2 is characterized by cold winters and moderately short, warm summers. Climax stands are composed of subalpine fir and hybrid white spruce with an understory containing falsebox (*Pachistima myrsinites* (Pursh) Raf.), black huckleberry (*Vaccinium membranaceum* Dougl.) and grouseberry (*Vaccinium scoparium* Leiberg) (Lloyd et al. 1990). The ESSFdc2 is typified by long, cold winters and short, cool summers. Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir comprise the canopy in climax stands; the understory is dominated by white-flowered rhododendron (*Rhododendron albiflorum* Hook), black huckleberry and Sitka valerian (*Valeriana sitchensis* Bong.) (Lloyd et al. 1990).

This was a retrospective study that took advantage of existing riparian buffers. In 1998, I located 10 experimental units throughout TFL #35 (Figure 1.2). I selected study sites that were similar with respect to stream size, clearcut age, surrounding forest type and consistency of riparian buffer width. Sample size was constrained by the availability of appropriate sites; treatments and controls were not selected randomly and were only replicated twice. Due to the uniqueness of each site, a nested experimental design was used (Hicks 1993), with replicates nested within treatments.

Treatments consisted of four different buffer widths, defined as “Very Narrow” (2-3 m), “Narrow” (11-15 m), “Medium” (30-34 m) and “Wide” (57-69 m) (Table 1.1) (Figure 1.3). Treated sites were located along small streams (≤ 5 m wide) with recent clearcut harvesting (≤ 4 yr) on one side and continuous forest on the other side. Control sites were placed along small streams (≤ 5 m wide) with ≥ 200 m of unharvested forest on both sides of the stream. All sites were surrounded by mature

forest and were at least 200 m from the next clearcut. Treated sites had at least one road leading into the study block; roads were absent from control sites.

Breeding Bird Sampling

Spot-mapping was used to survey breeding songbirds and determine territory density and location. This method involves a series of repeat visits to well-marked grids, within which the locations of all songbirds are recorded. At the end of the breeding season, location data are used to delineate territory boundaries for different individuals (Bibby et al. 1992).

I established a 4.5-ha grid at each site; this was less than the recommended area of 10 ha (Svensson and Taylor 1970) because of cutblock size limitations. Each grid was approximately 300 m long and 150 m wide, oriented lengthwise along the stream. Grid lines were flagged every 25 m; flagged markers were then georeferenced using a Global Positioning System (GPS) and plotted at a scale of 1:1500. I used these grid maps as census maps for recording all songbird observations. This permitted each bird observation to be digitized, entered into a Geographic Information System (GIS) database and assigned a georeference coordinate.

Spot-map surveys were carried out from 30 June – 15 July in 1998, and from 01 June – 13 July in 1999. Because of the time required to locate study sites and construct grids in 1998, only one survey was completed at each site and I was unable to delineate territories for density estimation. In 1999, sites were surveyed 7 times, meeting the minimum number of visits required by spot-mapping protocols (Svensson and Taylor 1970).

Two observers conducted the one survey in 1998, and four observers conducted the first four survey sessions in 1999. The remaining three sessions in 1999 were divided between two observers. Observers were trained over several days to standardize data collection. All observers surveyed the same plot over the same period and then compared results. By the end of the training period, observers were generating similar survey results. All surveys were completed between 0500 and 0900 hrs PST, and observers were rotated between sites to minimize observer bias. Survey start points were also rotated to prevent time-of-day bias. Surveys were not conducted in heavy rain or snow.

Territory Delineation with GIS

I used ArcView 3.1 (ESRI Inc. 1998) to delineate songbird territories from the 1999 survey data. All bird observations at each site and across all sessions were digitized and linked with a corresponding database. To aid in defining edge territories, the digital data included those individuals heard or seen up to 100 m beyond the grid boundaries. Database queries were used to select observations based on species, resulting in a separate map for each songbird species at each site, color-coded by session date. Countersinging and moving individuals were coded separately to help differentiate territorial males.

Songbird territories were delineated using criteria adapted from Svensson and Taylor (1970), Manuwal and Carey (1991) and Bibby et al. (1992). Territories were outlined using straight lines to connect the outer points of observations (Worton 1987) (Appendix 1). The effective number of visits was based on when each species was first observed on the study grids. For most species, this ranged from 5 to 7 visits;

accordingly, a minimum of 3 registrations of a singing male, from at least 3 separate sessions, was required to define a territory. Because of the short breeding season, records in a territory were an average of 6 days apart, not the 10 days recommended by Bibby et al. (1992).

I used ArcView to calculate the area of all territories inside and on the edge of each study grid. For each species, the number of territories in a grid was calculated by summing the number of complete territories and the proportion of each edge territory falling within the grid boundaries. The number of territories present in the cutblocks and buffers was calculated in the same way. I also summed territories across all species to yield the total number of territories for each grid, clearcut and buffer. I then divided the total number of territories for each species, and for all species combined, by the grid area (hectares) to calculate density (# territories per hectare) for each grid. Density values were also calculated for each cutblock and buffer by dividing the number of territories in each habitat by the cutblock area (ha) and the buffer area (ha), respectively.

Data Analysis

Songbird Community Characteristics

I calculated species richness, species diversity and community similarity values for each treatment. Species richness was simply the number of species with territories in each grid. Species diversity was calculated using both the Shannon-Wiener and Simpson diversity indices. These indices are sensitive to the rare and dominant species in a community, respectively (Krebs 1989). The Bray-Curtis index was calculated to evaluate the similarity of songbird communities across treatments

(Krebs 1989, Brower et al. 1990). This index of similarity is recommended for situations where species diversity is low and sample size is small (Krebs 1989). All indices were determined using the density of territories per hectare.

I used regression analysis to assess the relationship between riparian buffer width and each of total species richness, buffer species richness and species diversity (SigmaPlot SPSS Inc. 2001). All variables were tested for a normal distribution and equal variance; where necessary, variables were transformed using either the square-root or the \log_{10} transformation and re-tested for normality. Scatterplots of each variable vs. buffer width were used to determine the most appropriate regression model (if any) for testing (Zar 1996). A significance level of $\alpha = 0.05$ was used for all tests. I assessed the fit of each model with the coefficient of determination (r^2), the standard error of the estimate, the overall significance of the model and the significance of each parameter in the model (Zar 1996).

From examining species composition in the riparian buffers and the clearcuts, it was apparent that species fell naturally into broad habitat associations. I characterized these associations as *forest* (unharvested forest and buffers), *open habitat* (clearcuts) and *general* (clearcuts and buffers). Numerous researchers have also classified songbirds according to their broad habitat associations (Freemark and Collins 1992, Darveau et al. 1995, Gyug 1996, Whitaker and Montevecchi 1997, Davis et al. 1999, Hagar 1999, Whitaker and Montevecchi 1999). I used these classifications, in combination with species-habitat associations observed in my study area, to categorize species as either *forest*, *open-habitat* or *generalist* (Table 1.2, Appendix 2).

Songbird Density

At each site, I calculated the total density (# territories/ha) of all species in the entire grid, and in the buffer and clearcut. I also calculated the density of all forest and open-habitat species separately in the entire grid, buffer and clearcut. Finally, I calculated the density of each breeding species in each grid, buffer and clearcut. Only common species (i.e., those with territories on ≥ 3 study grids) were selected for further analyses. I used the Shapiro-Wilks goodness of fit procedure to test all density data for a normal distribution prior to statistical analysis (SPSS Inc. 1999). Where necessary, variables were either square-root or \log_{10} transformed and retested. Scatterplots were used to visually assess relationships between buffer width and the different density variables.

I used regression analysis to examine the effect of riparian buffer width on territory density within the grids (SigmaPlot SPSS Inc. 2001). Territory density was regressed against buffer width for all species combined, for forest and open-habitat species separately, and for the five most common species: dark-eyed junco (*Junco hyemalis*), golden-crowned kinglet (*Regulus satrapa*), Townsend's warbler, winter wren and yellow-rumped warbler (*Dendroica coronata*).

Model selection was based on the coefficient of determination (r^2), the standard error of the estimate, the overall significance of the model and the significance of each parameter in the model (Zar 1996). When different models generated similar significance values for the same variable, the most appropriate model was chosen based on the sum-of-squares technique (Hilborn and Mangel 1997) and the principle of parsimony (Burnham and Anderson 1998). Residuals were

plotted against predicted values as a final means of judging the fit of the model to the data (SPSS Applications Guide 1998).

Non-parametric analysis was performed on density data that could not be normalized through transformation (SPSS Inc. 1999). I used the Kruskal-Wallis one-way analysis of variance, with $\alpha = 0.05$, to assess the effect of riparian buffer width on the density of seven songbird species: American robin (*Turdus migratorius*), chipping sparrow (*Spizella passerina*), Lincoln's sparrow (*Melospiza lincolnii*), mountain bluebird (*Sialia currucoides*), Hammond's flycatcher (*Empidonax hammondii*), Swainson's thrush and varied thrush (*Ixoreus naevius*) (Zar 1996).

RESULTS

Community Characteristics

Forty-six bird species were recorded within the study grids during the 1999 spot-map surveys (Appendix 2). Thirty-six species were songbirds; the remainder consisted of three raptors, three woodpeckers, two corvids, one shorebird and one species of grouse. I considered songbirds as those species occurring within the Order Passeriformes, but excluded the Family Corvidae, due to their large territory sizes and lack of conspicuous territorial behaviour. Of the twenty songbird species that held territories within the grids (i.e., were recorded on ≥ 3 separate surveys), I classified nine as forest, eight as open-habitat and three as generalist (Table 1.2, Appendix 2). Of these, twelve species were present on ≥ 3 grids and were considered common (Appendix 2).

The Bray-Curtis community similarity index described the similarity in species composition among treatments (Table 1.3). Overall similarity was high (≥ 0.595); the greatest similarity occurred between the very narrow, narrow and medium treatments, and between the wide treatments and the unharvested forest. The greatest dissimilarity occurred between the wide and very narrow/narrow treatments, and between the unharvested forest and very narrow/narrow treatments.

Species richness within the grids was low at all study sites (Figure 1.4a), indicating a species-poor songbird community in general. The greatest richness occurred in the wide treatments and the lowest occurred in the very narrow treatments and the unharvested forest, although overall differences were small. Species diversity was also low across all treatments (Figure 1.4b). Despite measuring different aspects

of the community (*see* Methods), both the Shannon-Wiener and the Simpson indices showed the same pattern – that of maximum diversity in the wide treatments and minimum diversity in the unharvested forest.

Regression analysis did not reveal a significant relationship between riparian buffer width and either of total species richness, Shannon-Wiener diversity index or Simpson diversity index. However, there was a significant positive relationship between riparian buffer width and buffer species richness (Figure 1.5). The total number of species in the buffer grew rapidly with small increases in buffer width, and then began to plateau as buffer habitat occupied greater portions of the survey area. A power model yielded the best fit ($P < 0.001$), explaining 79% of the variation in the data.

Songbird Density

Regression analysis indicated a significant positive relationship between riparian buffer width and the total density (# territories/ha) of all species within the study grids (Figure 1.6a). The greatest increase in total density occurred between the narrow and wide buffers (Table 1.2). The logarithmic model provided the best fit and explained 59% of the variation in the data. Riparian buffer width also had a significant effect on the density (# territories/ha) of forest species within the study grids (Figure 1.6b). Density increased steadily from the very narrow to the wide buffers, after which the rate of increase slowed. The logarithmic model provided a simple, yet highly significant, description of the relationship and explained 88% of the variation in the data. Increasing buffer width did not have a significant effect on the density (# territories/ha) of open-habitat species within the study grids. Only in

the controls, where open habitat was completely lacking, were all open-associated species absent (Table 1.2).

I conducted regression analysis on the five most commonly occurring songbird species within the study grids (dark-eyed junco, golden-crowned kinglet, Townsend's warbler, winter wren and yellow-rumped warbler). Four species had significantly greater densities in wider buffers: golden-crowned kinglet, Townsend's warbler, winter wren and yellow-rumped warbler. There was no clear relationship between buffer width and dark-eyed junco density, although juncos were absent from the unharvested forest (Table 1.2).

Golden-crowned kinglet and Townsend's warbler densities displayed a similar relationship with buffer width (Figure 1.7 a, b). Density rose rapidly with small increases in width, and then slowed as buffers became wider and reached a maximum in the unharvested forest. In both cases, the logarithmic model yielded the best fit, explaining 89% of the variation in the kinglet data, and 85% of the variation in the warbler data. Although the maximum densities of golden-crowned kinglets and Townsend's warblers were similar, the slope of the regression model was slightly higher for kinglets, indicating a stronger response to small increases in buffer width.

Winter wrens and yellow-rumped warblers also showed significant responses to increasing buffer width, although the models failed to account for over half of the variation in the data. Winter wren density increased with width to a maximum in the unharvested forest (Figure 1.7c). A linear model provided the best fit and explained 43% of variability in the data. The density of yellow-rumped warbler territories also rose with increasing buffer width, but reached a peak in the wide buffers, then

declined again in the unharvested forest (Figure 1.7d). Although a quadratic model was significant only at $\alpha = 0.10$, it accounted for 48% of variation and provided the best fit to the yellow-rumped warbler data.

Non-parametric Kruskal-Wallis tests were conducted on the seven commonly occurring songbird species that did not exhibit normally distributed territory densities within the study grids (Table 1.4). At $\alpha = 0.05$, riparian buffer width did not have a significant effect on the density of any of the seven species. However, if the tests are considered exploratory and $\alpha = 0.10$ is used, buffer width had a significant negative relationship with the Lincoln's sparrow, and a significant positive relationship with the Swainson's thrush and the varied thrush.

DISCUSSION

Width Effects on Community Characteristics

The study area possessed a fairly simple songbird community, dominated by a few common species. Species number was similar to that observed in other high-elevation and boreal studies (Darveau et al. 1995, Schieck et al. 1995, Kinley and Newhouse 1997, Schmeigelow et al. 1997). The low richness and equitability, typical of high-elevation and boreal forests, is likely the result of the reduced productivity and short breeding seasons found in these environments (Able and Noon 1976, Sabo and Holmes 1983, Osborne and Green 1992, Folkard and Smith 1995). The assemblage of songbirds breeding in the study grids was characteristic of that found in montane forests throughout British Columbia (Gyug 1996, Kinley and Newhouse 1997, Wiebe and Martin 1997). Although numerous songbirds were considered 'rare' for the study area (i.e., recorded only once or twice), none of these species was provincially listed as threatened (blue-listed) or endangered (red-listed). Many of the species described as rare in this study (e.g., cedar waxwing (*Bombycilla cedrorum*), warbling vireo (*Vireo gilvus*), brown creeper) are actually common at the regional level. The forest species that were absent from the narrower buffers (e.g., Swainson's thrush, varied thrush, Hammond's flycatcher) are also considered regionally common.

Species richness and diversity were higher in the buffers than in the unharvested forest, and both values increased with buffer width. The increase in richness and diversity with buffer width may have been due to the influence of habitat heterogeneity (Triquet et al. 1990, Dickson et al. 1995, Gyug 1996, Hagar 1999, Meiklejohn and Hughes 1999). Grids containing very narrow and narrow buffers

were primarily composed of clearcut habitat and were inhabited mostly by open-habitat and generalist species. Grids containing medium and wide buffers incorporated a relatively large amount of forest adjacent to open habitat; accordingly, these sites had a mixture of generalist, open-habitat and forest species. The low richness and diversity recorded in the unharvested forest reflects the loss of species associated with clearcuts, forest openings and edges.

Increasing riparian buffer width had a positive effect on the number of species occurring in the buffers. Despite the presence of continuous forest on the opposite side of the stream, the richness of forest songbird species increased significantly with incremental changes in the amount of habitat. The observed effect of buffer width on buffer species richness implies that certain forest species may have been area-sensitive and/or edge-sensitive. Keller (1993) found a similar pattern for Neotropical migrants in streamside buffers and attributed it to the presence of various area-sensitive species (e.g., Acadian flycatcher [*Empidonax virescens*], red-eyed vireo [*Vireo olivacea*]) in wider buffers. The relationship between buffer width and species richness may also have been due to the increased availability of upland habitat in the medium and wide buffers, which attracted forest species not commonly associated with riparian habitats (Wiebe and Martin 1997).

Width Effects on Songbird Density

Total Density

The total density of all species and the density of forest species both showed significant responses to small changes in the amount of buffer habitat. The similarity of these patterns suggests that forest bird species were largely responsible for the

observed relationship between total density and buffer width. As with buffer species richness, density increased with buffer width despite the presence of contiguous forest on the opposite side of each stream, indicating the possible sensitivity of several forest species to small-scale changes in habitat availability. Similar results were yielded by two other studies with riparian buffers on one side of the stream only. Kinley and Newhouse (1997) found that the total density of all species differed significantly among buffer widths, with higher densities in wider buffers. Similarly, Darveau et al. (1995) found that forest songbirds used all remnant forest buffers, but that their densities significantly declined in narrow buffers (20 m) over a three-year period.

The density of open-habitat species did not change significantly with increasing riparian buffer width. Unlike their forest-dwelling counterparts, open-habitat species were not sensitive to small changes in the availability of their habitat. Although the ratio of buffer-to-clearcut within the study grids increased with increasing buffer width, the study grids were still surrounded by open habitat. These results suggest that the density of open-habitat species was primarily influenced by the availability of clearcut habitat on a larger scale.

Species-Specific Density

Most open-habitat species occurred at relatively low densities in the study grids, and all but the dark-eyed junco and the MacGillivray's warbler reached peak density in the very narrow (2-3 m) and narrow (11-15 m) buffer sites. The dark-eyed junco was the most abundant open-habitat species and was present in relatively high densities across all treatments. Juncos were frequently observed utilizing the forest

edge and residual patches of trees within the cutblocks for singing. Although all open-habitat species were common in the early seral habitat provided by the clearcuts, they were absent from the undisturbed forest. This contrasts with Davis et al. (1999), who found that species such as the American robin, chipping sparrow, Lincoln's sparrow and dark-eyed junco occurred in both early-seral and mid- to late-seral habitats in high-elevation forests. The lack of open-habitat species in the unharvested forests of this study may reflect a difference in structure (such as greater canopy closure and fewer canopy gaps) or a preponderance of open habitat available throughout the study area.

Generalist species occurred with the greatest density where both open and forest habitats were present, and appeared to benefit most from the juxtaposition of clearcuts and riparian buffers ≥ 30 m. Wilson's warblers were present only in medium (30-34 m) and wide (57-69 m) buffer sites, and yellow-rumped warblers reached maximum density in the wide buffer sites. Territories of both species included buffer and clearcut habitat, and individuals were frequently observed singing and calling from the forest edge. Yellow-rumped warblers also often used the small, residual patches of trees left in most cutblocks. In contrast, Kinley and Newhouse (1997) found the highest density of yellow-rumped warblers in medium buffers (37 m) and Whitaker and Montevicchi (1999) detected Wilson's warblers only within buffers. The density of these insectivorous species in the medium and wide buffers of my study may, in part, be a response to greater food availability. In western Newfoundland, Whitaker et al. (2000) linked the abundance of ubiquitous birds, such

as the yellow-rumped warbler, in riparian buffers to the elevated numbers of large-bodied flying insects found along the edges of lakeshore buffers.

All forest species reached their highest densities in the widest riparian buffers and the undisturbed forest. However, the absence of varied and Swainson's thrush from the medium and narrow buffers may indicate that buffers ≤ 34 m are not sufficient to provide suitable habitat for these species. Alternatively, these species were relatively uncommon in the study sites and may have been too sparsely distributed to sample effectively. Hagar (1999) found that the varied thrush was absent from most buffers, and Kinley and Newhouse (1997) observed it only in the widest buffers (70 m). Conversely, the sensitivity of Swainson's thrush to riparian buffer width may depend on ecosystem type or forest structure. Although Swainson's thrush has been characterized as an interior specialist in eastern Canada (Whitaker and Montevecchi 1997, 1999) and width-sensitive in western Canada (Gyug 1996), both Darveau et al. (1995) and Kinley and Newhouse (1997) recorded Swainson's thrush in all buffer widths.

Three forest species occurred in all riparian buffers: golden-crowned kinglet, Townsend's warbler and winter wren. The presence of these species in even the narrowest buffers suggests that, at least in a high-elevation forest, they may not be particularly sensitive to forest edges. Although they exhibited some sensitivity to area (i.e., higher densities in wider buffers), the three species did not seem to depend on interior forest habitat.

Golden-crowned kinglets were recorded in all buffers, with medium buffers (30-34 m) retaining approximately 60% of the kinglet density found in the

unharvested forest. Increasing the width to 60 m produced only a 10% further increase in density. These findings differ from those of other studies, where golden-crowned kinglets were described as highly area-sensitive. Whitaker and Montevecchi (1999) observed that golden-crowned kinglets were absent from all riparian buffers and Darveau et al. (1995) noted that kinglet density was very low in buffers <20 m. Hagar (1999) recorded low densities in even the widest buffers (40-70 m) and suggested that golden-crowned kinglets avoid edge and/or riparian habitats.

Townsend's warblers were also recorded in all buffers, although avoidance of riparian habitat was suggested by the observation that territories were only located in upslope areas in the unharvested forest. Medium buffers (30-34 m) retained 50% and wide buffers (57-69 m) retained 80% of the Townsend's warbler density found in the unharvested forest. Kinley and Newhouse (1997) noted that Townsend's warblers were present in all buffers, though at much lower densities than golden-crowned kinglets. In the high-elevation forests of southern B.C., Gyug (1996) observed that Townsend's warblers were absent from buffers <47 m and termed the species 'width-sensitive'. This range of results indicates that the sensitivity of Townsend's warblers to buffer width varies, perhaps in response to the changing nature of buffer habitats across the different studies.

Winter wrens were recorded in all buffers and most territories spanned the creek, even in the unharvested forest. Associated with, but not dependent upon riparian habitats (McGarigal and McComb 1992, Waterhouse 1998), winter wrens located their territories primarily along streams. Because a large portion of the riparian habitat was occupied in each buffer, territories along the stream did not

increase in number with buffer width. Instead, the number of territories that occurred in moist, upslope areas increased. Medium buffers (30-34 m) retained 65% and wide buffers (57-69 m) retained 80 – 90% of the density found in the unharvested forest, suggesting that winter wrens were not particularly sensitive to buffer width.

Whitaker and Montevecchi (1999) detected similar winter wren densities in both controls and buffers. However, Kinley and Newhouse (1997) recorded low numbers of winter wrens in all but the widest buffers (70 m), and Gyug (1996) found winter wrens to be absent from buffers <47 m. From these differing results, it seems that the winter wren, like the golden-crowned kinglet and the Townsend's warbler, exhibits a range of sensitivity to riparian buffer width.

Edge Effects

Forest edges have a range of effects on a number of variables, including microclimate, vegetation structure and vertebrate species distributions (reviewed in Kremsater and Bunnell 1999). Studies have documented a wide range of edge effect distances on birds, but many indicate that the greatest effects occur within the first 50 – 100 m into a forest (Gates and Gysel 1978, Hansson 1983, Vander Haegen and Degraaf 1996, Brand and George 2000, Brand and George 2001). A number of studies report increased bird species richness and density near edges, the result of incursions by species preferring the open and often more shrubby habitat that occurs at edges and in adjacent clearcuts (reviewed in Kremsater and Bunnell 1999). Conversely, forest-dwelling species exhibit an opposite response, avoiding the altered habitat and increased risk of predation/parasitism found along edges (Kroodsma

1982, Brand and George 2001, Flaspohler et al. 2001, but see Campi and Mac Nally 2001).

The riparian buffers in my study were not isolated strips of forest surrounded on all sides by clearcut habitat. Instead, buffers were on one side of the stream only, with continuous forest located both up and downstream, and across the stream. As a result, the stream nominally defined the width of each buffer. Small streams (i.e., ≤ 5 m) do not likely act as barriers to most forest songbirds. Hence, the study grids could have been measuring the response of songbirds to increasing distance from the forest/clearcut edge, as well as to changing amounts of clearcut and forest habitat within each grid. As buffer width decreased, the relative amount of forest within the study grid also decreased while the proportion of buffer habitat influenced by edge effects increased. The resulting patterns of forest bird richness and density were likely a combination of both factors.

In assessing the response of songbirds to riparian buffer width, it is difficult to separate the effects of forest edge from the effects of forest area. However, it may be hypothesized that the close proximity to edge in riparian buffers results in a lower richness and density of forest songbirds than would occur in forest interior conditions. If edge effects decrease as buffer width and distance from the edge increase, and the greatest influence of edge on songbirds occurs within 50 m of an edge, then narrower buffers are dominated by edge and wider buffers contain both edge and interior habitat. Consequently, narrower buffers would be predicted to possess a low number and density of forest species because they consist entirely of edge; wider buffers would be predicted to possess edge habitat with reduced numbers of forest birds, and

interior habitat with higher numbers of forest birds. Calculations of forest bird richness and density for each buffer in its entirety would therefore be a combination of lower numbers in the edge habitat and, for the wider buffers, higher numbers in the interior habitat. If the effect of edge could be removed, calculations of richness and density based only on interior habitat may yield higher values for the wider buffers. Although this would result in larger slope coefficients for the regressions of buffer width against buffer species richness and forest songbird density, it would not change the basic pattern of increasing richness and density with increasing buffer width.

Nonetheless, the evidence for negative edge effects on songbirds is not as strong in western forests fragmented by harvesting as in eastern forests fragmented by agriculture (Kremsater and Bunnell 1999). Edges between forest and clearcut habitats are not permanent; sharp edges gradually become less distinct as clearcut habitat matures into young forest. Studies conducted in the Pacific Northwest do not indicate a strong association between forest birds and interior forest (McGarigal and McComb 1995, Schieck et al. 1995). This suggests the possibility of an alternative hypothesis, where the effect of edge is minimal, and the increase in forest bird richness and density is primarily a function of forest area (buffer width). However, the sampling design and data collected in my study do not allow the effects of forest edge and relative forest area to be easily partitioned and independently evaluated. Given the nature of the data, all that can validly be concluded is that forest birds increase in richness and density with increasing riparian buffer width. The actual mechanism(s) causing this increase – whether edge effects, area effects or a combination of both – can only be hypothetically discussed.

Conclusions

Overall, wider riparian buffers appear to support a songbird community similar to that of unharvested forests. Results indicate that buffers 30 m wide can provide habitat for at least 50% of the forest species, at $\geq 50\%$ of the density, found in the unharvested forest. However, buffers of at least 60 m in width are required to maintain most forest species at up to 85% of the density found in unharvested forests. Likewise, Hagar (1999), Pearson and Manuwal (2001) and Kinley and Newhouse (1997) recommend minimum buffer widths of 40 m, 45 m and 70 m, respectively. However, riparian buffers are not islands – they are adjacent to clearcut habitat that will develop quickly into young forest, then slowly into mature forest. Davies et al. (1999) indicated that in the ESSF forests of east-central British Columbia, species such as the varied and Swainson's thrush inhabited forests as young as 40 years. Thus, narrower buffers that are unsuitable for some species will not remain so for long.

When making recommendations regarding riparian buffers, it is important to consider benchmarks. Recommended buffer widths are a guide for managers; they provide an idea of what species may be lost and what species may be maintained in buffers of certain widths. But if the management goal is to retain a full complement of forest songbird species in a harvested landscape, some *a priori* decision should be made as to how much of the community can be lost before management action is taken. One such benchmark could be loss of certain species that are indicative of ecosystem health and that are representative of the habitat needs of other species (e.g., woodpeckers represent secondary cavity nesters and indicate snag availability).

Within my study area, the point at which the decrease in number or density of forest species becomes greater than the loss of mature forest could be another benchmark. For example, if 50% of the forest within a defined area was removed and 80% of the forest species disappeared, the loss of species would be disproportionately high relative to the amount of forest harvested and should be cause for management concern.

At my study sites, the loss of forest species was not disproportionately greater than the loss of forest. Study grids with wide buffers had approximately 57% of the forest removed and lost about 20% of the forest songbird species; study grids with narrow buffers had approximately 90% of the forest removed and lost 50% of the forest species. At the stand level, my findings do not generate serious concern or require strong management action. Nonetheless, scale is an issue; highly mobile organisms such as songbirds, and bird species with large area requirements (e.g., hawks, owls and woodpeckers), should be assessed at a broader scale. Within TFL #35, the loss of forest birds could be measured at the watershed level. At a regional scale, benchmarks could be assessed at the biogeoclimatic zone or subzone level. A disproportionately high loss of species or individuals over a large area or within certain habitat types should necessitate a change in forest planning and management.

Table 1.1. Ecological characteristics of each study grid.

Buffer type	Mean buffer width (m)	BEC zone*	Elevation (m)	Aspect	Stream class**	Cutblock area (ha)	Harvest year
V. Narrow 1	3	ESSFdc2	1460	E	S3	23.4	1994
V. Narrow 2	2	ESSFdc2	1570	SE	S6	43.1	1997
Narrow 1	11	MSdm2	1370	E	S6	26.3	1996
Narrow 2	15	MSdm2	1480	SE	S6	30.9	1994
Medium 1	30	ESSFdc2	1500	N	S3	30.2	1995
Medium 2	34	ESSFdc2	1540	NE	S3	21.1	1994
Wide 1	69	MSdm2	1090	SE	S3	20.7	1997
Wide 2	57	MSdm2	1340	SE	S3	6.7	1996
Control 1	>150	MSdm2	1320	W	S6	NA	NA
Control 2	>150	ESSFdc2	1440	N	S3	NA	NA

* Meidinger and Pojar (1991)

** Province of B.C. (1995b)

Table 1.2. Habitat associations and mean density (territories/ha) (± 1 SE) of songbird species within the study grids in 1999.

Species ^A	Mean territories/ha (± 1 SE)			
	Very narrow	Narrow	Medium	Wide
Open-habitat species				
American robin	0.14 (0.02)	0.01 (0.01)	0.02 (0.02)	0.03 (0.03)
Chipping sparrow	0.16 (0.16)	0.19 (0.05)	0.07 (0.07)	0.15 (0.15)
Dark-eyed junco	0.50 (0.05)	0.37 (0.17)	0.49 (0.11)	0.65 (0.31)
Lincoln's sparrow	0.00 (0.00)	0.14 (0.04)	0.07 (0.02)	0.00 (0.00)
MacGillivray's warbler	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Mountain bluebird	0.14 (0.01)	0.00 (0.00)	0.06 (0.06)	0.00 (0.00)
Savannah sparrow	0.08 (0.08)	0.00 (0.00)	0.04 (0.04)	0.00 (0.00)
White-crowned sparrow	0.06 (0.06)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Total mean density (open)	1.06 (0.37)	0.70 (0.26)	0.75 (0.32)	0.91 (0.52)
Generalist species				
Townsend's solitaire	0.00 (0.00)	0.09 (0.09)	0.00 (0.00)	0.00 (0.00)
Wilson's warbler	0.00 (0.00)	0.00 (0.00)	0.17 (0.17)	0.00 (0.00)
Yellow-rumped warbler	0.20 (0.11)	0.13 (0.10)	0.27 (0.07)	0.49 (0.02)
Total mean density (generalist)	0.28 (0.11)	0.22 (0.19)	0.45 (0.25)	0.65 (0.15)
Forest-habitat species				
Boreal chickadee	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.50 (0.50)
Golden-crowned kinglet	0.02 (0.01)	0.32 (0.13)	0.38 (0.03)	1.09 (0.04)
Hammond's flycatcher	0.00 (0.00)	0.00 (0.00)	0.16 (0.16)	0.20 (0.01)
Red-breasted nuthatch	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Ruby-crowned kinglet	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.07 (0.07)
Swainson's thrush	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.19 (0.10)
Townsend's warbler	0.08 (0.05)	0.22 (0.03)	0.25 (0.05)	0.90 (0.23)
Varied thrush	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	0.32 (0.02)
Winter wren	0.22 (0.06)	0.11 (0.04)	0.18 (0.06)	0.39 (0.10)
Total mean density (forest)	0.32 (0.01)	0.64 (0.11)	0.99 (0.32)	3.20 (0.35)
Overall mean density	1.58 (0.48)	1.56 (0.35)	2.17 (0.25)	3.69 (0.89)
				3.39 (0.32)

A = Scientific names given in Appendix 2

Table 1.3. Similarity values for the Bray-Curtis Community Similarity Index.

	Very narrow	Narrow	Medium	Wide
Narrow	0.998			
Medium	0.839	0.838		
Wide	0.596	0.595	0.739	
Uncut Forest	0.635	0.634	0.783	0.955

Table 1.4. Results for Kruskal-Wallis tests of treatment effect on non-normally distributed songbird density data (degrees of freedom for each test = 4).

Species	Chi-square value	Significance (P-value)
Lincoln's sparrow	8.862	0.065
Swainson's thrush	7.945	0.094
Varied thrush	7.821	0.098
American robin	5.834	0.212
Chipping sparrow	2.781	0.595
Hammond's flycatcher	3.912	0.418
Mountain bluebird	7.596	0.108

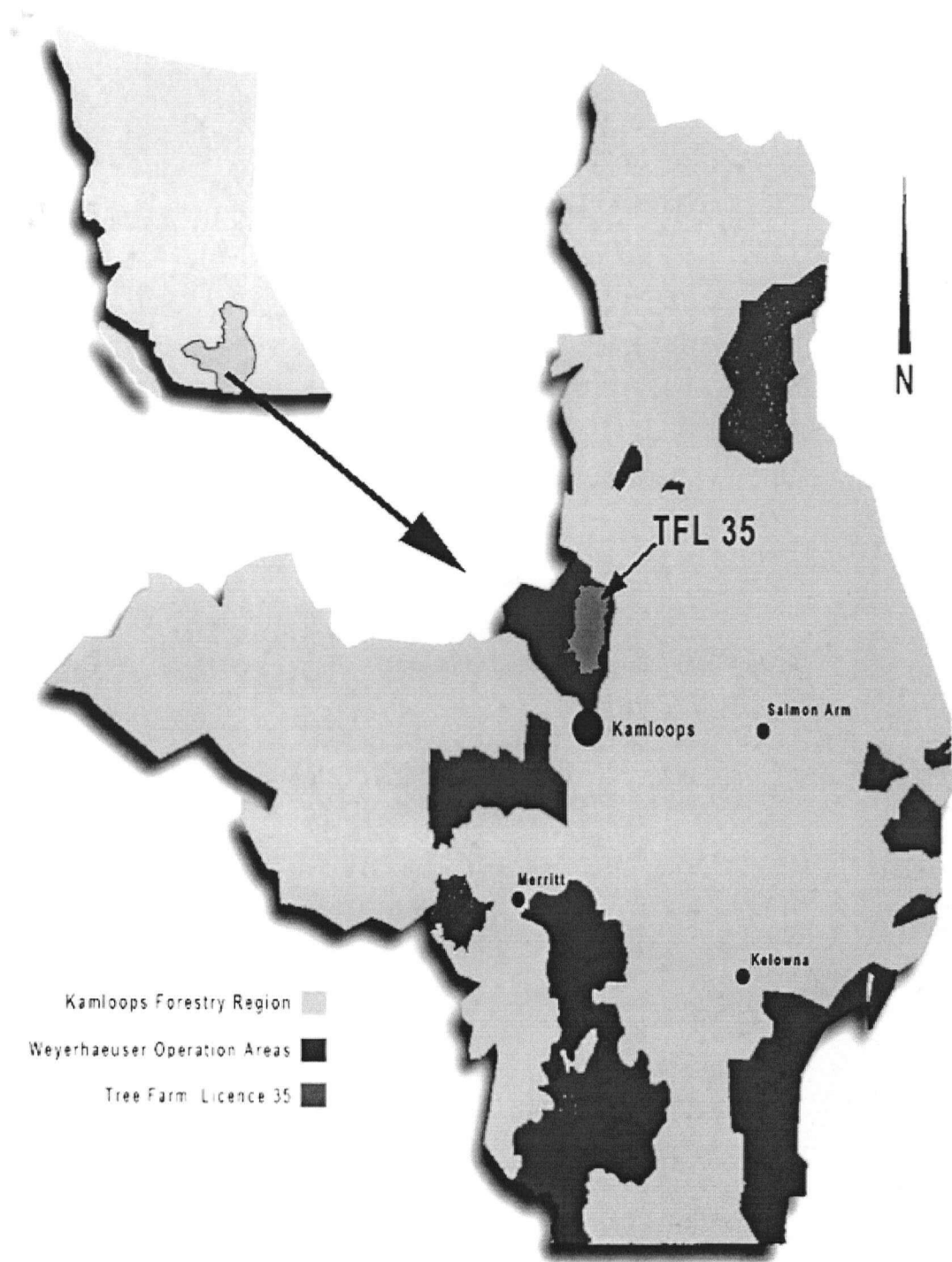


Figure 1.1. Location of Tree Farm License (TFL) 35 within the Kamloops Forest Region (KFR), in the south-central portion of British Columbia.

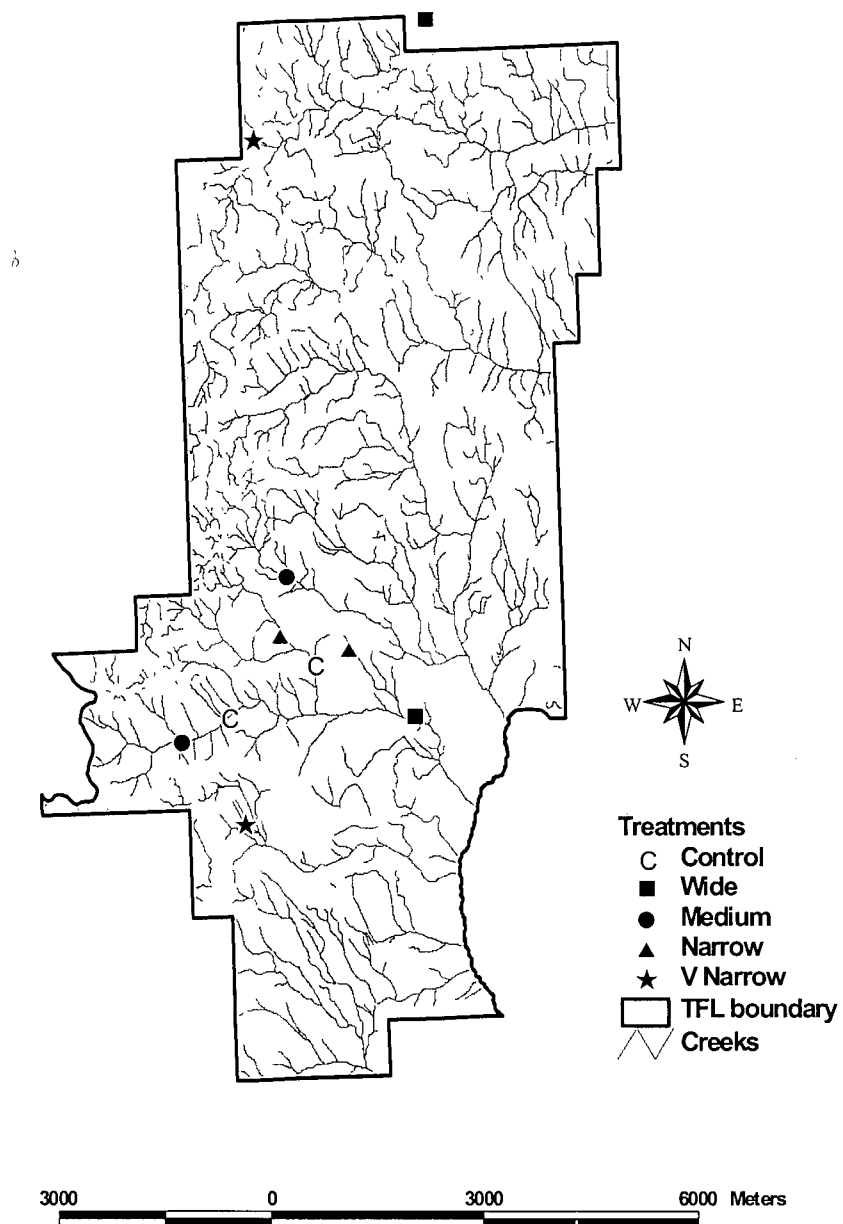


Figure 1.2. Location of study sites within TFL #35. TFL #35 is situated approximately 30 km north of the city of Kamloops, British Columbia.

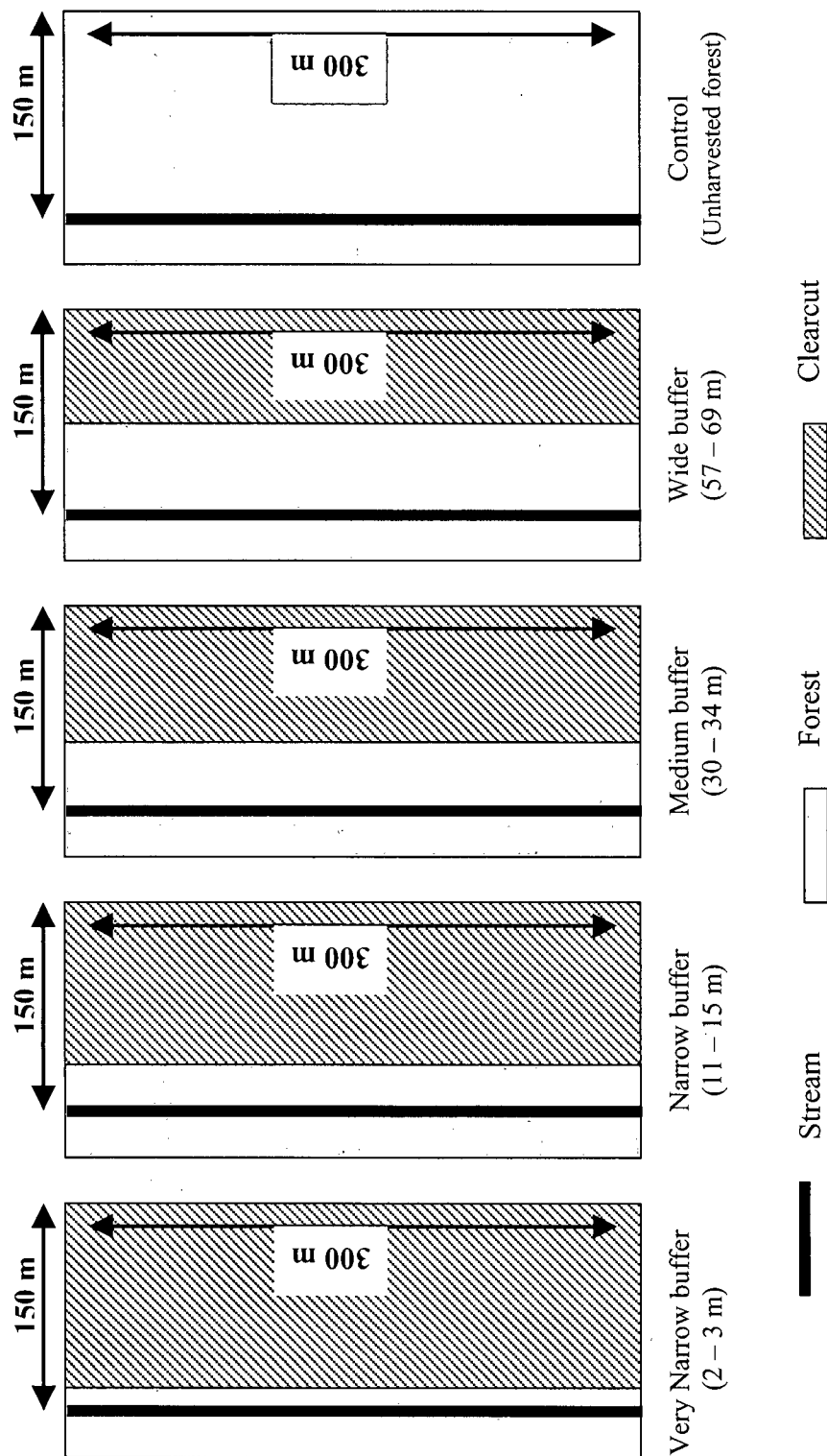
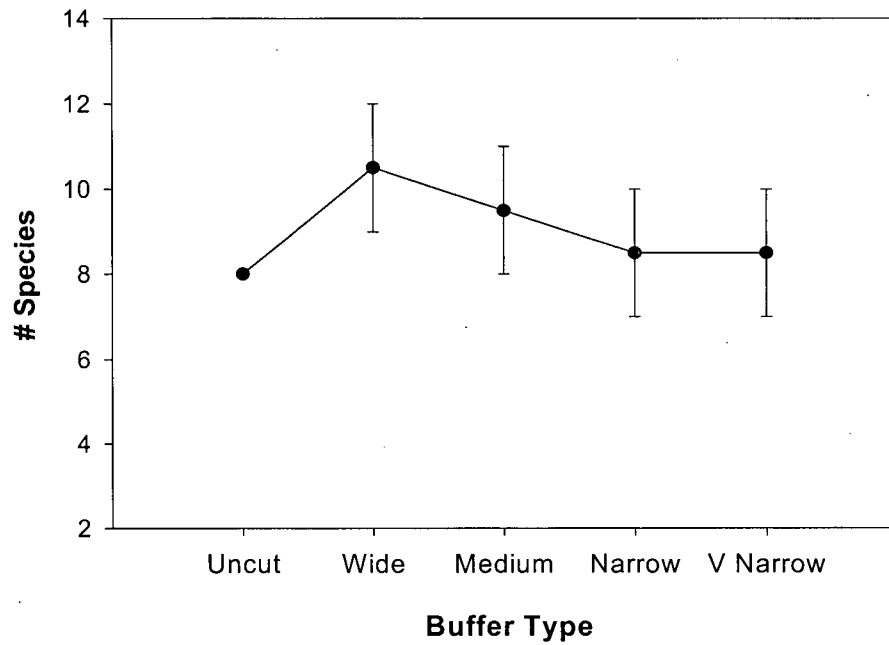


Figure 1.3. Graphical representation of treatments, depicting the 150 m x 300 m spot-map grids and each buffer width on one side of the stream and continuous forest on the other.

A.



B.

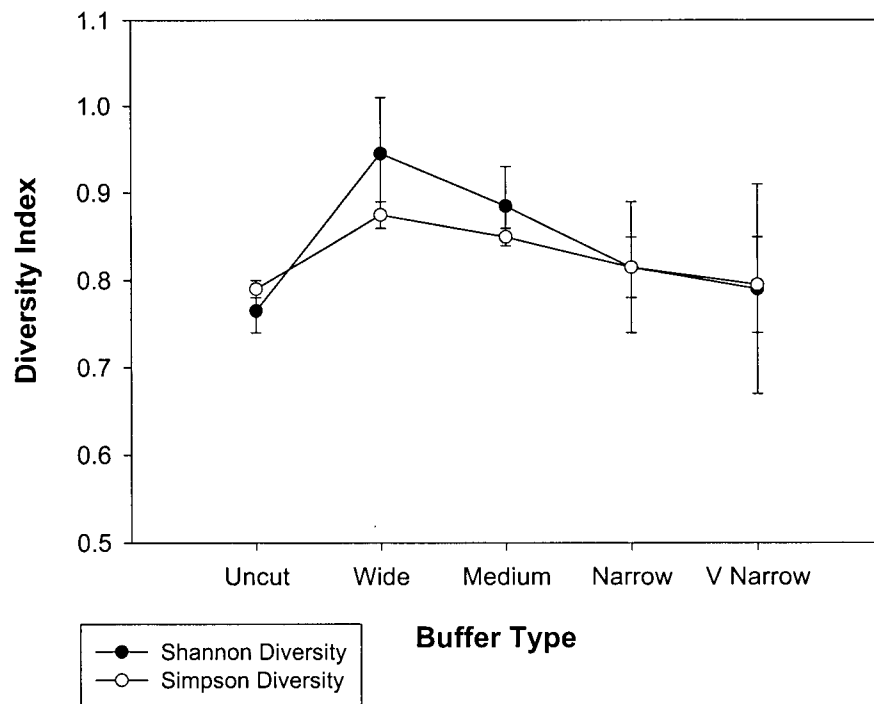


Figure 1.4. (a) Mean species richness (± 1 SE), and (b) mean Shannon-Wiener and Simpson diversity (± 1 SE) in study grids across buffer types. For each buffer type, $n = 2$.

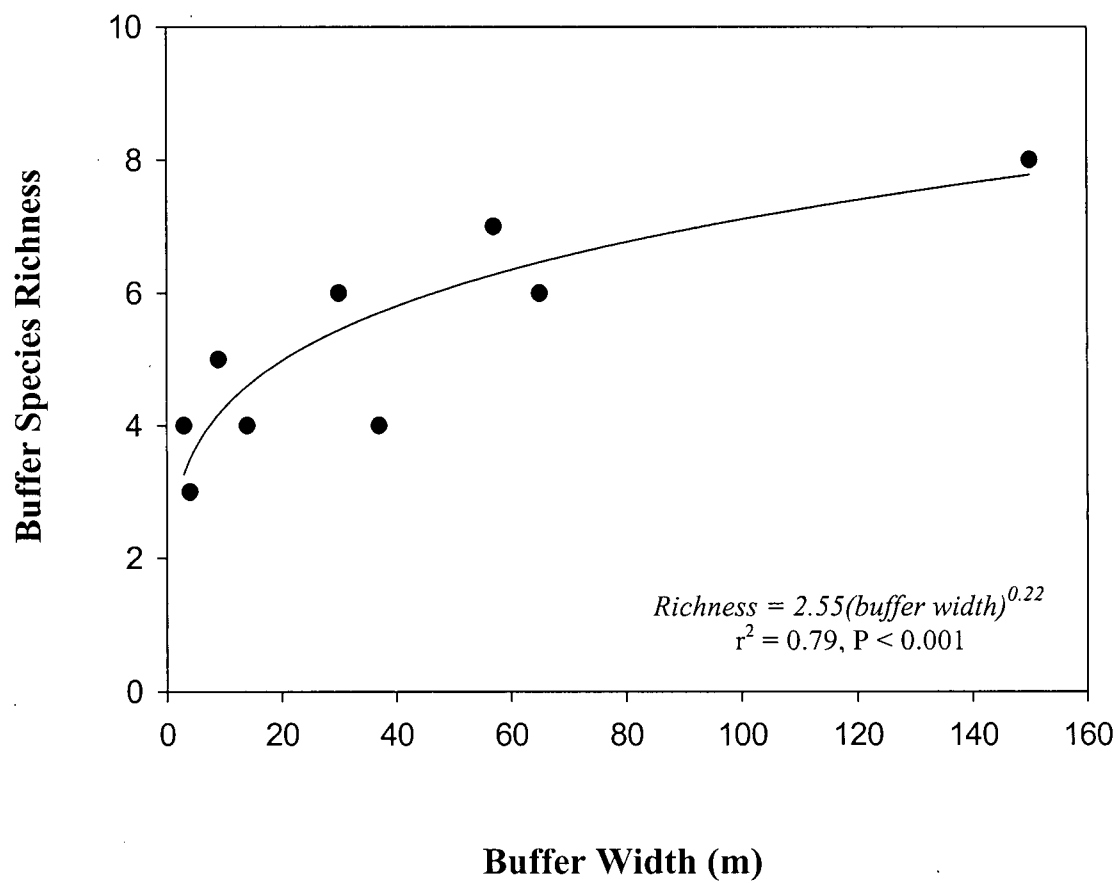


Figure 1.5. Relationship between riparian buffer width and species richness in the buffers only.

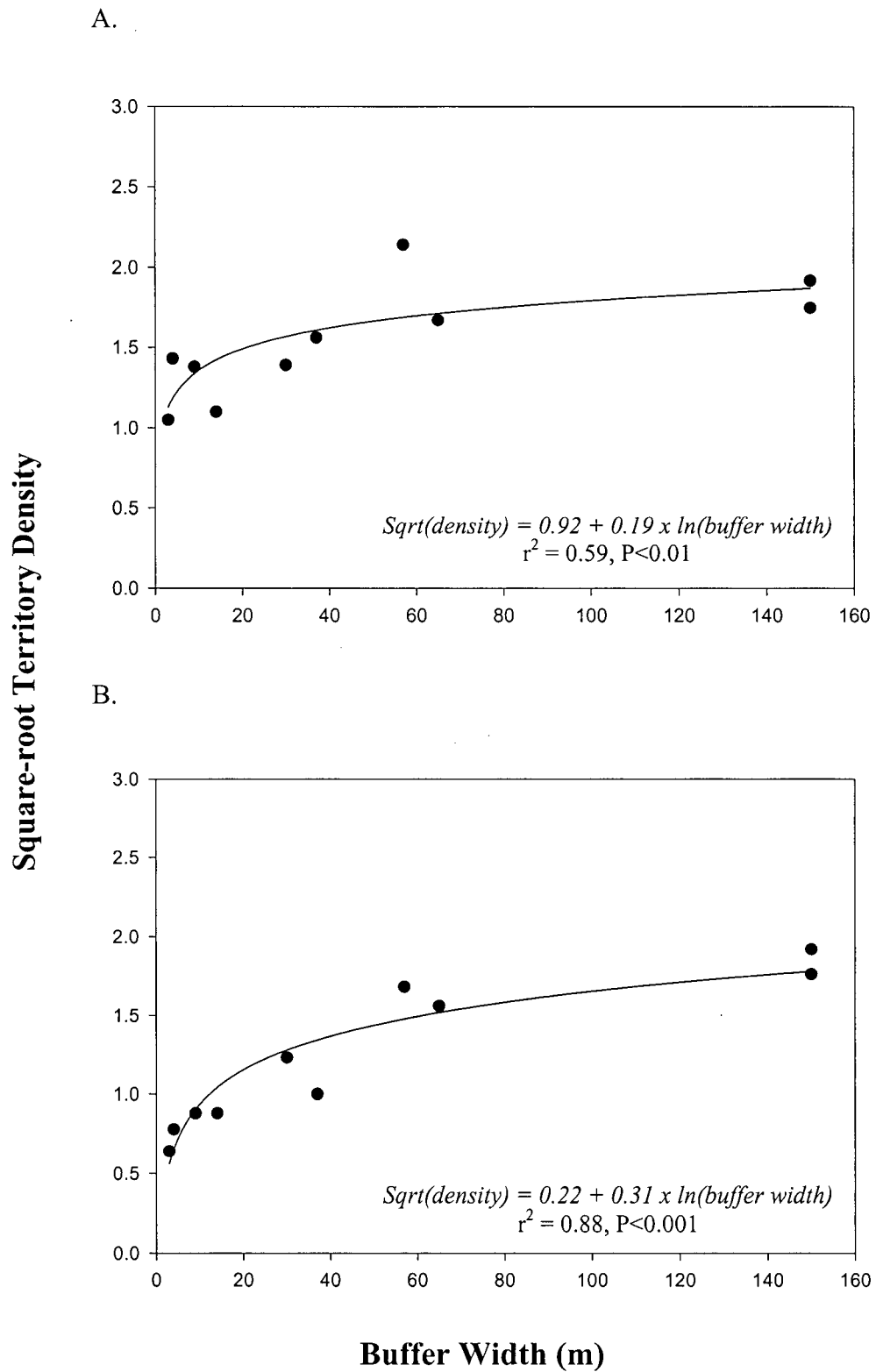


Figure 1.6. Relationship between riparian buffer width and the territory density (square-root transformed) of (a) all species combined, and (b) forest species, within the study grids.

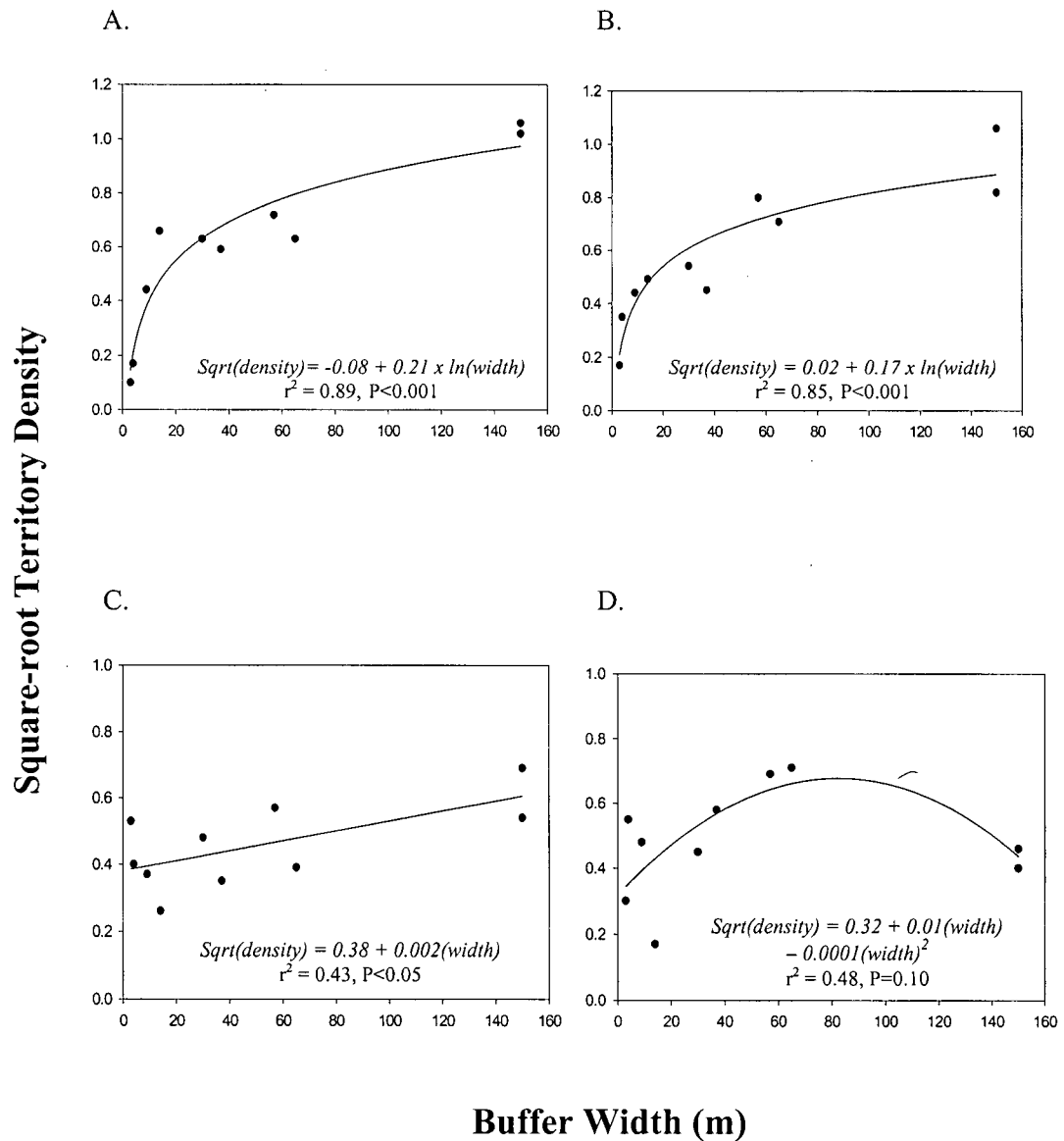


Figure 1.7. Relationship between riparian buffer width and the territory density (square-root transformed) of (a) golden-crowned kinglets (b) Townsend's warblers (c) winter wrens, and (d) yellow-rumped warblers, within the study grids.

CHAPTER 2. Vegetation characteristics of riparian buffers and the use of riparian buffers by foraging forest songbirds.

INTRODUCTION

Studies of forest fragmentation effects on songbirds have demonstrated a strong relationship between forest area and species composition (Whitcomb et al. 1981, Blake and Karr 1984, Faaborg et al. 1995). In particular, research on forest patch sizes (Galli et al. 1976, Freemark and Collins 1992, Schmiegelow et al. 1997) and riparian buffer widths (Darveau et al. 1995, Thurmond et al. 1995, Hagar 1999) has shown that many forest-dwelling species are constrained by habitat area and are absent from small forest patches.

It has been theorized that area-dependent changes in songbird communities are produced by area-dependent changes in the forest environment (Ambuel and Temple 1983, Lynch and Whigham 1984). When harvesting occurs, adjacent residual forests experience a number of edge effects, including significant microclimate changes (Chen et al. 1995) that can extend several hundred meters into the forest and alter vegetation structure and composition. Reduced forest area can also cause the loss of important habitat components, such as spatial variability in plant species and forest structure (Freemark and Merriam 1986). Many studies have focused on the relative importance of forest area and forest habitat in determining the composition of songbird communities in fragmented landscapes. Askins et al. (1987) hypothesized that the environment (forest size, type of vegetation) within and immediately adjacent to a forest patch was the primary determinant of avian richness and density.

Similarly, Robbins (1989), Blake and Karr (1987), and Doherty et al. (2000) proposed

that patch size, isolation and habitat characteristics all contributed to songbird density and distribution with varying degrees of influence.

Identifying the habitat attributes with which songbirds are associated can help to predict fragmentation effects on songbirds (Ambuel and Temple 1983). Many avian studies have investigated species-habitat relationships to help determine the impacts of human disturbance (Anderson and Shugart 1974, Clark et al. 1983, Hansen et al. 1995, Hagar et al. 1996). Multivariate and regression techniques have been applied to examine relationships between bird richness or abundance and a range of vegetation variables. Significant associations have been found with such attributes as tree species richness and canopy cover (James and Wamer 1982), canopy volume, tree density and understory cover (Clark et al. 1983), and the density of small shrubs (Swift et al. 1984). Multiple regression methods have also been used to develop species-specific habitat models. Models derived for western forests have correlated the abundance of common forest-dwelling songbirds with tree density, tree diameter and tree species (Morrison et al. 1987, Hansen et al. 1995, Hagar et al. 1996).

Songbird habitat models may help to identify some important habitat attributes, but they have often met with limited success when validated or tested against independent data sets (Stauffer and Best 1986, Morrison et al. 1987). An alternative means of examining songbird habitat use is to observe the behaviour of individual birds in the field. Behaviour sampling can yield information on species-specific patterns of utilization and preferences for certain vegetation attributes (MacArthur 1958, Robinson and Holmes 1982, Sabo and Holmes 1983, Osborne and Green 1992). Observations of songbird behaviour have also been used to examine

how habitat alteration affects foraging behaviour and community structure (Mauer and Whitmore 1981, Mahony et al. 1997, Brotons et al. 1998). Behaviour sampling can therefore provide researchers with additional information on patterns of habitat use by songbirds in response to forest harvesting.

This chapter examines the forest attributes with which songbirds are associated, and the effects of riparian buffer width on those attributes. My objectives were to: (1) measure changes in forest vegetation across buffers of different widths, (2) determine if the density of forest songbirds is related to changes in buffer vegetation, (3) describe foraging habitat use by four songbird species, and (4) quantify the influence of riparian buffer width on the movements of four songbird species. I hypothesized that decreasing riparian buffer width would result in various edge effects, including reduced tree density and cover of tall shrubs (due to harvesting disturbance and windthrow), and increased cover of low shrubs and herbaceous plants (due to increased light levels). I predicted that these changes in forest structure would correlate with forest bird density independently of buffer width. Finally, I predicted that narrower riparian buffers would restrict the movements of forest birds and result in activities that were concentrated along the stream, rather than in the upland.

METHODS

Habitat Sampling

Habitat mapping and vegetation sampling were used to describe each study site. I mapped large-scale features to make broad comparisons between habitat types and the distribution of species territories. I used vegetation sampling to measure the finer-scale attributes of habitat structure and composition.

Habitat mapping was conducted in July and August 1998. Major habitat features were recorded onto survey maps (1:1500) and included riparian buffers, root masses, wildlife trees, slash and blowdown piles, and steep slopes. I then digitized these habitat features into ArcView 3.1 (ESRI Inc. 1998) and added them to the map of each study grid. Within the GIS, I overlaid the habitat maps with territory locations to display territory position relative to the different habitat features. Digital Terrain Resource Information Management (TRIM) maps and forest cover data were provided by Weyerhaeuser Canada. These included vegetation, topographical and harvest information for areas surrounding the study sites. Layering this graphical information onto the study grid maps allowed the comparison of study sites with respect to elevation and adjacent stand features.

Vegetation was sampled in July and August 1998. I systematically placed 12 circular vegetation plots (0.03 ha) throughout each spot-map grid, at increasing distances from the stream: 10 m, 40 m, 70 m and 125 m (Appendix 3). Two 20-m line transects were placed within each vegetation plot, oriented at right angles to each other and intersecting at the plot center. Vegetation plots were used to measure

canopy attributes; line transects were used to sample understory and ground cover attributes.

Vegetation plots were divided into four quadrants and the number of trees in each quadrant was tallied by species and diameter-at-breast-height (dbh) class (Noon 1980). I defined diameter classes as: 10–20 cm, >20–40 cm, >40–60 cm and >60 cm. All live trees >10 cm dbh and all standing dead snags >10 cm dbh and >1.5 m height were included. To estimate canopy height, a Suunto clinometer and hip chain were used to measure the height of one tree from each DBH class present within the plot. Canopy cover along each cardinal direction from the center of the plot was estimated with a convex densiometer (Martin et al. 1997).

I used the line-intercept method (Cook and Stubbendieck 1986) to measure shrub cover by species and height class along the two line transects in each vegetation plot. Height classes were defined as: 0–1.0 m, >1.0–3.0 m, >3.0–5.0 m and >5.0 m. The distance (meters) covered by each shrub that intersected the meter tape was recorded, along with the species of shrub and the height class. The percent cover of each shrub species in each height class was then calculated as the total distance intersected divided by the entire transect length (40 m), multiplied by 100.

I used the point-intercept method (Bonham 1989) to estimate ground cover, by cover class. Ground cover classes were defined as: herb, grass, moss, lichen, coarse woody debris, litter and bare ground. A wooden rod with a pointed metal end and a carpenter's level was dropped at 2 m intervals along both line transects. Any cover type that was intersected by the metal point was recorded. The percent cover of each class was then calculated as the number of times the ground cover type was

intersected divided by the total number of times the point was dropped (20), multiplied by 100.

Behaviour Sampling

I chose focal individual sampling with continuous recording to sample foraging behaviour (Altmann 1974, Lehner 1987). My first objective was to record the foraging activities of individuals to determine which foraging substrates, vegetation species and vegetation layers were used most frequently. My second objective was to record the distances and directions moved by foraging individuals to determine how songbird movements were influenced by riparian buffer width. The winter wren and the yellow-rumped warbler were chosen as the primary focal species for behavioural observations. The winter wren, a cavity-nesting insectivore, was chosen to represent species that utilize the ground and shrub layers for foraging and/or nesting. The yellow-rumped warbler, also an insectivore, was chosen to characterize species that primarily dwell in the mid to upper canopy layers. Additional data were collected on the Townsend's warbler and the golden-crowned kinglet.

Songbird behaviour was sampled from 22 June 1999 to 28-July 1999. Observations were conducted within the study grids from 0700 – 1200 hrs PST, during the most active period of the day. An individual bird was followed for a maximum of 30 minutes and foraging activities were continuously recorded with a tape recorder. There was no minimum recording time. Although sites were sampled an equal number of times, all species were not necessarily observed at each site during each session; as a result, species observations were not distributed evenly

across all sites. I assumed that samples were independent, though some individual birds were likely sampled more than once at each site.

For each session, data were recorded under seven categories: habitat, activity, substrate, relative position, height above ground, movement direction and distance traveled. *Habitat* included the forest, forest-clearcut edge, clearcut and residual tree patches within the clearcut. *Activity* classes included five different foraging methods – ground gleaning, bark gleaning, foliage gleaning, hover-glean and hawking (Erich et al. 1988). *Substrate* referred to the item on which an activity occurred and included ground, herb, coarse woody debris, root mass, shrub, snag and tree (sapling, pole or mature). *Relative position* assigned the location of a bird to low, mid or upper shrub/trunk/canopy (where applicable), and *height* referred to the estimated height of the bird above the ground while on a substrate. *Movement direction* was defined according to a set of angles numbered relative to the stream (Figure 2.1a) and *distance* was the estimated number of meters flown between substrates.

Data Analysis

Forest Structure

All vegetation variables were tested for a normal distribution using normal probability plots and the Kolmogorov-Smirnov goodness of fit procedure (SPSS Inc. 1999). All percent cover variables were arcsin-square-root transformed prior to analysis. I transformed additional non-normal variables using the \log_{10} transformation, then retested for normality. Vegetation data included the following variables for each plot:

- basal area (m^2/ha), canopy cover, tree species richness;

- total shrub cover, coniferous and deciduous shrub cover in each height class and in total, conifer seedling/sapling species richness, deciduous shrub species richness, number of shrub layers;
- cover of coarse woody debris, bare ground, litter, moss, grass and herbaceous plants.

I used a one-way analysis of variance to test if riparian buffer width had an effect on individual vegetation variables (SPSS Inc. 1999). Analysis included the continuous variables listed above and used only the data from the vegetation plots in the buffers and unharvested forest (i.e., excluded clearcut vegetation data). Variables were tested with a nested model, where replicates were nested within treatments, and a significance level of $\alpha = 0.05$ was used for each test. Bonferroni multiple comparison tests were used on the variables for which riparian buffer width had a significant effect.

I used factor analysis with Equamax rotation to reduce the number of vegetation variables in order to describe overall forest structure (Tabachnick and Fidell 1996). Analysis included all vegetation variables (25 in total) and used only the data from the vegetation plots in the buffers and unharvested forest. I used the correlation matrix and principal components method of extraction, and selected the number of factors based on eigenvalues (> 1.0) and scree plots. The scree plot consists of eigenvalues plotted against factors; the point at which a line drawn through the points changes slope indicates the approximate number of factors in the data. Variables with component loadings greater than ± 0.55 were selected for factor interpretation; a conservative cut-off value of 0.55 was used following the

recommendation of Comrey and Lee (1992). I then used regression analysis to explore the relationship between riparian buffer width and the resulting forest structure factors (SigmaPlot SPSS Inc. 2001). Each factor was regressed against buffer width separately, using a significance level of $\alpha = 0.05$. I assessed the fit of each model with the coefficient of determination (r^2), the standard error of the estimate, the overall significance of the model and the significance of each parameter in the model (Zar 1996).

Songbird-Habitat Associations

Songbird Density and Forest Structure

I used partial correlations to test the relationship between forest structure and the richness and density of forest songbird species (SPSS Inc. 1999). Because previous analyses indicated that buffer width had a significant effect on both songbird richness/density (Chapter 1) and forest structure, partial correlation coefficients were calculated to test the relationship between birds and habitat while controlling for the effects of buffer width. Forest structure was represented using the four factors derived from the factor analysis. Partial correlations were computed between mean factor scores and each of forest species richness, forest species density, and the density of golden-crowned kinglets, Townsend's warblers and winter wrens. Scatterplots of mean factor scores against each songbird variable were used to assess whether or not the assumption of a linear relationship was met (Tabachnick and Fidell 1996). A significance level of $\alpha = 0.05$ was used for each partial correlation.

Habitat Use and Movements

Activity budgets were calculated for each of the four study species, summarizing the proportion of total time spent in each activity and on each substrate. I also summarized the proportion of time spent in each habitat type and, for canopy-dwelling species, the proportion of time spent in each canopy layer. Data were pooled across all sites and both sexes; I did not examine differences in habitat use between treatments or gender. Male wood warblers tend to forage higher in the canopy than females during the breeding season (Morse 1968). Because male warblers are more conspicuous and were therefore sampled more often, combining data for both genders may have overestimated mean foraging heights for the yellow-rumped and Townsend's warblers.

To explore species-specific movement patterns across riparian buffer widths, I combined treatments into three classes: Narrow (Very Narrow + Narrow buffers), Wide (Medium + Wide buffers), and Uncut Forest. I also reduced the eight movement angles to three classes: movements *parallel* to stream (1, 5), movements *perpendicular* to stream (3, 7), and movements *diagonal* to stream (2, 4, 6, 8) (Figure 2.1b). For each of the four study species, I calculated the mean distance moved in each direction class in each treatment. I then used the Kruskal-Wallis non-parametric analysis of variance to test for differences in movement distance (1) between treatment classes and (2) within each treatment class (SPSS Inc. 1999). Because the analyses were exploratory, and the statistics were used as descriptors rather than for hypothesis testing, a significance level of $\alpha = 0.10$ was used for each test.

RESULTS

Forest Structure

General Description

The total basal area/ha of live trees within the forest increased with riparian buffer width, reaching a maximum in the wide buffers and the unharvested forest (Figure 2.2a). The unharvested forest had significantly greater basal area than did the very narrow buffers ($F_{4,5}=5.21$, $P<0.05$). Canopy cover also increased with buffer width to reach a maximum in the unharvested forest. The wide buffers and the unharvested forest had significantly greater canopy cover than the very narrow buffers ($F_{4,5}=10.37$, $P<0.01$) (Figure 2.2b).

Primary tree species in the riparian buffers were hybrid white spruce and subalpine fir, with some lodgepole pine and Douglas-fir. As an indication of habitat diversity, the change in canopy composition with increasing distance from the stream was assessed in medium buffers, wide buffers and the unharvested forest. Although there was little change in composition with distance from the stream in medium buffers (Figure 2.3a), both wide buffers and the unharvested forest had less hybrid white spruce and more lodgepole pine and Douglas-fir (Figures 2.3b, 2.3c).

Shrub cover increased with riparian buffer width to reach a maximum in the unharvested forest, though differences across treatments were not significant. Low shrubs (≤ 1.0 m) reached their highest cover in the narrow buffers; conversely, shrubs >1.0 m had their greatest cover in the unharvested forest. The cover of coniferous shrubs increased steadily with buffer width; the cover of deciduous shrubs varied across treatments, but was greatest in the unharvested forest (Figure 2.4). Coniferous

shrubs included tree seedlings and saplings; common deciduous species included falsebox, black gooseberry (*Ribes lacustre* (Pers.) Poir.), black huckleberry and thimbleberry (*Rubus parviflorus* Nutt.).

Although ground cover varied across treatments, the effect of riparian buffer width was significant only for coarse woody debris (Table 2.1). Plots in the unharvested forest contained the lowest mean cover of coarse woody debris and were significantly different ($F_{4,5}=9.85$, $P<0.01$) from the wide buffers, which possessed the greatest mean cover. The unharvested forest also had the lowest mean cover of bare ground and litter, and the greatest mean cover of moss.

Width Effects on Forest Structure

Twenty-three vegetation variables were used for factor analyses, though only 12 variables had component loadings greater ± 0.55 in the final analysis (Table 2.2). Four factors explained 68% of the variation in the vegetation data. Each variable loaded highly on one factor only, facilitating interpretation of each factor. Decreasing coarse woody debris cover and increasing basal area and canopy cover represented the first factor, which I described as ***Tree Cover***. The second factor, called ***Coniferous Shrub Cover and Richness***, was associated with increasing coniferous shrub cover, number of coniferous seedling/sapling species and number of shrub layers. The third factor was described as ***Herb Cover*** and had a positive loading of herbaceous ground cover and a negative loading of litter cover. The fourth factor, called ***Deciduous Shrub Cover and Richness***, had increasing deciduous shrub cover and species richness, increasing grass cover and decreasing moss cover.

Together, the first two factors (Tree Cover + Coniferous Shrub Cover/Richness) explained 44.6% of variation in the data and exhibited the greatest change across treatments. In general, wide buffers and the unharvested forest had higher scores along both axes than did narrow and very narrow buffers (Figure 2.5). Vegetation plots in the medium buffers were relatively evenly distributed along both axes.

Regression analyses of factor scores against riparian buffer width yielded a positive and significant relationship between width and Tree Cover. Coniferous Shrub Cover/Richness also exhibited a positive, though not significant, relationship with width. There was no relationship between buffer width and either of Herb Cover or Deciduous Shrub Cover/Richness. The logarithmic model gave the best fit for Tree Cover versus buffer width ($P < 0.001$), explaining 87% of the variation in the data (Figure 2.6). Both Tree Cover and Coniferous Shrub Cover/Richness increased rapidly with small increases in buffer width, and then slowed once a width of approximately 35 m was reached.

Songbird-Habitat Associations

Songbird Density and Forest Structure

I used partial correlations to determine the influence of each factor on the richness and density of forest songbird species within the study grids, while controlling for the influence of buffer width. Scatterplots indicated a positive linear relationship between forest songbird richness/density and each of Tree Cover and Coniferous Shrub Cover/Richness. Neither songbird variable showed a relationship with either of Herb Cover or Deciduous Shrub Cover/Richness. Once partial

correlations removed the effect of buffer width, neither forest species richness nor density had a significant relationship with any of the four factors (Table 2.3).

Partial correlations were also used to test the width-independent influence of forest structure on the density of golden-crowned kinglets, Townsend's warblers and winter wrens. Scatterplots showed a positive linear relationship between the density of both golden-crowned kinglets and Townsend's warblers and each of Tree Cover and Coniferous Shrub Cover/Richness. Winter wren density did not exhibit a distinct relationship with any of the four factors. Once the influence of buffer width was controlled for, the density of Townsend's warblers and winter wrens was not significantly related to any of the forest structure factors (Table 2.3). By contrast, the density of golden-crowned kinglets was positively and significantly related to Coniferous Shrub Cover and Richness.

Habitat Use and Movements

A total of 165 minutes of foraging activity was recorded for the four species. Winter wrens were observed at 8 sites for a total of 21 minutes. Yellow-rumped warblers were recorded at 7 sites for 73 minutes. Golden-crowned kinglets were observed at 7 sites for a total of 41 minutes, and Townsend's warblers were recorded at 4 sites for a total of 30 minutes.

Foraging winter wrens gleaned from bark, ground and foliage (Figure 2.7a). The greatest proportion of foraging time was spent on coarse woody debris and on the ground; root masses and mature Douglas-fir trees were used to a lesser extent (Figure 2.7b). Winter wrens were only recorded foraging in the uncut forest and the riparian buffers, though they were occasionally observed singing in the clearcuts.

Yellow-rumped warblers were frequently observed foliage gleaning and singing concurrently (Figure 2.8a). Foliage gleaning was occasionally interspersed with hover-gleaning; bark and ground gleaning were observed less often. Mature and pole-sized trees, mainly Douglas-fir, subalpine fir and lodgepole pine, were the most frequently used foraging substrates (Figure 2.8b). The mid-canopy layer was used for bark gleaning, and both mid and upper canopy layers were used for foliage gleaning and singing (Figure 2.8c). Yellow-rumped warblers foraged in all habitat types, though the primary habitats used were the riparian buffers, buffer edges and residual tree patches in clearcuts.

Golden-crowned kinglets were most often observed foliage gleaning, though hover-gleaning was interspersed (Figure 2.9a). Mature and pole-sized trees, primarily hybrid white spruce and subalpine fir, were used extensively for foraging (Figure 2.9b). The mid-canopy layer was utilized for all types of gleaning; foraging was infrequently observed in the lower and upper canopy layers (Figure 2.9c). Golden-crowned kinglets spent most of their time foraging in the unharvested forest and riparian buffers, though they were also observed along buffer edges and in residual tree patches dispersed throughout the adjacent clearcut.

Townsend's warblers were observed using a combination of foliage gleaning and hover-gleaning (Figure 2.10a). Foraging occurred on both pole-sized and mature hybrid white spruce and subalpine fir (Figure 2.10b); individuals used the lower, mid and upper canopy layers equally (Figure 2.10c). Townsend's warblers were occasionally observed foraging along buffer edges, but were most often seen in the riparian buffers and the unharvested forest.

Buffer width appeared to influence the movement patterns of winter wrens (Figure 2.11a). Across treatments, wrens moved more in the perpendicular direction in the unharvested forest than in the narrow and wide buffers ($\chi^2=8.35$, $df = 2$, $P<0.05$). Distances moved in the parallel and diagonal directions were similar across treatments. Within each treatment, distances moved in each direction were different in the narrow buffers ($\chi^2=20.17$, $df = 2$, $P<0.01$) and the wide buffers ($\chi^2=6.64$, $df = 2$, $P<0.05$), but not in the unharvested forest. In both the narrow and wide buffers, wrens moved mostly in the upstream and downstream direction, rather than towards and away from the stream.

Buffer width did not seem to strongly affect the movement patterns of yellow-rumped warblers (Figure 2.11b). Across treatments, individuals moved more upstream and downstream in narrow buffers than in wide buffers, but the difference was not significant. Distances moved in both the perpendicular and the diagonal directions were similar across treatments. Within each treatment, the distances moved in each direction were significantly different in the narrow buffers ($\chi^2=5.23$, $df = 2$, $P<0.10$), but not in the wide buffers. Yellow-rumped warblers moved equally in all directions in wide buffers, but mostly upstream and downstream in narrow buffers.

Buffer width also did not seem to have a strong influence on the movement patterns of golden-crowned kinglets (Figure 2.12a). Between treatments, individuals moved greater distances upstream and downstream in the wide and narrow buffers than in the unharvested forest, but the difference was not significant. Distances moved perpendicular and diagonally to the stream were similar across treatments.

Within each treatment, the distances moved in each direction were not significantly different, though kinglets in both narrow and wide buffers moved the least in the perpendicular direction and the most in the upstream and downstream directions.

Buffer width influenced the movement patterns of Townsend's warblers (Figure 2.12b). Across treatments, individuals moved significantly more perpendicular to the stream in the unharvested forest than in the buffers ($\chi^2=3.16$, $df = 1$, $P<0.10$). Distances moved in the parallel and diagonal directions were similar across treatments. Within each treatment, the distances moved in each direction were significantly different in the buffers ($\chi^2=4.83$, $df = 2$, $P<0.10$), but not in the unharvested forest. Within the buffers, Townsend's warblers moved mostly in the upstream and downstream direction, rather than towards and away from the stream.

DISCUSSION

Width Effects on Forest Structure

Changes in forest vegetation occurred with increasing riparian buffer width, particularly in the canopy and understory layers. Wider buffers possessed higher moss, tall shrub and canopy cover, more vegetation layers and species, and larger trees than did narrower buffers. Because distance from the edge increased with increasing buffer width, these changes in vegetation were likely due to edge effects. Edge effects are often experienced along forest-clearcut boundaries (Voller 1998). In the Pacific Northwest, forest edges exhibit reduced canopy cover, stem density and basal area, and elevated rates of tree mortality and windthrow (Chen et al. 1992). In my study, windthrow along buffer edges contributed to lower basal area and canopy cover, and ground disturbance (from harvesting) and increased light levels likely resulted in the low moss and high litter cover observed in the narrower buffers. Given that edge effects on vegetation do not appear to penetrate as far into the forest as microclimate effects (Kremsater and Bunnell 1999), the narrower buffers in my study likely consisted entirely of edge habitat, whereas the wider buffers were more characteristic of interior forest habitat.

Forest structure, as described by factor analysis, also exhibited the influence of edge effects. The first factor (Tree Cover) was significantly and positively related to buffer width; the second factor (Coniferous Shrub Cover and Richness) also had a positive, though not significant, relationship with buffer width. Tree Cover essentially described features of undisturbed forest habitat and separated narrow buffers from wide buffers and the unharvested forest. Coniferous Shrub Cover and

Richness broadly described the increased regeneration that has been shown to occur within the first 30 – 60 m of a forest-clearcut boundary (Chen et al. 1992). Overall, my results indicate that edge effects on forest vegetation decrease as riparian buffer width (and therefore distance from the edge) increases.

Songbirds and Buffer Width vs. Forest Structure

The richness of forest songbird species was not significantly related to forest structure. Similar to the area effects noted by Freemark and Merriam (1986), Blake and Karr (1987) and Askins et al. (1987), buffer width was the primary influence on species richness. A positive relationship between species richness and habitat area has been observed by many researchers (Galli et al. 1976, Forman et al. 1976, reviewed in Connor and McCoy 1979, Wiens 1989). The density of forest songbird species was also not significantly related to forest structure. Similar results were described by Askins et al. (1987) and Doherty et al. (2000), who found that patterns of songbird density in forest fragments were strongly associated with fragment area and were unrelated to vegetation structure. Likewise, Ambuel and Temple (1983) were unable to find any area-related changes in vegetation structure that influenced songbird abundance.

The densities of two common forest species, the winter wren and the Townsend's warbler, were highly correlated with riparian buffer width but not with forest structure. Given the strong relationship between density and buffer width for each species (Chapter 1), associations with habitat structure may have been too subtle to detect. However, other research into the habitats used by these species has indicated that such relationships do exist. In the central interior of B.C., Davis et al.

(1999) found Townsend's warblers to be positively correlated with the abundance of snags, and winter wrens to be positively correlated with total basal area, coarse woody debris volume and snag abundance. Hansen et al. (1995) showed that winter wren abundance was related to the total density of large diameter trees. Hagar et al. (1996) also found wren abundance to be correlated with the density of large diameter conifers and hardwoods, as well as the cover of coniferous shrubs. Although each model was developed from a different study site with a different set of measured variables, they all point to the importance of various canopy attributes.

The density of golden-crowned kinglets was related both to buffer width and to a descriptor of coniferous shrub cover and richness. Davis et al. (1999) found that golden-crowned kinglets were associated with total basal area, basal area of large trees and snag abundance. Hansen et al. (1995) showed that golden-crowned kinglets were significantly correlated with total tree density, and Hagar et al. (1996) found that kinglets were related to the percent cover of pole-sized and mature trees. In light of these models, it is difficult to explain why the density of a canopy-dwelling species like the golden-crowned kinglet would be associated with the percent cover of coniferous shrubs (seedlings and saplings). It is possible that the increased cover of coniferous shrubs, mainly saplings ≤ 10 cm dbh, afforded more foraging opportunities for kinglets. It is also possible that the cover of coniferous shrubs was related to some other aspect of forest structure that was not measured and with which golden-crowned kinglets were associated.

Although my analyses did not reveal distinct relationships between songbirds and forest structure, the influence of edge effects on buffer vegetation may in part

explain the pattern of increasing forest bird density and richness with buffer width. The long, thin medium and narrow buffers had a high ratio of edge to area. Because they possessed lower canopy cover, basal area and shrub cover than the wide buffers and the unharvested forest, they presented fewer foraging and nesting opportunities for some forest songbirds. In addition to the constraints of buffer width, edge effects and decreased resource availability may have further limited species presence and territory density in narrower buffers.

Habitat Use and Movements

My observations of foraging songbirds indicated that certain habitat features were used differently by the four study species (winter wren, yellow-rumped warbler, Townsend's warbler, golden-crowned kinglet). By incorporating this data with habitat use information from other sources, species-specific inferences may be made regarding the potential effects of area-related vegetation changes in riparian buffers.

Winter wrens prefer dark, relatively dense forests with abundant coarse woody debris, root masses and understory (Godfrey 1986, Davis et al. 1995, Campbell et al. 1997). However, they are flexible with respect to habitat type and will also occur along edges, in logging slash and in more open forests with shrubby understory (Campbell et al. 1997). In my study area, winter wrens favoured coarse woody debris and root masses for foraging. Because winter wrens spend much of their time ground gleaning (Sabo and Holmes 1983) and nest in root masses, tree cavities and creek banks (Waterhouse 1998), habitat elements such as downed wood, shrubs and snags are important to them. The ability of this species to utilize a variety of habitat types may make it less sensitive to logging in and adjacent to riparian areas. At the same

time, the lower basal area, canopy cover and shrub cover found in riparian buffers may decrease the suitability of buffer habitat for wrens. The removal of snags from buffers (to meet safety regulations) can lead to the loss of potential nesting locations, though this loss may be offset by the increased amount of downed wood that results from windthrow. Overall, winter wrens may not be seriously affected by the changes in forest structure that occur in riparian buffers, as long as critical elements (i.e., canopy cover, wildlife trees, shrub cover) are retained.

The yellow-rumped warbler is found in relatively open coniferous and mixed-wood stands (Godfrey 1986) and exhibits little habitat specificity (Hunt and Flaspohler 1998). This species demonstrates foraging plasticity – the ability to ‘make the best’ of a bad situation by exploiting resources in different ways as forest conditions change (Morse 1968). The yellow-rumped warbler is a generalist arboreal forager that uses all parts of the tree (Hunt and Flaspohler 1998), though higher use of the mid and lower canopy layers has been documented (MacArthur 1958, Sabo and Holmes 1983). In my study area, yellow-rumped warblers were flexible in their choice of substrate, tree species, canopy strata and habitat type for foraging. They were observed most often on pole-sized and mature trees and used both mid and upper canopy layers. Because of their preference for more open conifer stands at high elevations (Campbell et al. 2001) and their ability to forage in a broad range of microhabitats, yellow-rumped warblers may be unaffected by the changes in canopy structure that occur in riparian buffers as long as some larger trees are retained (Hunt and Flaspohler 1998).

Townsend's warblers occupy fir and montane spruce-fir forests, favouring late successional unharvested stands (Wright et al. 1998). This species has been positively correlated with crown closure, tall conifers, high basal area, number of coniferous saplings and dense deciduous understory (Campbell et al. 2001, Wright et al. 1998). Townsend's warblers forage primarily in the upper canopy, on both coniferous and deciduous trees (Wright et al. 1998, Godfrey 1986). In my study area, they used all canopy layers and foraged both on pole and mature trees. Because of their preference for dense, mature forests with abundant understory, this species may be adversely affected by the structural changes that occur in riparian buffers. In addition, any selective harvesting of tall, large diameter conifers in buffers will remove preferred nesting and foraging locations (Wright et al. 1998). However, the fact that Townsend's warblers were recorded at low density even in narrow buffers (Chapter 1) suggests that individuals will occupy riparian buffers as long as important habitat features (i.e., moderate canopy cover, some larger trees) are maintained.

Golden-crowned kinglets breed in a wide variety of forest types, but prefer boreal and subalpine forests (Ingold and Galati 1997). Although this species is usually found in dense, old growth or mature second growth forests (Campbell et al. 1997), it also occurs in logged areas, open and mixed-wood forests (Ingold and Galati 1997). Golden-crowned kinglets exploit a range of foraging maneuvers and substrates, focusing mostly on the lower and mid canopy (Sabo 1980), but also using the upper canopy layer (Sabo and Holmes 1983). In my study area, individuals foraged primarily in the mid canopy layer, using both pole-sized and mature trees. While golden-crowned kinglets are reliant on the canopy for foraging and nesting,

their flexibility with respect to forest type and foraging location suggests that they may not be particularly vulnerable to area-related vegetation changes in riparian buffers. The presence of golden-crowned kinglets in narrow buffers, albeit at low density (Chapter 1), indicates that they are tolerant of reduced canopy cover and basal area, provided that some mature trees are retained.

The retention of trees and tree patches in cutblocks may also provide additional habitat for certain species. Both golden-crowned kinglets and yellow-rumped warblers were observed foraging in retention patches within clearcuts. In particular, yellow-rumped warblers used both single trees and tree patches for foraging and singing perches. Residual trees can make cutblock habitat more attractive to forest bird species (Norton and Hannon 1997, Schieck et al. 2000, Schieck and Hobson 2000). In western boreal forests, harvest areas with tree retention patches (especially hardwoods) contain bird communities similar to those found in older forests (Schieck et al. 2000). Although larger patches attract more forest species than do smaller patches (Schieck and Hobson 2000), even the retention of single trees can provide habitat features for some forest species.

Differences in songbird movement patterns were observed between riparian buffers and the unharvested forest. Overall, birds foraging in riparian buffers appeared to be constrained by buffer width. In unharvested stands (and wide buffers for yellow-rumped warblers), birds foraged in all directions equally; individuals moved about the same distance upstream and downstream as they did towards and away from the stream. In buffers, movements into the upland were truncated; individuals tended to move greater distances upstream and downstream than they did

towards and away from the stream. Robinson and Holmes (1982) found that foraging birds moved just far enough to take them into new search areas. Riparian buffers may therefore increase the energy demands of individuals that are forced to seek prey over longer distances than in undisturbed forests.

Conclusions

The changes in vegetation that were observed across riparian buffers of different widths were likely the result of edge effects. Although changes in forest structure and forest songbird density were related to buffer width, they did not appear to be correlated with each other. Two possible reasons for this exist: (1) the appropriate vegetation variables were not measured, or were measured at too coarse a scale, or (2) forest birds were responding to edge effects besides those related to forest structure (e.g., competitive interaction with open-habitat species, increased predation, etc.)

The foraging behaviours and habitat requirements of the species observed in my study and in others indicate a certain degree of flexibility. Most common forest species can probably adapt to the variations in vegetation structure that occur in riparian buffers, provided that critical habitat elements like large trees, moderate canopy cover and downed wood are retained. However, the needs of specialist species were not addressed by my study. These species are likely to be less flexible and therefore more vulnerable to changes in forest structure. Their general absence from riparian buffers in the study area may reflect an inability to adjust to habitat modifications.

Table 2.1. Mean percentage cover of ground cover types across treatments and in the uncut forest.

	% Cover (± 1 S.E.)			
	Very Narrow	Narrow	Medium	Wide
Coarse woody debris*	16 (1) ^{AB}	15 (2) ^{AB}	15 (3) ^{AB}	17 (2) ^A
Bare ground	6 (1)	3 (3)	2 (1)	4 (3)
Litter	18 (8)	14 (9)	13 (3)	21 (5)
Herbaceous species	33 (22)	45 (7)	52 (4)	28 (7)
Grass species	5 (3)	8 (3)	1 (1)	3 (0)
Moss species	6 (4)	18 (5)	13 (3)	25 (1)
				9 (1) ^B
				0 (0)
				13 (5)
				40 (2)
				4 (4)
				36 (14)

* Letters A, B and AB indicate significant differences at $\alpha = 0.05$, as determined by a one-way ANOVA with Bonferroni multiple comparisons tests.

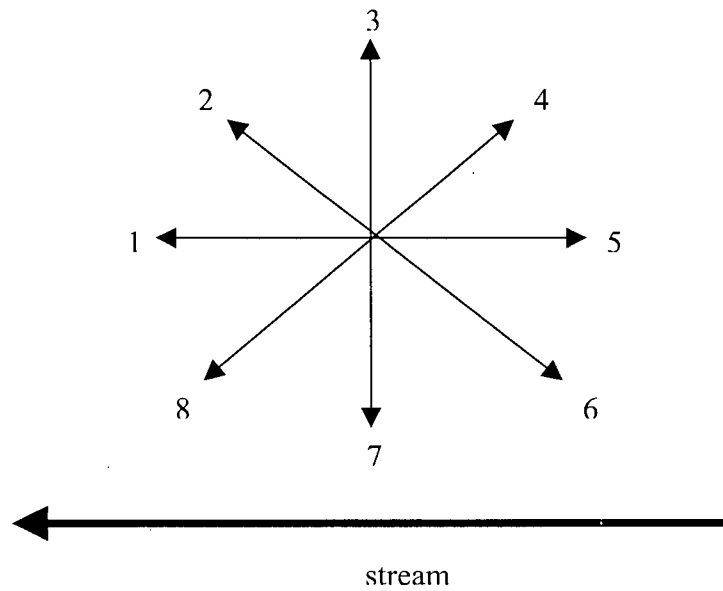
Table 2.2. Results of factor analysis with Equamax rotation. Only vegetation variables with component loadings ≥ 0.55 are shown.

Vegetation Variable	Tree Cover (FA 1)	Conifer Shrub Cover (FA 2)	Herb Cover (FA 3)	Deciduous Shrub Cover (FA 4)
Total basal area (m ² /ha)	0.79	-	-	-
Canopy cover (arcsin transformed)	0.77	-	-	-
# conifer seedling or sapling species	-	0.81	-	-
Coniferous shrub cover (arcsin)	-	0.82	-	-
Deciduous shrub cover (arcsin)	-	-	-	0.67
# shrub layers	-	0.66	-	-
# deciduous shrub species	-	-	-	0.56
Litter cover (arcsin)	-	-	-0.89	-
Coarse woody debris cover (arcsin)	-0.64	-	-	-
Grass cover (arcsin)	-	-	-	0.71
Herb cover (arcsin)	-	-	0.85	-
Moss cover (arcsin)	-	-	-	-0.57
Eigenvalue	3.33	2.03	1.60	1.21
% variance explained by factor	27.77	16.89	13.33	10.09
Total % variance explained	27.77	44.67	57.99	68.09

Table 2.3. Partial correlation values for the richness and density of forest songbird species vs. each of the four forest structure factors. Buffer width is the variable controlled for in each correlation. Two-tailed tests of significance were performed with $\alpha = 0.05$. For each variable, the partial correlation coefficient and the (significance level) is shown. Significant correlations are indicated with an *.

Songbird Variable	Tree Cover (FA 1)	Conifer Shrub Cover (FA 2)	Herb Cover (FA 3)	Deciduous Shrub Cover (FA 4)
Forest species richness	0.417 (P = 0.264)	0.226 (P = 0.559)	- 0.045 (P = 0.907)	0.119 (P = 0.760)
Forest species density	0.512 (P = 0.159)	0.416 (P = 0.264)	0.054 (P = 0.891)	0.225 (P = 0.561)
Golden-crowned kinglet density	0.591 (P = 0.094)	0.682 (P = 0.044) *	0.640 (P = 0.063)	0.306 (P = 0.423)
Townsend's warbler density	0.531 (P = 0.141)	0.576 (P = 0.104)	0.253 (P = 0.511)	0.641 (P = 0.063)
Winter wren density	- 0.330 (P = 0.385)	- 0.582 (P = 0.100)	- 0.386 (P = 0.305)	0.141 (P = 0.718)

A.



B.

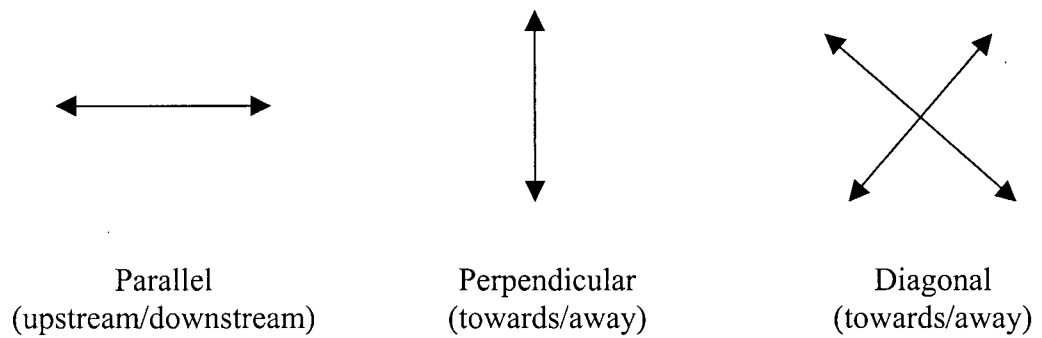


Figure 2.1. (a) Direction angles (relative to stream) used to record songbird movements, and (b) movement classes used for analysis.

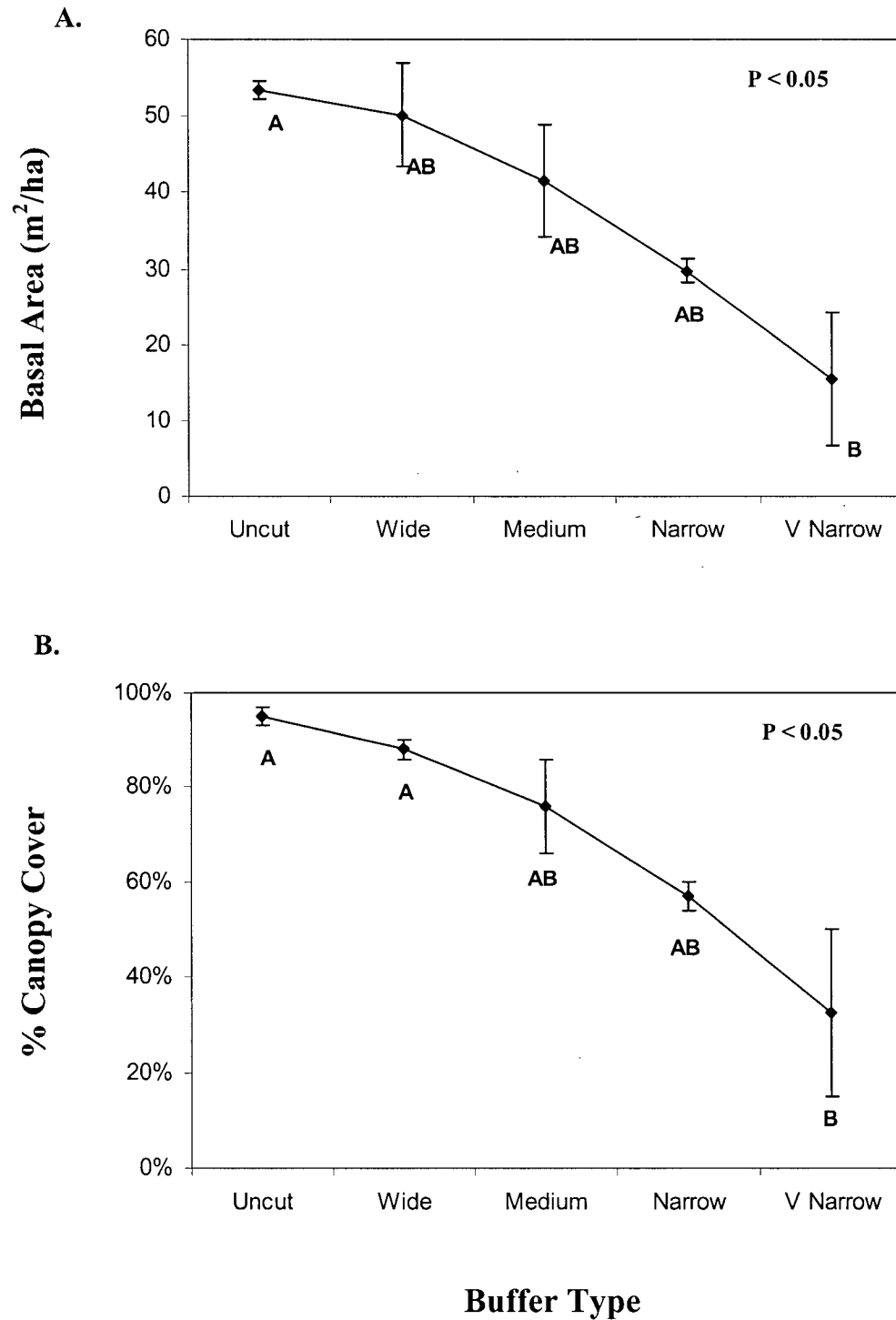


Figure 2.2. (a) Mean basal area (± 1 SE), and (b) mean % canopy cover (± 1 SE) in forest plots across treatments. Letters indicate significantly different treatments, based on one-way ANOVA with Bonferroni multiple comparisons.

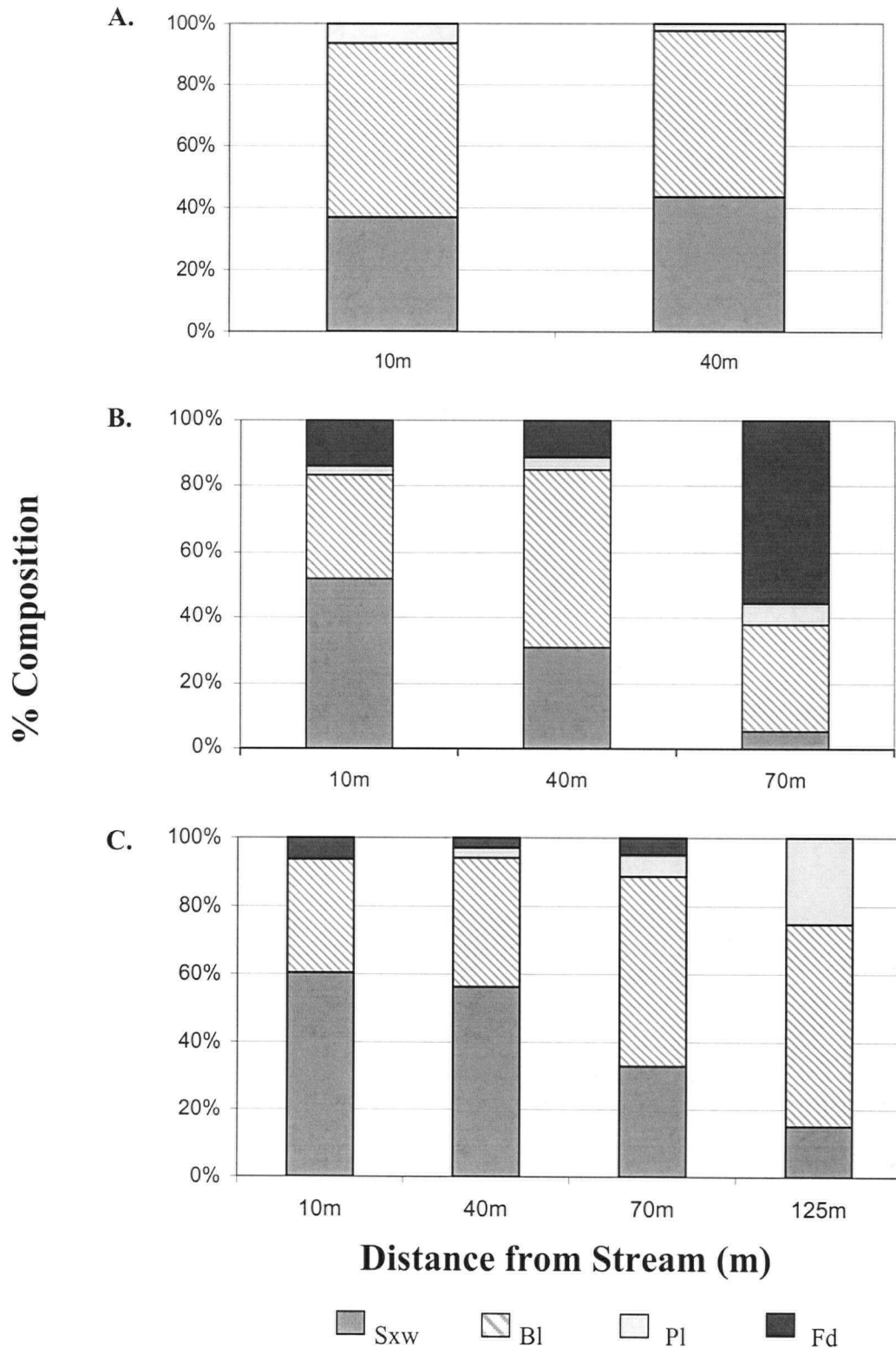


Figure 2.3. Changes in % tree species composition with distance from stream in (a) medium buffers, (b) wide buffers, and (c) the uncut forest. Sxw = hybrid white spruce; Bl = subalpine fir; Pl = lodgepole pine; Fd = Douglas-fir.

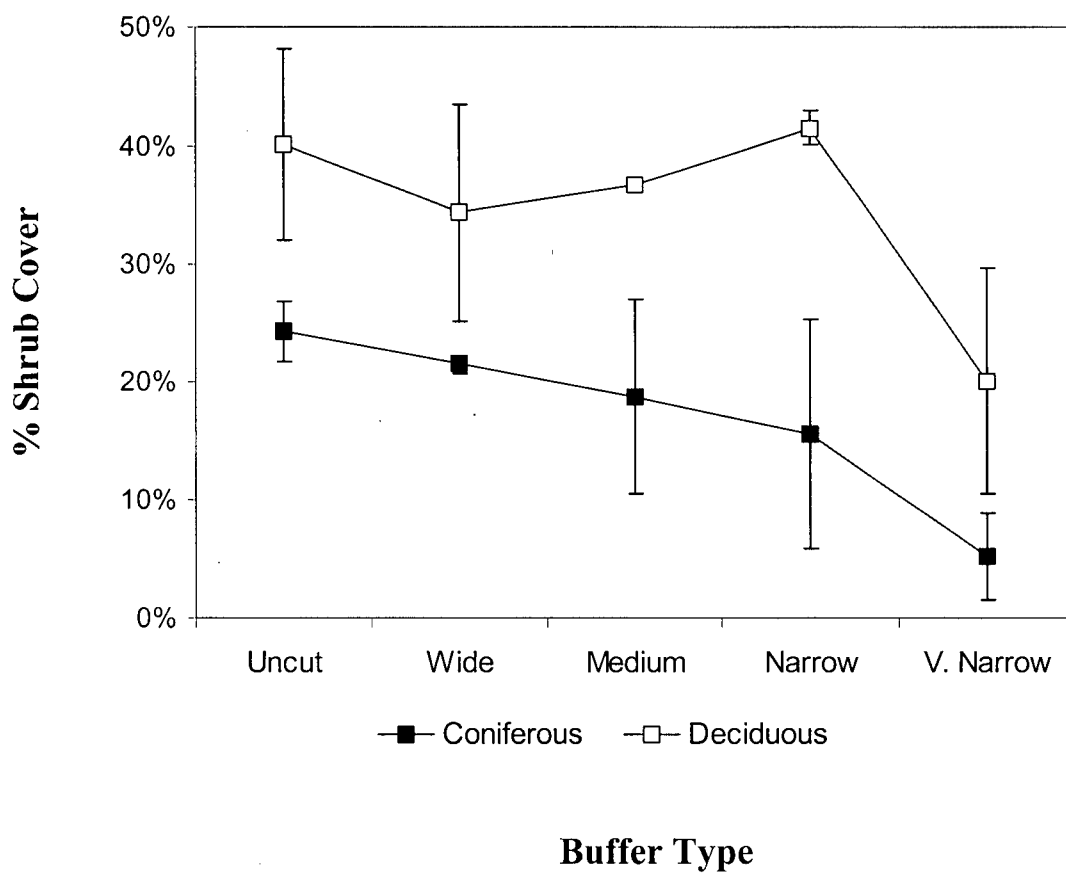


Figure 2.4. Mean % cover of coniferous and deciduous shrubs (± 1 SE) in forest plots across treatments.

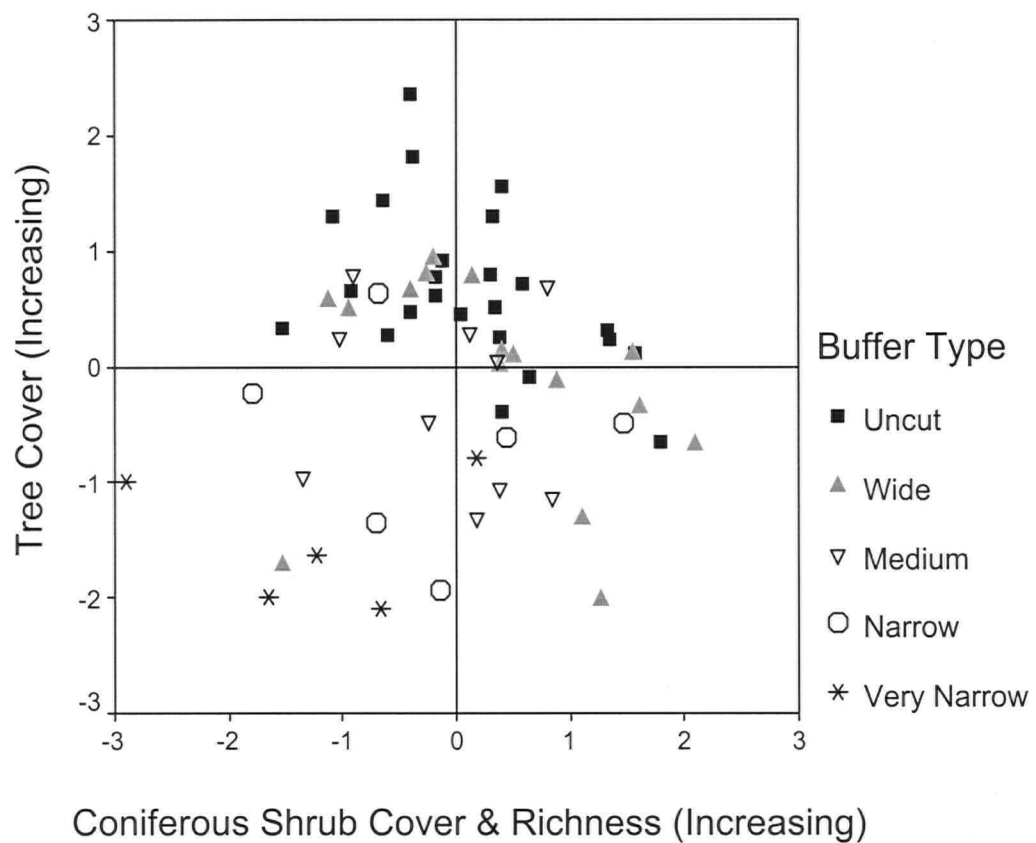


Figure 2.5. Scatterplot of Factor 1 (Tree Cover) scores against Factor 2 (Coniferous Shrub Cover + Richness) scores, by buffer type.

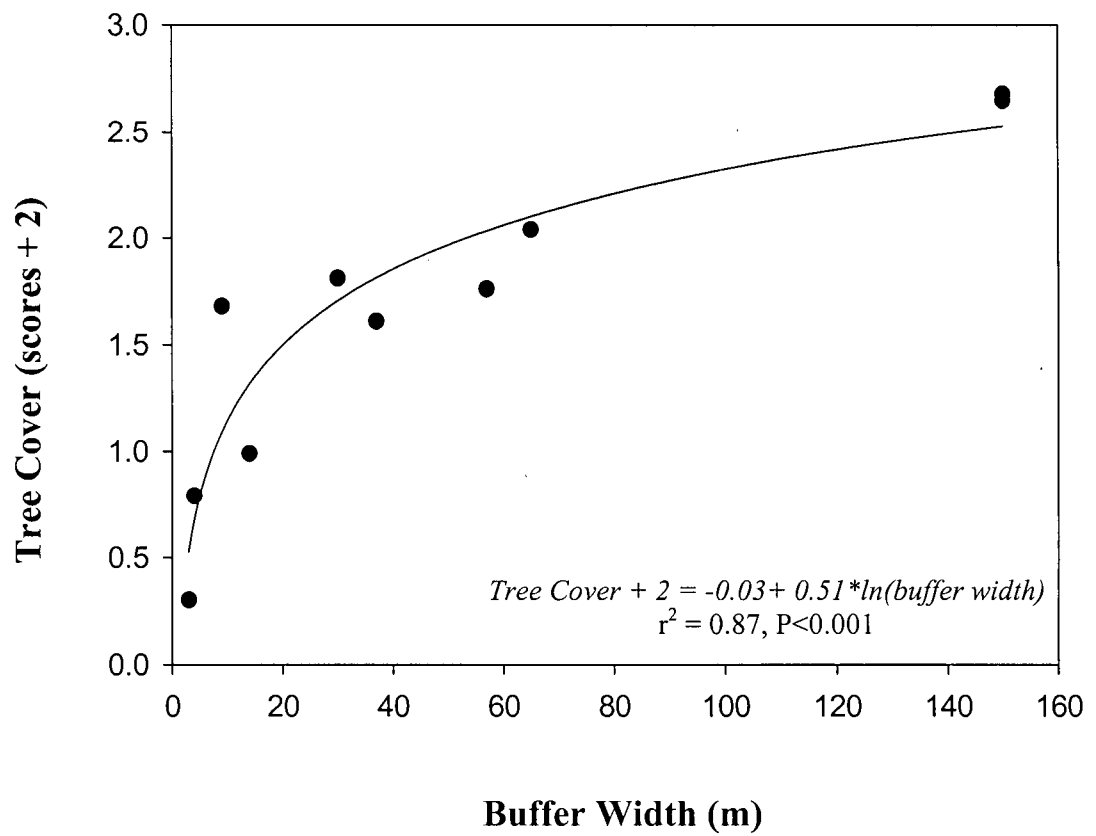
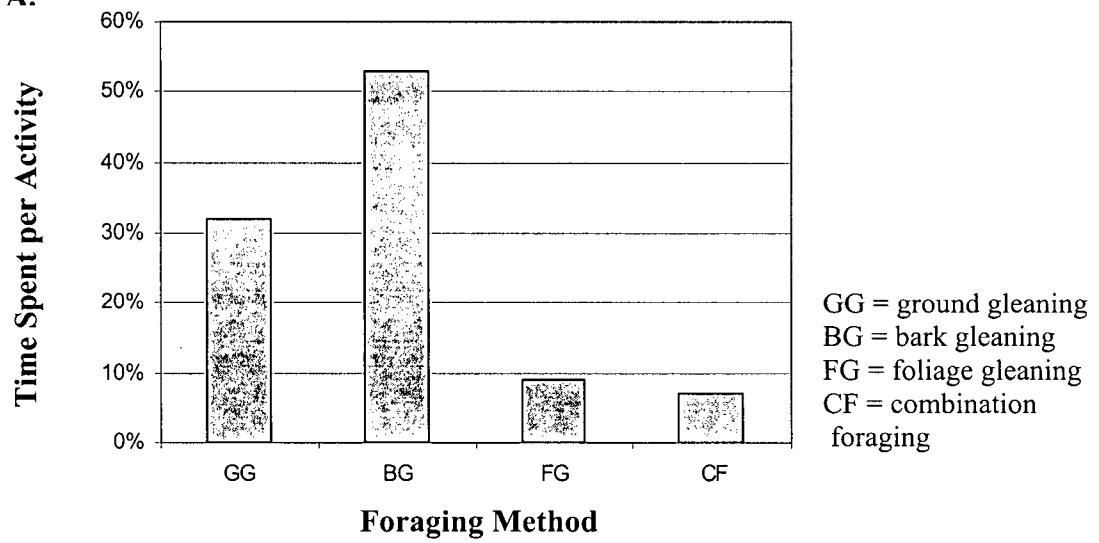


Figure 2.6. Relationship between riparian buffer width and Tree Cover (Factor 1 scores + 2).

A.



B.

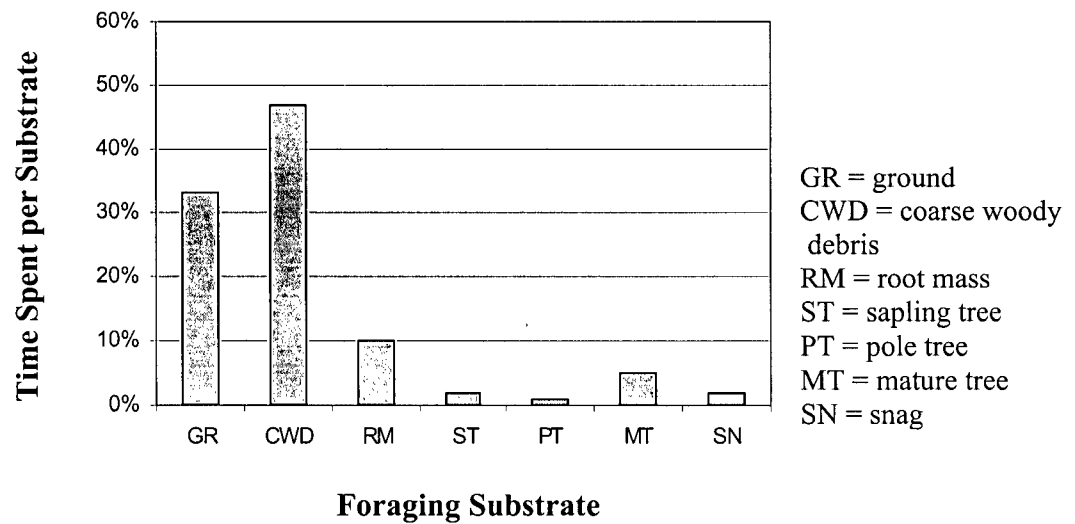


Figure 2.7. Winter wren activity budget. Proportion of time spent (a) engaged in foraging activities, and (b) foraging on different substrate types.

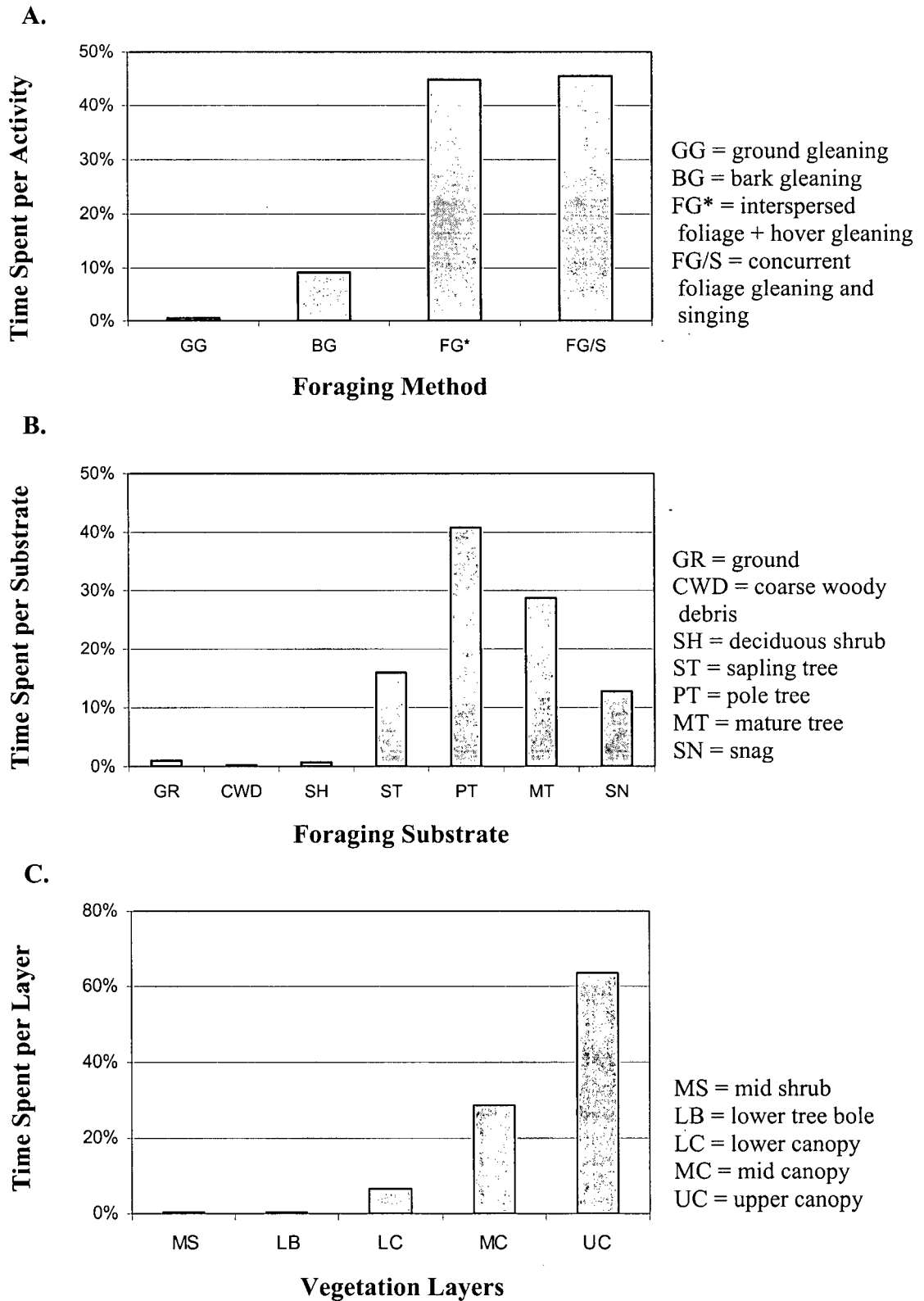


Figure 2.8. Yellow-rumped warbler activity budget. Proportion of time spent (a) engaged in foraging activities, (b) foraging on different substrate types, and (c) foraging in different vegetation layers.

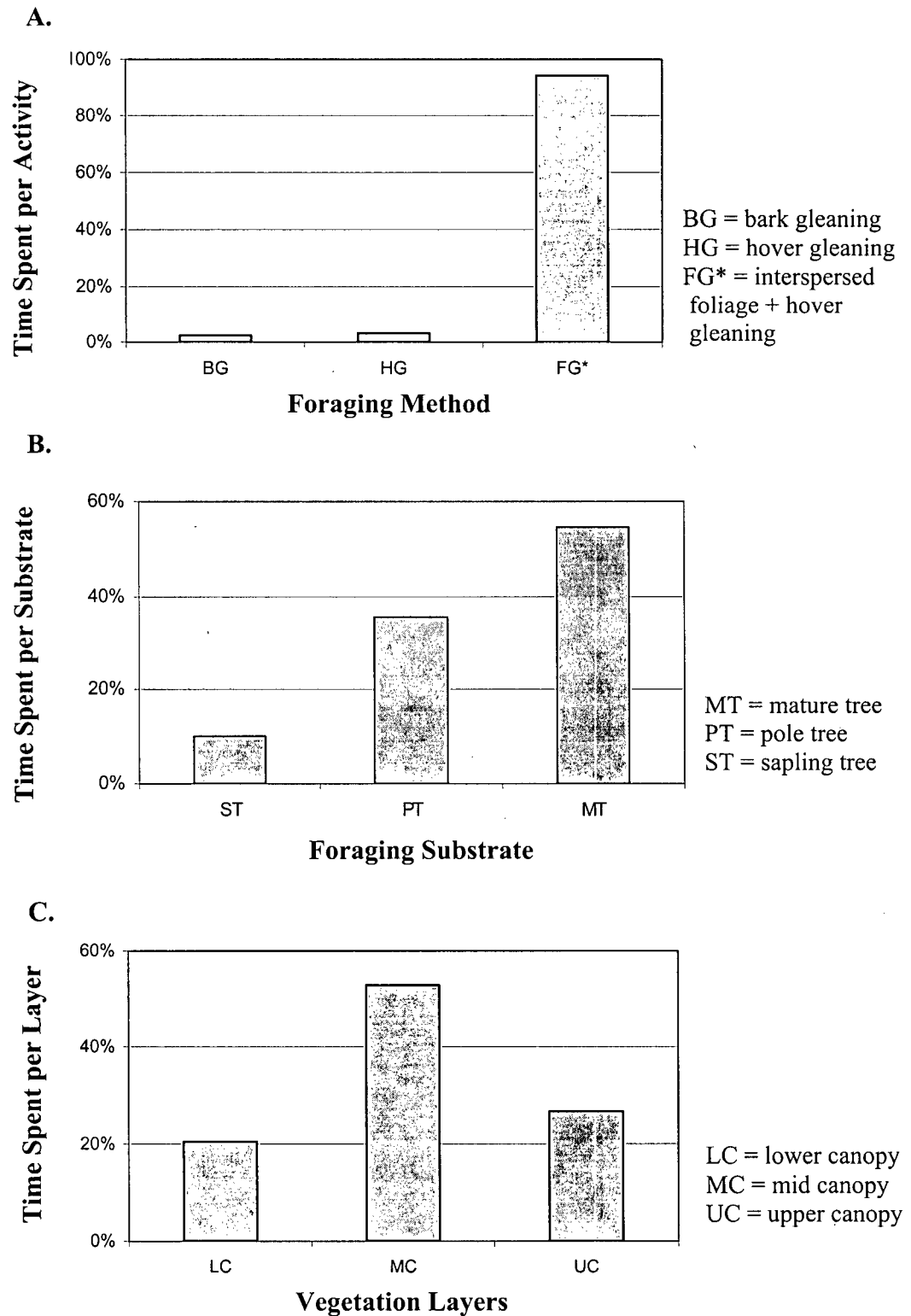


Figure 2.9. Golden-crowned kinglet activity budget. Proportion of time spent (a) engaged in foraging activities, (b) foraging on different substrate types, and (c) foraging in different vegetation layers.

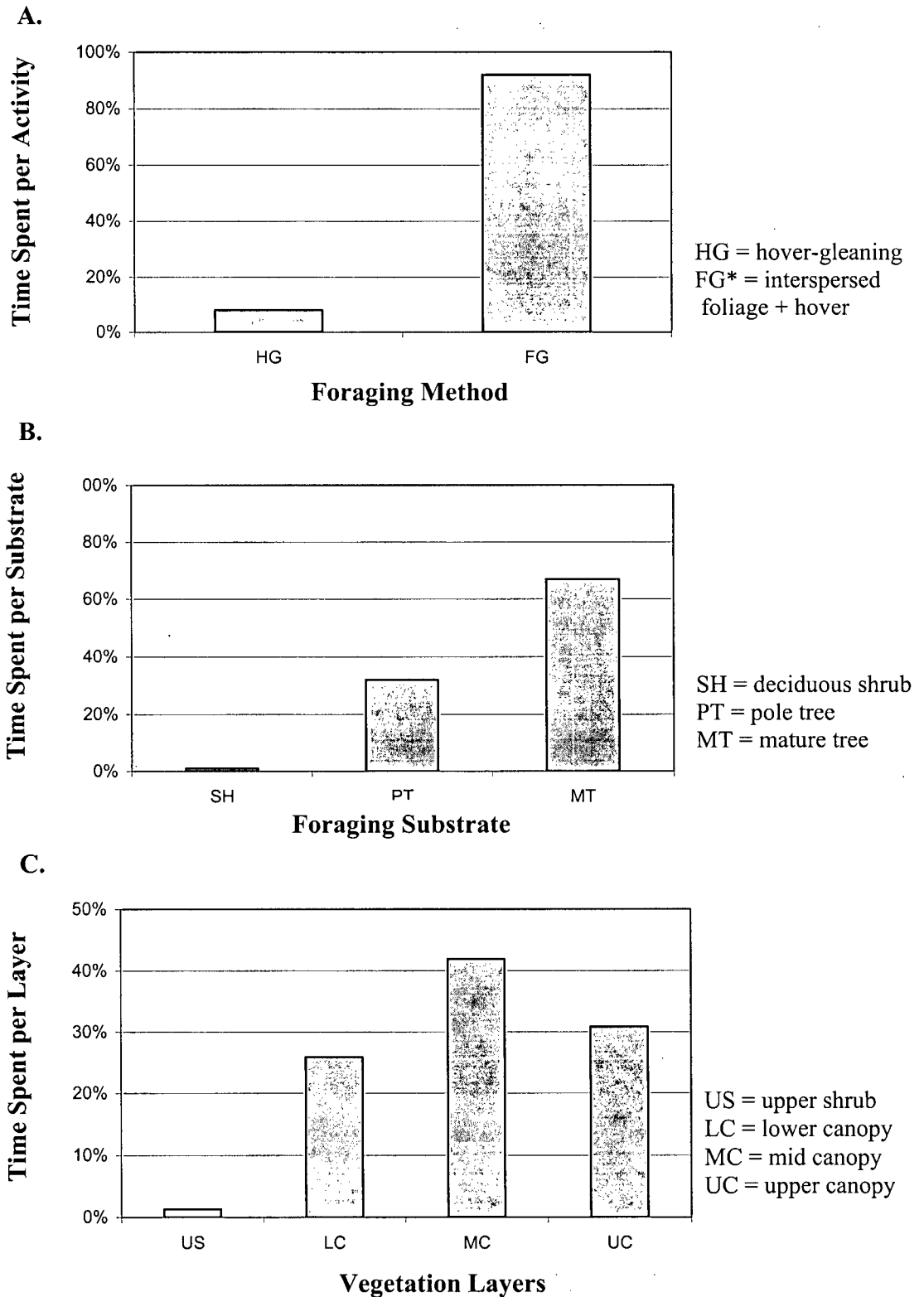


Figure 2.10. Townsend's warbler activity budget. Proportion of time spent (a) engaged in foraging activities, (b) foraging on different substrate types, and (c) foraging in different vegetation layers.

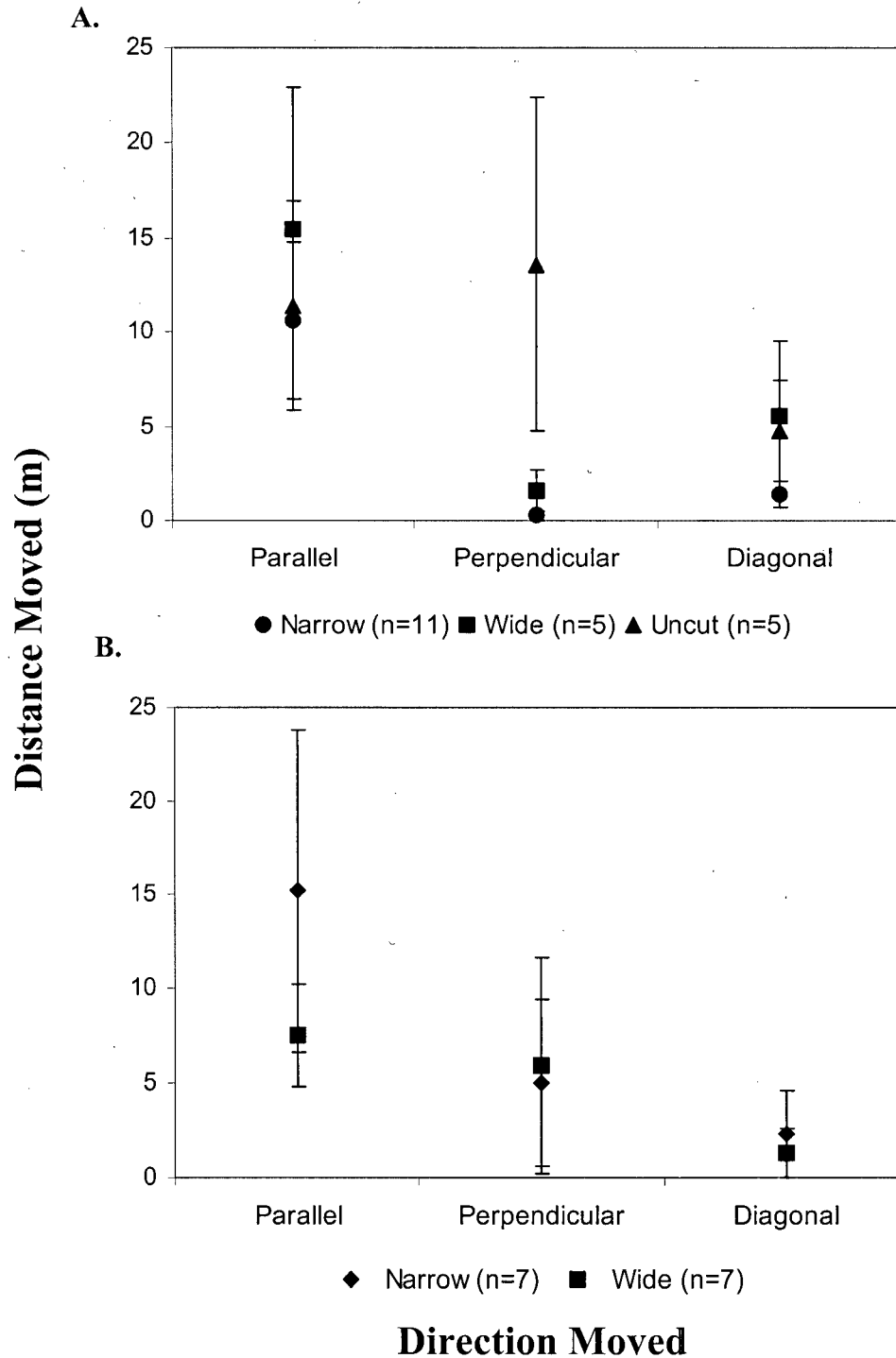


Figure 2.11. Mean distance moved (± 1 SE) in directions relative to stream by (a) winter wrens, and (b) yellow-rumped warblers. Sample sizes are given in each legend. (Parallel = upstream/downstream; Perpendicular = directly towards/away from stream; Diagonal = towards/away from stream at an angle).

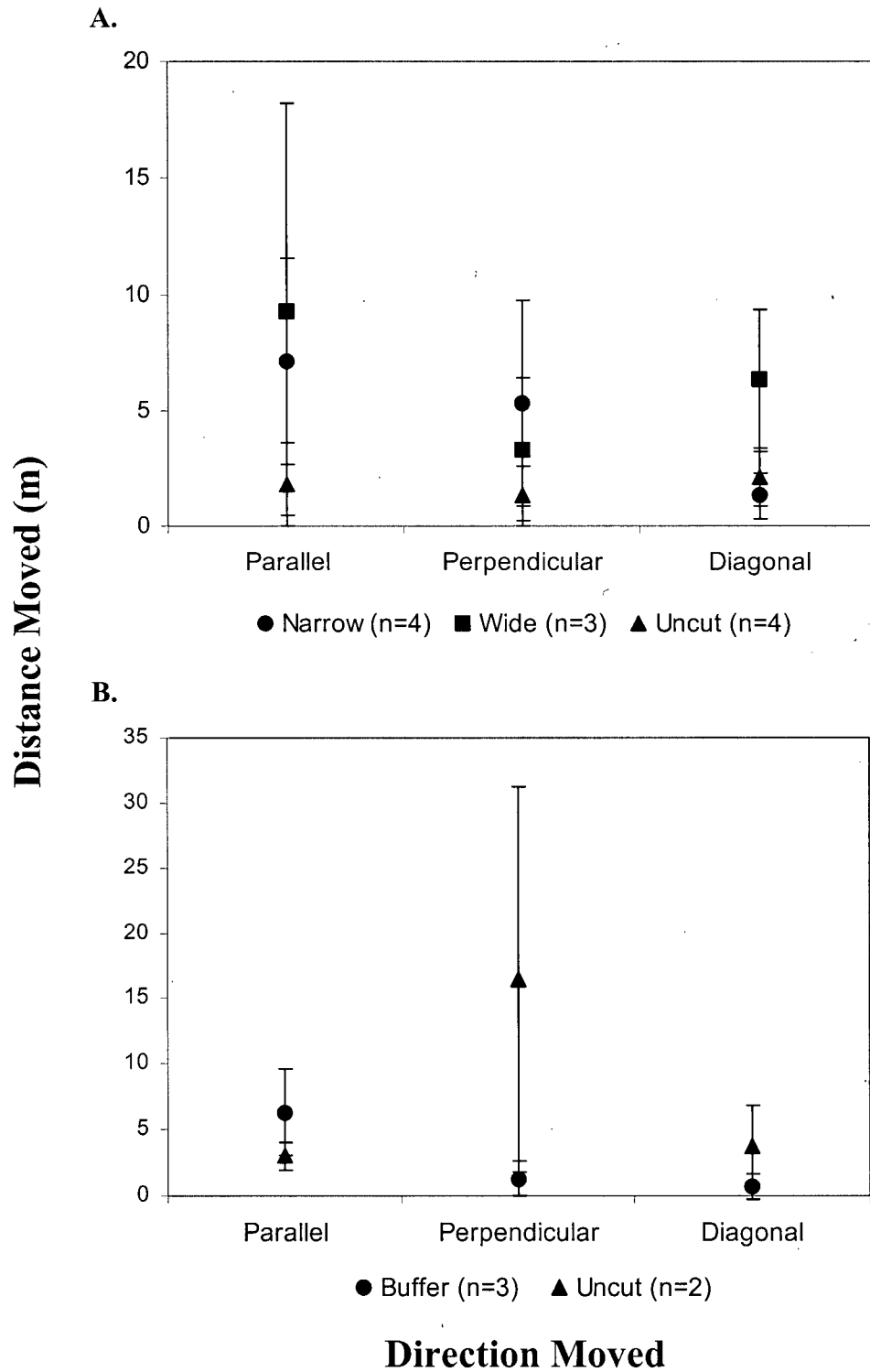


Figure 2.12. Mean distance moved (± 1 SE) in directions relative to stream by (a) golden-crowned kinglets, and (b) Townsend's warblers. Sample sizes are given in each legend. (Parallel = upstream/downstream; Perpendicular = directly towards/away from stream; Diagonal = towards/away from stream at an angle).

CONCLUSIONS AND RECOMMENDATIONS

Species are frequently classified based on their response to landscape structure or habitat fragmentation, but the data to support these classifications are often lacking (Villard 1998). For example, empirical evidence for edge avoidance in species thought to depend on forest interior is scant and few species appear to be “true” forest-interior specialists (Villard 1998). Most forest songbirds in my study area did not demonstrate the same degree of edge avoidance and area-sensitivity as found in other studies (e.g., Darveau et al. 1995, Gyug 1996, Hagar 1999, Whitaker and Montevecchi 1999, Pearson and Manuwal). Changes in the density of different forest species basically tracked changes in buffer width; there were no obvious thresholds below which the loss of forest species was disproportionately greater than the loss of buffer habitat.

There are several possible landscape-level explanations for these stand-level observations. First, the study area is still surrounded by forest at both the local and the regional level. Proximity to other local populations can influence the occupancy of forest fragments by birds (Villard 1998). Both Trzcinski et al. (1999) and McGarigal and McComb (1995) found that the distribution of forest songbirds was positively correlated with forest cover across the landscape. Askins et al. (1987) found that the density of “forest-interior” birds was higher in heavily forested regions, concluding that the dispersal of birds from surrounding forests is important to maintain populations in forest fragments. Second, the study area occurs in a naturally heterogeneous landscape that has been historically disturbed by fire and insect outbreaks (Province of B.C. 1995a). Because the forest birds inhabiting this

landscape have adapted to natural disturbance at various scales, they are likely more resilient to anthropogenic disturbances such as harvesting (Schieck et al. 1995, Schmiegelow et al. 1997). Third, many songbird declines in fragmented landscapes have been attributed to brown-headed cowbird parasitism (Brittingham and Temple 1983, May and Robinson 1985, Robinson 1992). There were no cowbirds recorded either in or around my study grids, leading me to conclude that brown-headed cowbirds were largely absent from the study area. Although confirmation of this would require a more detailed study with experienced observers, it is unlikely that cowbird nest parasitism is having a strong effect on the local songbird population.

Overall, riparian buffers provided usable habitat for forest songbirds breeding in the study area. Buffers were used by the winter wren, a riparian-associated species, and by various non-riparian species. Even those species considered “upland specialists”, such as the golden-crowned kinglet, Hammond’s flycatcher and Townsend’s warbler (McGarigal and McComb 1992, Martin and Wiebe 1997, Pearson and Manuwal 2001), established territories in the buffers. Riparian buffers \geq 60 m in width were used by almost every species observed in the unharvested forest, but even the narrower buffers provided some habitat for several forest species. Although wide riparian buffers are not likely to meet the needs of all forest songbirds, the range of buffer widths created by current forest practices appears to provide suitable habitat for many songbirds in the study area.

Study Limitations

The restricted temporal scope of this study is one major limitation to the generality of my research. Songbird data were collected for one breeding season only

due to logistical constraints. North American songbird populations frequently exhibit moderate to large-scale annual fluctuations in species abundances (Folkard and Smith 1995, Schmiegelow et al. 1997) and in observed relationships between species abundance and habitat area (Blake and Karr 1987). The winter that preceded the sampling season was particularly long and harsh, likely resulting in decreased songbird numbers and possibly in the general absence of certain species that should have been more common (e.g., red-breasted nuthatch, brown creeper, hermit thrush). Thus, the extrapolation of conclusions from this one year of abnormal weather to other milder years is unreliable. The study also did not incorporate both pre- and post-treatment sampling; the absence of any pre-treatment data precludes the assumption of true replication. In addition, site tenacity in songbirds can produce local densities that reflect past, rather than present habitat quality (Van Horne 1983). Without longer-term data for the study area, it is impossible to know whether or not the patterns exhibited during the 1999 breeding season are representative of general trends and true conditions.

A second limitation of this study is the lack of any nesting or productivity data. The density of individual species and of all species combined was used to indicate the ability of riparian buffers to provide suitable breeding habitat. This assumes that bird density and habitat quality are positively correlated. Without any supporting nesting success and productivity data, however, this assumption may be misleading or even incorrect (Van Horne 1983). The singing males recorded in the buffers may have been "floaters", subdominant males forced into sub-optimal habitat where they were unable to attract mates. Alternatively, males in the buffers may have

successfully attracted females, but the negative influence of edge effects subsequently resulted in low nesting or fledging success. Thus, riparian buffers thought to be of adequate width to maintain breeding songbirds may actually be acting as habitat sinks (Van Horne 1983). Further research that incorporates measures of fitness would be required to determine whether or not riparian buffers truly contribute to viable populations of forest songbirds.

A third limitation of the research is the transferability of the data and results. The relationships between species density and buffer width that were defined through regression analysis should be viewed as descriptive, rather than predictive. Because of the small sample size and low level of replication, there are not sufficient data to extrapolate these relationships beyond the study area or buffer widths sampled. In addition, the study examined streams with a riparian buffer on one side and contiguous forest on the other side. Although harvesting on one side of the stream is a common practice within TFL #35, it is not the method applied in all managed forests. If the buffers had been isolated by upland harvesting on both sides of the stream, the density of forest birds would have likely been much lower and some species (e.g., varied thrush) may have been entirely absent (but see Waterhouse and Harestad 1999). Patches that are too small to support certain species can do so only if additional, suitable habitat exists nearby (Blake and Karr 1987). Thus, the presence of unharvested forest across the stream allowed buffers to support more individuals and more species than would have occurred in isolated buffers. The conclusion that a minimum riparian buffer width of 30 m is needed to provide habitat for most forest

songbirds would not be valid if extrapolated to similar forest types with isolated riparian buffers.

Management Recommendations

The recommendations listed below are intended to act as a guide for forest managers, particularly those working within TFL 35 and other, similar high-elevation forest types. Although these practices may not necessarily be employed across the entire managed landscape, they can be applied to portions of the landscape to meet specific management objectives.

1. *Variable-width buffer retention.* Results of my research indicate that a minimum riparian buffer width of 30 m is required to provide habitat for many forest songbird species in the study area. In other studies however, the same forest species exhibited high variability with respect to width-sensitivity (Darveau *et al* 1995, Gyug 1996, Kinley and Newhouse 1997, Hagar 1999, Manuwal and Pearson 2001). This variability makes it difficult to propose an absolute minimum riparian buffer width. Instead, I recommend variable-width buffers that make use of site-specific topography. For example, wide buffers can be assigned to riparian areas that are inoperable due to steep slopes in exchange for greater volumes extracted from riparian areas that may be particularly susceptible to windthrow. In this way, patches of wide forested buffers will be interspersed with sections of stream having little or no buffering – an alternative to having long, narrow buffers that provide little habitat and can be subject to high rates of blowdown.

2. *Single-side harvesting.* The contiguous forest on the opposite of each stream likely contributed to the songbird densities that were observed in the riparian buffers. Removing timber along only one side of a stream in each pass will increase the value of the retained buffer as usable habitat for forest songbirds. The isolation of buffers by concurrent harvesting on both sides of a stream is not recommended.
3. *Retention of structure in clearcuts.* Residual patches of live trees retained in clearcuts were utilized for foraging and singing by various songbird species, including dark-eyed juncos, yellow-rumped warblers, golden-crowned kinglets and Townsend's warblers. Single live trees and snags were also utilized for foraging and perching. The retention of living and dead deciduous and coniferous trees in harvested areas can provide important habitat elements to both open-habitat and forest songbird species. The continued maintenance of these structural features, in both dispersed and clumped distributions, is recommended.
4. *Additional conservation strategies.* Riparian buffers retained in harvested areas can mitigate the effects of habitat loss for numerous forest songbird species. The juxtaposition of clearcuts and forested buffers can even increase songbird richness and diversity across the landscape. However, the maximization of species richness and diversity should not be the only goal of management. It is necessary to consider the composition of the songbird community and the continued maintenance of both common and rare species. Even wide buffers will not support all species – songbirds with a high degree

of area-sensitivity will require large patches of unharvested forest for breeding habitat. Thus, it is important to consider the use of additional conservation strategies, such as Old Growth Management Areas (Ministry of Forests 1995), to sustain a complete forest bird community.

5. *Monitoring songbird numbers.* Monitoring is an integral component of any wildlife management strategy. Recommendations made from this study are based on a single year of data and may not be sufficient to maintain songbird species and numbers over time. The implementation of a monitoring program, even a basic survey of songbird presence/absence every 2 or 3 years, is highly recommended. One cost-effective way to gather monitoring data is to request that a North American Breeding Bird Survey route be established within the management area. This would allow the collection of annual data, by an experienced observer, for the long-term monitoring of local population trends.

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APPENDIX 1: An example of territory delineation for the Townsend's Warbler in a wide buffer site.



APPENDIX 2: Songbird species list, species abbreviations, status and classification for the study area.

<u>Latin Name</u>	<u>Common Name</u>	<u>Abbreviation</u>	<u>Status</u> ¹	<u>Classification</u> ²
<i>Cinclus mexicanus</i>	American dipper	AMDI	NT, R	
<i>Turdus migratorius</i>	American robin	AMRO	T, C	O ^{2, 4, 5, 7, 8}
<i>Poeciles atricapilla</i>	Black-capped chickadee	BCCH	NT, U	
<i>Poecile hudsonica</i>	Boreal chickadee	BOCH	T, U	F ^{2, 5, 7, 9}
<i>Certhia americana</i>	Brown creeper	BRCR	NT, R	
<i>Bombycilla cedrorum</i>	Cedar waxwing	CEWA	NT, R	
<i>Spizella passerina</i>	Chipping sparrow	CHSP	T, C	O ^{2, 3, 4, 5, 7}
<i>Corvus corax</i>	Common raven	CORA	NT, U	
<i>Junco hyemalis</i>	Dark-eyed junco	DEJU	T, C	O ^{2, 3, 5, 6, 7, 8, 9}
<i>Empidonax oberholseri</i>	Dusky flycatcher	DUFL	NT, R	
<i>Coccothraustes vespertinus</i>	Evening grosbeak	EVGR	NT, U	
<i>Regulus satrapa</i>	Golden-crowned kinglet	GCKI	T, C	F ^{2, 3, 4, 5, 6, 7, 8, 9}
<i>Perisoreus canadensis</i>	Gray jay	GRJA	NT, U	
<i>Empidonax hammondi</i>	Hammond's flycatcher	HAFL	T, C	F ^{5, 6, 8}
<i>Picoides villosus</i>	Hairy woodpecker	HAWO	NT, R	
<i>Catharus guttatus</i>	Hermit thrush	HETH	NT, R	
<i>Charadrius vociferus</i>	Killdeer	KILL	T, U	
<i>Melospiza lincolni</i>	Lincoln's sparrow	LISP	T, C	O ^{2, 3, 5, 7}
<i>Oporornis tolmiei</i>	McGillivray's warbler	MGWA	T, U	O ^{5, 6, 8}
<i>Sialia currucoides</i>	Mountain bluebird	MOBL	T, C	O ⁵
<i>Poecile gambeli</i>	Mountain chickadee	MOCH	NT, U	
<i>Colaptes auratus</i>	Northern flicker	NOFL	NT, U	
<i>Aegolius acadicus</i>	Northern saw-whet owl	NSWO	NT, R	
<i>Contopus cooperi</i>	Olive-sided flycatcher	OSFL	NT, R	
<i>Vermivora celata</i>	Orange-crowned warbler	OCWA	NT, R	
<i>Pinicola enucleator</i>	Pine grosbeak	PIGR	NT, U	

<i>Carduelis pinus</i>	Pine siskin	PISI	NT, U	F ^{2, 4, 5, 7, 8, 10}
<i>Sitta canadensis</i>	Red-breasted nuthatch	RBNU	T, U	
<i>Loxia curvirostra</i>	Red crossbill	RECR	NT, U	
<i>Buteo jamaicensis</i>	Red-tailed hawk	RTHA	NT, R	
<i>Regulus calendula</i>	Ruby-crowned kinglet	RCKI	T, U	F ^{2, 5, 7, 10}
<i>Passerculus sandwichensis</i>	Savannah sparrow	SASP	T, U	O ⁷
<i>Falciennis canadensis</i>	Spruce grouse	SPGR	NT, R	
<i>Catharus ustulatus</i>	Swainson's thrush	SWTH	T, C	F ^{2, 3, 4, 5, 7, 8, 10}
<i>Buteo swainsoni</i>	Swainson's hawk	SWHA	NT, R	
<i>Picoides tridactylus</i>	Three-toed woodpecker	TTWO	NT, U	
<i>Myadestes townsendi</i>	Townsend's solitaire	TOSO	T, U	G ⁵
<i>Dendroica townsendi</i>	Townsend's warbler	TOWA	T, C	F ^{3, 5, 6, 8}
<i>Tachycineta bicolor</i>	Tree swallow	TRSW	NT, U	
<i>Ixoreus naevius</i>	Varied thrush	VATH	T, C	F ^{3, 5, 6, 8}
<i>Vireo gilvus</i>	Warbling vireo	WAVI	NT, R	
<i>Contopus sordidulus</i>	Western wood-pewee	WWPE	NT, R	
<i>Zonotrichia leucophrys</i>	White-crowned sparrow	WCSP	T, U	O ^{5, 6}
<i>Wilsonia pusilla</i>	Wilson's warbler	WIWA	T, U	G ^{2, 3, 5, 7, 8}
<i>Troglodytes troglodytes</i>	Winter wren	WIWR	T, C	F ^{1, 2, 3, 4, 5, 6, 7, 8, 10}
<i>Dendroica coronata</i>	Yellow-rumped warbler	YRWA	T, C	G ^{2, 3, 4, 5, 7, 9}

¹ STATUS: T = held territory in study grid

NT = did not hold territory in study grid

R = rare (observed only once or twice)

U = uncommon (territories on <3 study grids OR observed several times outside study grids)

C = common (territories on ≥3 study grids)

² CLASSIFICATION – applied only to species with territories on study grids – includes authorities used to classify:

F = forest-associated species

O = open-habitat species

G = generalist

AUTHORITIES:

- 1 = Austen et al. 2001
- 2 = Darveau et al. 1995
- 3 = Davis et al. 1999
- 4 = Freemark and Collins 1992
- 5 = Gyug 1996
- 6 = Hagar 1999
- 7 = Hobson and Bayne 2000
- 8 = Schieck et al. 1995
- 9 = Whitaker and Montevecchi 1997
- 10 = Whitaker and Montevecchi 1999

APPENDIX 3: An example of plot layout for vegetation sampling within a wide buffer site.

