Bird use of epiphyte resources in an old-growth coniferous forest of the Pacific Northwest

by

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ABSTRACT

Epiphytes play important ecological roles in the Pacific Northwest and elsewhere, but the resources they provide for birds are poorly known. If epiphytes are an important foraging and nesting resource for birds, current and future forest management activities may have negative effects on bird community diversity and abundance. I used mountain-climbing techniques to access the forest canopy to: 1) assess whether species and foraging guilds use host and epiphyte resources in the same proportions relative to their availability; and 2) evaluate whether canopy-level and ground-level point count assessments are comparable methods for detecting forest birds.

I studied epiphyte use by birds in the T. T. Munger Research Natural Area, an old-growth coniferous forest in the southern Washington Cascades. Approximately 30% of all foraging records (N=735) occurred on epiphyte substrates. Chestnut-backed Chickadee, Red-breasted Nuthatch, Brown Creeper, Hairy Woodpecker and Gray Jay used epiphytes disproportionately, based on log-likelihood ratio tests. Bark insectivores and omnivore scavengers used cyanolichen and other lichen and bryophytes disproportionately, relative to their availability. Use of lichen substrates was more frequent than other epiphytes in the mid- and upper-crown, compared with more frequent use of bryophytes than other epiphytes in the lower-crown. Alectorioid lichens were used with hanging and probing behaviors, whereas foraging bouts on cyanolichen and other lichen substrates involved a greater variety of foraging maneuvers and postures. *Pseudotsuga menziesii* and *Tsuga heterophylla* were used disproportionately more frequently than any other tree species, relative to their availability when epiphyte substrates were used. Although ground-level foraging observations were important for determining which resources were used in the mid- to lower-canopy and understory, ground-based observers could not reliably evaluate which resources were used by small passerines in the upper canopy. Use of epiphyte substrates for foraging appears to be a function of observer location, rather than actual resource selection. Similarly, the location of the observer was an important determinant for recording the height of bird foraging activity.

More species and individuals were recorded at the canopy-level than at the ground-level and detection frequencies increased at the canopy level when sampling radii exceeded 30 m. Although there were no differences in the rank order of species detections between canopy and ground-level observers, the canopy-level observer detected a more species rich community, relative to observer detections captured at the ground level.

Non-vascular epiphytes increased the inner canopy rugosity and provided important ecological functions for higher trophic levels, including nesting and foraging habitat. In Oregon and Washington, 100 bird species that breed in coniferous forests use bryophyte, lichen or mistletoe in their nests. To provide prime foraging and nesting habitat for forest birds, land managers should consider the epiphyte vegetative community structure within foraging and nesting habitat. Forest managers should implement forest practices that maintain old-growth structural characteristics to enhance epiphyte assemblages and associated bird species communities.

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These arboricolous plants turn tree limbs into Babylonian hanging gardens.

Edward O. Wilson, *The Diversity of Life*

CHAPTER 1

INTRODUCTION

Epiphytes fulfill important ecological functions in forest ecosystems (Coxson and Nadkarni 1995, Rhoades 1995). Epiphytic cryptogams intercept precipitation, fog and mist, and retain aerosol-delivered nutrients, fix nitrogen (Pike 1978, Nadkarni 1986, Nash 1996); and supply forests with a nutrient subsidy via litterfall and throughfall (Reynolds and Hunter 2004). These arboreal communities also provide critical microhabitats for invertebrates, and vertebrate resources for insectivorous and non-insectivorous bird species (Pettersson *et al*. 1995, Muir *et al*. 2002). Coniferous forests in the Pacific Northwest (PNW) harbor a tremendous diversity of epiphytes, which reach their greatest diversity in old-growth stands (McCune 1993). Canopy epiphyte biomass in the PNW is as high as 2.6 tons ha^{-1} (McCune 1993) and lichens alone may contribute up to 7.5 kg ha^{-1} yr^{-1} of nitrogen to nutrient poor forests (Pike 1978).

Considerable ornithological research has been conducted in the PNW, most studies have primarily focused on patterns of avian abundance and distribution between different aged stands and forest types (e.g., Manuwal 1991, Manuwal and Carey 1991, Ruggiero *et al.* 1991, Sharpe 1996). These studies have positively correlated bird species richness and species abundance with old-growth forest, with the relationship attributed to complex structural features of the forest. The crowns of old-growth conifers offer tremendous structural diversity in foliage, branch forms, snags, cavities and epiphytic communities (Shaw *et al.* 2002). However, no studies in the PNW have considered the ecological relationship of epiphytic resources and birds, due to the difficulty of accessing the canopy for direct observations (Munn and Loiselle 1995), the apparent lack of epiphyte specialists (Sillett 1994), and the focus of research on the two federally threatened species (the Northern Spotted Owl (*Strix occidentalis caurina*) and Marbled Murrelet (*Brachyramphus marmoratus*)). Thus, the ecological roles of and resources that PNW epiphytes provide for vertebrates are poorly known, particularly for birds.

My primary objective was to assess bird use of epiphytes. Research in tropical forests has demonstrated that birds use canopy epiphytes extensively, and their presence in forests may contribute to bird community diversity (Terbough 1980, Nadkarni and Matelson 1989, Nadkarni 1994, Sillett 1994). Tropical birds are rewarded with nectar, resins, or pollen, rewards that do not exist in temperate coniferous forest canopies because the temperate arboreal epiphyte community is almost entirely composed of non-vascular plants (McCune *et al*. 2000). Epiphytes may add to the available pool of ecological niches, or auxiliary resources by increasing the surface area of the forest canopy. This hypothesis has been proposed (Nadkarni and Matelson 1988) and tested (Cruz-Angon *et al.* 2008) in tropical forest ecosystems but has not been tested in temperate forests.

Mosses and lichens are used by temperate coniferous forest birds as nesting substrate (Sharnoff and Rosentreter 1998), but do these birds also use these substrates for foraging? A diverse range of biotic and abiotic variables affect bird foraging patterns and substrate selection, but optimal foraging theory suggests that birds will optimize and maximize their successes in procuring food by spending most of their foraging efforts searching substrates most likely to harbor rewards (Pyke 1984, Morse 1990). Differential foraging strategies by foraging guilds and their representative species contribute to increased niche partitioning and increased forest diversity. I collected foraging observations from the canopy and ground level to determine the relative frequency of specific substrates use by foraging birds. This revealed the relative importance of each substrate for each species and respective foraging guild, and allowed a comparison between species and foraging guilds. My alternate hypothesis is that there are difference among species and foraging guilds: species and foraging guilds will use epiphytes disproportionately using dissimilar foraging strategies and behaviors.

The importance of canopy epiphytic resources has been documented for certain temperate bird species. The federally threatened Marbled Murrelet uses an epiphytic moss (*Isothecium* spp.) extensively as a nesting substrate (Hamer and Nelson 1995). Sillett (1994) reported that some birds use epiphyte resources in parts of their range during certain times of the year, although he also noted that there were no epiphyte specialists in temperate and arctic North America and Greenland. Birds avoided fruticose lichen and foliose species presumably because the lichens contained anti-herbivory compounds (Sillett 1994). However, PNW canopy foliose lichen and bryophyte mats provide suitable microhabitat for, and harbor a unique assemblage of arthropods (Winchester and Ring 1994, Schowalter and Ganio 1998, Behan-Pelletier and Eamer 2001). Thus, temperate forest epiphytes provide foraging birds rewards, albeit indirectly. I suggest that all epiphyte functional groups provide additional vertical and horizontal strata that increase the structural and functional diversity of canopy resources, thus increasing foraging and nesting opportunities for insectivorous birds.

Birds may contribute to epiphyte reproduction by acting as agents of dispersal for vascular and non-vascular plant species (Rhoades 1995, Benzing 2004). This could account for higher epiphyte species richness (McCune *et al*. 2000) and an increase in bird abundance reported in the upper canopy, relative to the ground level and lower canopy (Shaw *et al*. 2002). Therefore, not only may epiphytes provide “new” resources for birds otherwise limited to resources of the host tree, but also the birds could be facilitating dispersal of propagules and spores among epiphyte populations.

Branch forms and branch distribution influence the composition of epiphytic communities in old-growth forests, and epiphytes within old-growth forest canopies are not randomly or evenly distributed: the foliage supports the bulk of epiphytic lichen biomass, followed by branches, and finally trunks (Clement and Shaw 1999). Vertical stratification of epiphytic functional groups occurs (McCune 1993, Clement and Shaw 1999, McCune *et al*. 2000) and vertical stratification also occurs in some songbird assemblages (Shaw *et al.* 2002). Thus, I postulate that the gradient in epiphyte groups might influence vertical stratification observed in birds if certain epiphytes groups are more important foraging resources than other epiphyte groups.

The response of epiphytes to forestry practices has received considerable attention in the past three decades (McCune 1993). Experimental studies have documented that certain epiphytes are dispersal limited while others may be limited by substrate or micrometeorological conditions (Pike 1978, McCune 1993, Peck and McCune 1997, Sillett and Goslin 1999). Although we can generally predict how certain epiphyte species respond to changes in age class and canopy structural modifications, we cannot predict how these changes alter epiphyte communities and associated fauna, including bird communities. The effects of forest management on lichen and invertebrate communities and passerine birds have been investigated in other countries (Pettersson *et al.* 1995, Uliczka 1999). For example, Uliczka (1999) correlated the absence of certain lichen and bird species in heavily managed boreal forests in southern Sweden. This hole in our knowledge limits our ability to manage lands to promote biodiversity.

In the PNW, forest management goals for state and federal forests (the “matrix”) entail harvest rotations of 40 to 80 years, stands that have poorly developed epiphyte communities (McCune 1993). Thus, if epiphytes are an important foraging and nesting resource for birds, current and future management activities may have negative effects on bird community diversity and abundance. Spickler *et al*. (2006) suggested that epiphyte productivity and the associated humus mats that develop in old-growth conifer crowns may maintain a diverse community of nutrient dependant organisms. These structurally complex crowns of old-growth forest stands may contribute to increased foraging opportunities for birds, which might account for higher bird species richness and abundances reported for old-growth stands, relative to young stands (Manuwal 1991, Huff and Raley 1991, Huff *et al.* 1991).

A secondary objective was to assess whether point counts conducted at the ground level are a reliable census technique for forest birds. Point counts are a common census technique used to estimate species richness, densities and abundances of bird populations. The accuracy and precision of these estimates relies on them meeting certain assumptions (Bibby *et al*. 1992, Buckland *et al*. 1993). Among-observer sources of bias and error associated with these estimates vary according to environmental factors including vegetation and background noise (e.g., Waide and Narins 1988, Kissling and Garton 2006, Simons *et al*. 2007, Pacifici *et al*. 2008). Ground-based techniques, such as double-observer sampling, have been developed to assess the amount of error and bias in these distance sampling estimates (e.g., Kissling and Garton 2006). However, few studies have evaluated among-observer variability, particularly when double-observer sampling is conducted simultaneously and vertically in dense forests with high canopies (Waide and Narins 1988, Anderson 2009). This evaluation is important because one of the key assumptions of distance sampling theory is that the probability of detecting all birds at the plot center is 1, which is unlikely in forests with high canopies (DeSante 1981). For example, ground-level observers in a tropical forest underestimated the population of singing canopy birds by as much as 50% (Waide and Narins 1988, Anderson 2009). Thus, if more species and individuals could be recorded by a canopy observer, relative to a ground-level observer, then species richness and abundances that characterize a temperate forest stand may historically have been underestimated, since most forest bird assessments are conducted at ground level. Among-observer variability of canopy- and ground-level point counts were compared to assess whether ground-level point count assessments are a reliable method for detecting forest birds. I postulate that point counts conducted at the canopy level facilitate a more comprehensive assessment of species richness, abundance and detection frequencies in both fixed and unlimited radii plots.

The study was comprised of two parts: 1) a literature review of North American species accounts of bird use of epiphytes and 2) field surveys. I provide information on the roles that epiphytes provide for PNW forest birds, and compare differences between canopy- and ground-level observers. My goals are to:

1. Quantify the frequency of bird use of epiphyte resources, and whether birds use epiphyte resources in proportion to their availability, relative to other forest resources;
2. Identify foraging guild or species epiphyte specialists;
3. Identify the epiphyte foraging strategies used by foraging guilds and species;
4. Compare species richness and relative abundances between canopy- and ground-level observers in variable circular plot point counts;
5. Suggest epiphyte/bird roles in forest ecology; and
6. Outline management implications of these findings.

CHAPTER 2

LITERATURE SUMMARY OF BIRD USE OF MOSSES AND LICHENS

Introduction

Although lichens and mosses are considered critical components of many food chains, there is a paucity of published information on the ecological roles that these non-vascular plants provide for wildlife, especially birds (Sharnoff and Rosentreter 1998). Most literature on the matter has focused on lichens as an important forage base for caribou and other ungulates. For instance, the North American Caribou (*Rangifer tarandus*) is known to eat pendant epiphytic forage lichens that cloak old-growth forest canopies, including species of *Alectoria*, *Bryoria*, and *Usnea* (Richardson and Young 1977).

Although it was generally accepted that birds use lichens and bryophytes for nest structure, function and ornamentation, the listing of the Northern Spotted Owl and Marbled Murrelet as federally-threatened species validated the importance of bryophytes and lichens as nesting material as well as food for a variety of birds, bats, and rodents dependant on old-growth forests (FEMAT 1993). The Northern Spotted Owl and Marbled Murrelet rely either directly or indirectly on the presence of these cryptogams. For instance, the Marbled Murrelet uses moss mats as a nesting platform, and the Northern Spotted Owl eats Northern Flying Squirrel (*Glaucomys sabrinus*), which uses lichens and moss extensively for food and in its nests (FEMAT 1993).

Birds use bryophytes and lichens as inner or outer nest lining, or for ornamentation of the outside, and the nest functions provided by bryophytes and lichens include insulation, camouflage, and possibly predator avoidance mechanisms. Lichens and bryophytes also provide North American passerines with a forage base by affording invertebrates both food and protective environments for shelter, oviposition and pupation sites (Seaward 1977, Smith 1982). Lichen- and bryophyte-associated invertebrates include terrestrial fauna such as mites, annelids, mollusks and other arthropods (Gerson and Seaward 1977, Gerson 1982). These invertebrates provide a foraging base for vertebrates including insectivorous birds.

If birds use mosses and lichens extensively for nesting substrate and forage, then the presence of these non-vascular plants may contribute to bird community diversity in these temperate forests. A review of the literature was warranted to identify the bird species that use cryptogams in nest construction and use lichens or mosses directly as a food source.

Methods

I reviewed the literature on bird use of epiphytic resources (primarily bryophytes and lichens) as nesting substrates in North America (Gabrielson and Jewett 1970; Seward 1977, Ehrlich *et al*. 1988; Marshall *et al*. 2003, Baicich and Harrison 2005, Wahl *et al.* 2005; and two surveys of lichens and their use by North American wildlife and invertebrates [Sharnoff and Rosentreter 1998, Sharnoff 1998]). In addition; I reviewed a subset of entries (239 species) from the Birds of North America online electronic resource (Cornell Lab of Ornithology 2009), which included 151 bird species known to breed in forested habitats in Oregon (Oregon Bird Records Committee 2008, Marshall *et al*. 2003) and Washington (Washington Ornithological Society 2008, Wahl *et al.* 2005). The species reviewed included all members of the Orders Falconiformes, Strigiformes, Apodiformes, Piciformes, and Passeriformes, and species that breed in coniferous forests (e.g., Ruffed Grouse, Band-tailed Pigeon). The species accounts in the citations were reviewed to determine the number of bird species that use epiphytic resources for nesting in a) North America, and b) and Oregon (OR) and Washington (WA).

Results

Of a total of 670 bird species that nest in North America (Baicich and Harrison 2005), at least 279 species (42%) use one or more of the five common epiphyte substrates: 1) bryophyte, 2) lichen, 3) Spanish Moss, 4) epiphytic rootlets, and 5) mistletoe, for nesting, including structural, nest ornamentation or lining purposes (Table 1; see Appendix A for a complete list of species and substrate use). Nearly 40% (262 species) of North American birds use either lichens or bryophytes as a nesting substrate or as nesting material. At least 21 North American birds use the epiphytic vascular plant, Spanish moss (*Tillandsia usneoides*) as nest material (Appendix A).

Of the 151 bird species that breed in coniferous forests of OR and WA, 98 species (65%) use either lichen or moss; and 45 species (30%) use both lichen and moss as nesting material (Table 1). Thus, the proportion of birds that use bryophytes and breed in OR and WA coniferous forests is almost double the proportion of North American birds that use bryophytes. Similarly, although not quite as extreme, a greater proportion of WA and OR forest breeding birds use lichens (35%), relative to the proportion of North American birds that use lichen (19%). In OR and WA coniferous forests, all seven thrush (Turdidae) and six hummingbird species (Trocholidae) use either bryophyte or lichen as nesting material (Appendix A). All nine crows and jays (Corvidae), except one (Black-billed Magpie), use bryophytes in their nests. Similarly, 10 of 11 OR and WA breeding fringilline finches (Fringillidae) use either moss or lichen. Bryophytes and lichens are frequently used as nesting material by 8 of 12 (67%) tyrant flycatchers (Tyrannidae), and by 8 of 11 wood warblers (Parulidae).

At least 14 bryophyte and ten lichen genera are used by breeding birds in coniferous forests: The bryophyte genera used included *Alsia*, *Brachythecium*, *Calliergon*, *Dendroalsia*, *Dicranum*, *Eurhynchium*, *Homalothecium*, *Hypnum*, *Isothecium*, *Pogonatum*, *Pohlia*, *Polytrichum*, *Porella*, and *Sphagnum*. The bryophyte genera *Alsia*, *Dicranum*, *Hypnum*, *Isothecium*, and *Porella* generally have epiphytic forms, whereas *Eurynchium* is primarily terrestrial although *Eurynchium* often grows on the bases of tree boles and on fallen logs. The lichen genera included *Alectoria*, *Bryoria*, *Cladonia*, *Evernia*, *Hypogymnia*, *Parmelia*, *Physcia*, *Ramalina*, *Sphaerophorus*, and *Usnea*. With the exception of *Cladonia*, all lichen genera are generally epiphytic, growing on bark and wood of coniferous and deciduous trees (McCune and Geiser 1997). Twenty North American bird species use *Usnea* lichen as either the primary structure or lining for their nest substrates (Table 2). Eleven of the 20 species that use *Usnea* lichen breed in OR and WA and locate their nests in coniferous trees; seven species, Fox Sparrow, Golden-crowned Kinglet, Gray Jay, Hutton's Vireo, Marbled Murrelet, Red Crossbill and Ruby-crowned Kinglet are year-round residents, and all four tyrant flycatchers are neotropical migrants.

Several bird species that breed in coniferous forests use nests made almost entirely of mosses. Examples include the Winter Wren (Hejl *et al*. 2002), Marbled Murrelet (Nelson 1997) and Golden-crowned Kinglet (Ingold and Galati 1997). A Hammond Flycatcher nest described by Sakai (1988) was comprised of two epiphytic lichens (*Hypogymnia inactiva* and *Ramalina menziesii*), and five bryophytes (including the epiphytic moss *Isothecium* sp., and liverwort, *Porella navicularis*). Two other Neotropic migrants (Pacific-slope Flycatcher and Hutton's Vireo) use the epiphytic lichen *R. menziesii*.

Table 1: Summary data for bird use of nesting material in North America, and for birds that breed in coniferous forests of Washington and Oregon**.**

NORTH AMERICA	**No. of Species**	**Percent*,****
bryophyte	223	33
lichen	127	19
mistletoe	10	1
lichen or bryophyte	262	39
lichen and bryophyte	88	13
Spanish moss	21	3
either bryophyte, lichen, Spanish Moss, epiphytic rootlets or mistletoe	279	42
WASHINGTON AND OREGON		
Coniferous forest breeding birds**	151	23
bryophyte	90	60
lichen	53	35
lichen or bryophyte	98	65
lichen and bryophyte	45	30
either bryophyte, lichen, or mistletoe	100	66

* percentages are based on a total of 670 species occurring in North America (Baicich and Harrison 2005); and ** 151 breeding birds in Washington and Oregon (Marshall *et al*. 2003, Wahl *et al*. 2005)

Table 2: North American birds that use *Usnea* lichen as nesting material.

English Name	**OR/WA breeder?**	**Nest host/location**	**Winters in OR/WA**
Red-shouldered Hawk	yes	Deciduous tree	yes
Marbled Murrelet	yes	Conifer	yes
Olive-sided Flycatcher	yes	Conifer	no
Dusky Flycatcher	yes	Deciduous tree, Conifer, Shrub	no
Pacific Flycatcher	yes	Deciduous tree, Conifer	no
Hammond's Flycatcher	yes	Deciduous tree, Conifer	no
Gray Jay	yes	Conifer	yes
Golden-crowned Kinglet	yes	Conifer	yes
Ruby-crowned Kinglet	yes	Conifer	yes
Bohemian Waxwing	no	Conifer	yes
Philadelphia Vireo	no	Deciduous tree	no
Hutton's Vireo	yes	Deciduous tree, Conifer	yes
Northern Parula	no	Deciduous tree	no
Blackburnian Warbler	no	Conifer	no
Blackpoll Warbler	no	Conifer	no
Fox Sparrow	yes	Conifer	yes
Rusty Blackbird	no	Conifer, Shrub	yes
Common Grackle	no	Deciduous tree, Conifer	no
Red Crossbill	yes	Conifer	yes
Common Redpoll	no	Shrub	yes

Discussion

Thus, many bird species use cryptogams in nest construction. This literature review was not exhaustive since many nest details were defined in broad categories. For some species, the nest descriptions provided were coarse categories, such as “plant debris” or “plant fibers”, whereas for others, the nest details were meticulous. For instance, the nest of the Townsend’s Warbler was described as being “lined with moss fruiting stems and hair”, and the Worm-eating Warbler uses hair moss stems in the genus *Polytrichum* (Baicich and Harrison 2005). For some species, the breeding ecology and nest details are poorly understood (e.g., Hermit Warbler [Pearson 1997]). These data should also be considered an underestimate because several North American species use abandoned nest sites or are brood parasites of species known to use epiphytes for nest substrates (e.g., genera *Molothrus*). Furthermore, the nest substrate data in the literature reviewed did not specify whether the bryophytes and/or lichen used were epiphytic forms. Bryophyte and lichen forms may be terrestrial, epilithic (dwelling on rocks) or epiphytic.

This literature search more than doubled the number of North American birds that use lichens in their nests to 127 species, from 45 (Richardson and Young 1977). The common use of lichens by birds for nesting is believed to be an evolutionary adaptation that aids in nest concealment (Richardson and Young 1977). That the terms decoration and ornamentation are often used to describe lichen use diminishes the functional ecological role of lichens. Not only do lichens provide aesthetic and camouflage, lichens likely play a significant role in maintaining nest health, since several lichen species (e.g., *Lobaria pulmonaria*) have antimycobacterial properties (Boustie and Grube 2005). Lichens waterproof nests by shedding water (Ehrlich *et al*. 1988), and darker-colored lichens used often as nest material in colder climates (e.g., *Bryoria* spp.) have insulating properties, because they more readily absorb solar radiation than lighter-colored materials. Because 19% of North American birds (and 35% of birds that breed in coniferous forests in OR and WA) use lichens for nesting substrates, birds may function as a dispersal agent. This has important implications for lichen conservation and management objectives of many dispersal-limited epiphyte species. However, birds may or may not represent a significant pathway of dispersal.

Birds rarely use lichens or bryophytes as food, except in times of food shortages (Sillett 1994, Rhoades 1995). Possible explanations for the limited use of these cryptogams are the low caloric value and presence of toxic compounds (Rhoades 1995). However, there were several accounts of species eating bryophytes, but fewer accounts for lichen. Most accounts were for species that breed in the colder climates of North America (e.g., the Red-throated Loon, Brant, and three cogenerics of Ptarmigan, White-tailed, Willow, and Rock Ptarmigan) (Palmer 1962, Martin and Hik 1992, Braun *et al*. 1993, Hannon *et al*. 1998). Sporophyte capsules of *Distichum incinatum* comprised a substantial proportion of the crop contents of some Willow Ptarmigan chicks (Martin and Hik 1992). Possible explanations for these Canadian Arctic breeders eating mosses might be because several arctic bryophytes contain higher percentages of lipids, relative to their vascular plant counterparts (Pakarinen and Vitt 1982), providing high quality food.

Canopy epiphytic mosses and lichens indirectly provide important food sources for invertebrates, and egg laying sites, on which birds depend (Gerson and Seaward 1977). Any modification or disruption of these epiphyte communities may have a deleterious effect for higher trophic levels.

CHAPTER 3

STUDY SITE AND METHODS

The field survey component included 1) foraging data collected from fixed-area plots and walking transects, and 2) simultaneous canopy- and ground-level variable circular plot point counts.

Study Area

The field study site was the 478 ha Thornton T. Munger Research Natural Area (RNA) located in the 4208-ha Wind River Experimental Forest located in the southern Cascade Range of Washington State (latitude N 45°49’13.76”, longitude W 121°57’06.88”; Fig. 1). Sampling was conducted in an approximately 500-year-old Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) – western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) coniferous forest (Shaw *et al.* 2004). The RNA supports a transitional vegetation zone between the Western Hemlock Zone and the Pacific Silver Fir Zone (Franklin and Dyrness 1973). The RNA occurs on an extinct shield volcano, topography is gentle, and elevation ranges from 335 m to 610 m (Meyers and Fredricks 1993). The climate is characterized by summer droughts, winter snow events, with mean annual precipitation of approximately 2.2 m per year (Shaw *et al.* 2004). The Wind River Canopy Crane Research Facility located in the southeastern portion of the RNA, has facilitated extensive forest canopy research in this old-growth forest ecosystem. Previous work on epiphytic abundance and distribution (McCune 1993, Clement and Shaw 1999, McCune *et al*. 2000, Shaw *et al*. 2002, Nadkarni and Sumera 2004) has been conducted in the vicinity.

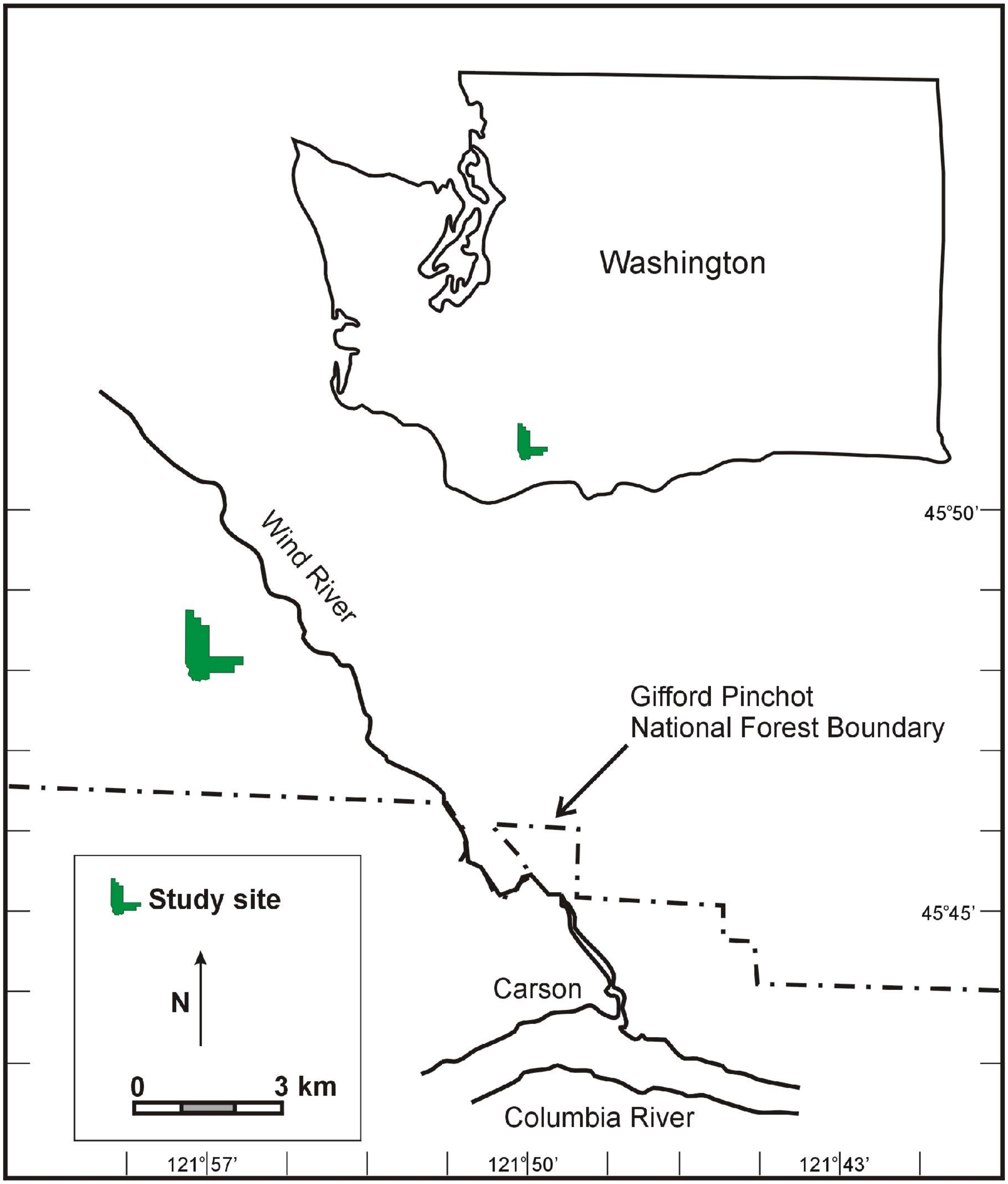

Figure 1: Location of Study Area.

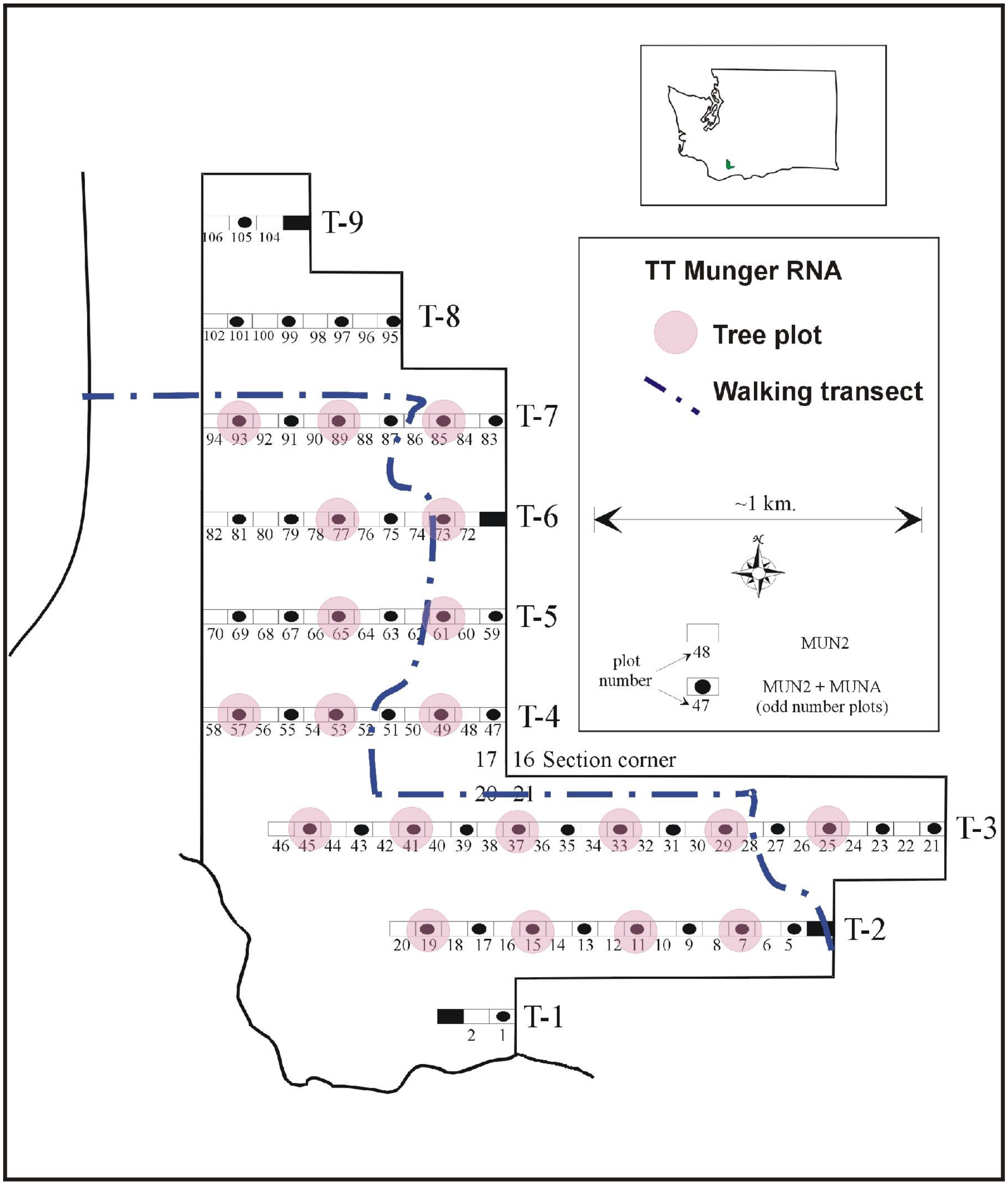

Figure 2: Location of Tree Plots and Walking Transect in the T. T. Munger Research Natural Area.

Foraging Observations

I followed the field research protocol of Nadkarni and Matelson (1989) and Sillett (1994), and used two sampling procedures to collect data on bird foraging behavior and substrate use: 1) fixed-area plots (hereafter referred to as Tree Plots), and 2) Walking Transects. Surveys were conducted between 25 April and 7 July 2005 for a total of 40 survey days totaling 337.6 survey hours: 122.7 Tree Plot hours (mean survey length = 3.07 hrs, SE = 0.02); and 214.9 Walking Transect hours (mean survey length = 5.4 hrs, SE = 0.03). Total distance traversed during the Walking Transects was 96 km, which captured approximately 288 km^2 of the RNA. The 20 Tree Plots captured approximately 1.4 km^2 of the RNA.

Tree Plots

Twenty Tree Plots were selectively located in existing permanent growth and mortality study plots located within the RNA (Meyers and Fredricks 1993, Fig. 2). Tree Plots were 30 m radius semi-circular viewing arenas at two levels in the forest: i) lower zone: 0 – 30 m; and ii) upper canopy-level zone: 30 m – 60 m (Fig. 3). In general, Tree Plots were located a minimum distance of 400 m from another. In each Tree Plot, a dominant or codominant tree was selected as the climbing tree with the following criteria: 1) safety, 2) a suitable viewing arena around which the observations could be conducted, and 3) within the long term monitoring plots in the RNA.

The cumulative mean number of dominant, codominant and intermediate trees per Tree Plot was 21.2 (± 1.2 SE), with the majority of these tree classes represented by *T. heterophylla* (11.7 ± 1.1 SE) and *P. menziesii* (6.1 ± 1.1 SE) (Table 3). The maximum number of dominant and codominant *P. menziesii* and *T. heterophylla* within any given plot was 17 (120 ha^{-1}) and 15 (106 ha^{-1}), respectively. The total number of trees per plot (excluding suppressed trees) ranged from 12 to 31 (85 to 219 trees ha^{-1}). Including all tree classes, the mean number of trees per plot was 42.6 (± 4.0 SE), with 17 to 89 trees per plot (approximately 120 to 630 trees ha^{-1}). *Thuja plicata* is generally rare across the plots with the exception of the southeastern portion of the RNA. Cover, based on Lemmon (1956), of the overstory canopy vegetation within the 30 m-radius plot ranged from 75% to 95%. For additional information on RNA vegetation composition, see Meyers and Fredericks (1993) and Shaw *et al.* (2004).

Table 3: Mean number of trees (± SE) per Tree Plot by species and crown class[1].

Tree Species	Dominant	Codominant	Intermediate	Suppressed	Total
Pseudotsuga menziesii	4.44 (0.76)	1.50 (0.52)	0.19 (0.10)	0.00	6.13 (1.14)
Tsuga heterophylla	4.56 (0.85)	3.06 (0.58)	4.06 (0.51)	8.88 (1.43)	20.56 (1.74)
Abies spp.	0.19 (0.10)	050 (0.20)	1.50 (0.44)	6.19 (2.75)	8.5 (2.76)
Thuja plicata	0.94 (0.94)	0.13 (0.13)	0.13 (0.09)	0.00 (0.00)	1.19 (1.12)
Taxus brevifolia	---	---	---	4.81 (1.30)	4.81 (1.30)
Cornus nuttallii	---	---	---	0.44 (0.27)	0.44 (0.27)
Snags	---	---	---	---	4.69 (1.12)
Total	10.69 (0.80)	5.63 (0.77)	5.94 (0.80)	20.38 (4.02)	42.63 (4.03)

[1] Smith *et al*. 1997

In each Tree Plot, a climbing rope was placed in the target tree to allow the canopy observer to gain access to the upper canopy approximately 30 m above the forest floor (Fig. 3). At least one day prior to data collection, trees were rigged and the perimeter of the 30-m semicircular viewing arena (ground level) was marked with flagging tape. The climbing rope was set the day before to minimize disturbing birds. On the morning of the observations, one observer ("the upper zone observer") gained access to the upper zone using single rope climbing methods (Perry 1978). The upper zone observer was located in a fixed position, perched on a "tree seat" attached to the bole of the tree, enabling the observer to conduct observations in a 180° viewing arena while seated or standing and minimizing damage to sensitive canopy resources. The upper zone observer was not expected to affect bird behavior (Nadkarni and Matelson 1989). A second observer on the forest floor ("the lower-zone observer") documented observations in the lower zone. The lower-zone observer walked around the periphery of the 30 m semicircular viewing arena to maximize detections, and the observers surveyed the zones simultaneously. Only one Tree Plot was surveyed on any given day so that observations could be conducted during the mornings when bird activity was greatest. The foraging observation sessions were typically initiated within 1 hour after dawn, and lasted three hours.

The mean height of the tree seat from where the canopy observer conducted the foraging observations and canopy-level point counts was 31.4 m (± 0.2 SE). The maximum tree seat height was 43 m, in a *P. menziesii*, and the lowest canopy observation location was 25 m, in a *T. heterophylla* (Appendix B). The overall height of the forest canopy was between 40 and 70 m. Seventy percent of the dominant and codominant trees climbed were *T. heterophylla*, the remaining trees were *P. menziesii* (25%) and one *Abies grandis* (5%).

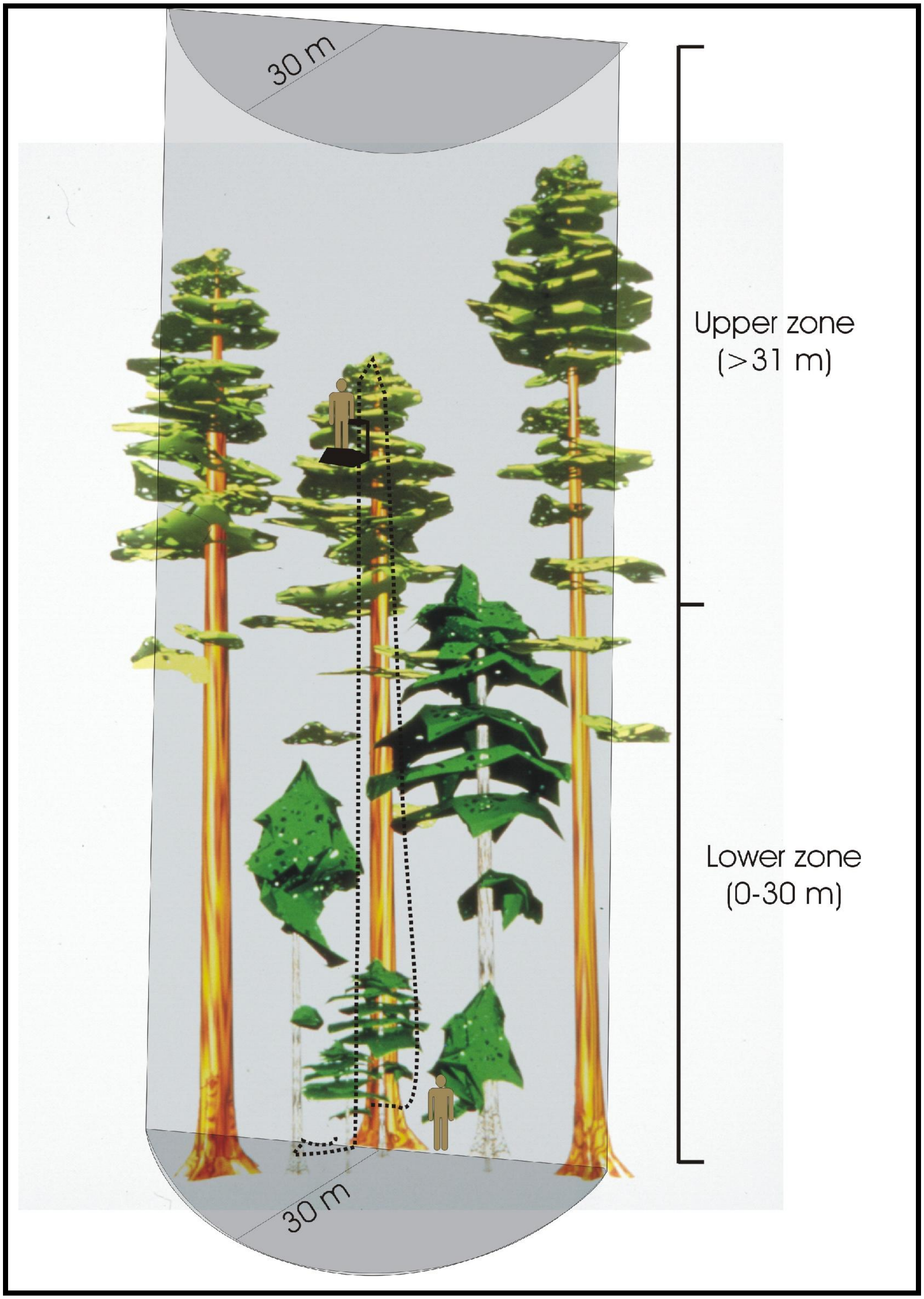

Figure 3: Conceptual Rendering of the Tree Plot Sampling Area.

Walking Transects

The Walking Transects followed an existing 4.8 km trail through the RNA (Fig. 2). Two observers conducted the Walking Transect surveys at ground level, with observers beginning foraging observations at opposite ends of the Walking Transect. Flagging tape denoted each 0.1 km interval, allowing observers to calculate distances along the transect. They recorded foraging birds opportunistically while walking along the survey route, and also paused at each 0.1 km marker for 3 min (Weikel and Hayes 1999). Individual bird activities were recorded if they occurred within 30 m of either side of the trail. To avoid collecting sequential conspecific observations in the Walking Transects, sequential records for most small passerines (e.g., Chestnut-backed Chickadee and Golden-crowned Kinglet) were only collected after moving >80 m from the prior observation; sequential foraging data for larger passerines (e.g., Hairy Woodpecker, Red Crossbill and Gray Jay) were only considered when distances between observations exceeded 200 m. The Walking Transect survey concluded when the observers met. The Walking Transects did not overlap or interfere with any of the Tree Plots (Fig. 2).

Foraging Data Collection

Individual birds were observed for the entire period they were visible within the Tree Plot viewing arena or within 30 m of either side of the Walking Transect trail. Each foraging sequence was timed and the following data were recorded: 1) foraging substrate (e.g., epiphyte versus host, see below), 2) tree species, 3) estimated bird height in the tree, 4) crown class (dominant, codominant, intermediate and suppressed, Smith *et al.* 1997), 5) horizontal crown zone (inner, mid and outer) and vertical crown zone (above, upper, mid, lower and below live crown, Lyons *et al.* 2000), 6) tree position (on what structure in the tree was the bird, e.g., bole, foliage, branch), 7) tree condition (live or dead), 8) type of foraging maneuver, 9) foraging posture, and 10) location along the transect (Walking Transect only). As a bird foraged, we noted when a bird changed substrates, tree species, foraging behaviors, or foraging height. Therefore, any change was considered a sequential foraging sequence, and multiple foraging sequences were recorded for the same individual. Foraging behaviors (postures and maneuvers) followed Remsen and Robinson (1990). Foraging postures included hang, hang upside-down, hop, lean into, perch, reach under, reach up, sally, and short flights. Foraging maneuvers included glean, hammer, peck, pluck, probe, and search.

Epiphytes were defined as bryophytes and lichens growing directly on the surface of living trees and shrubs or dead stumps or logs. Epiphyte categories (following McCune 1993) to classify epiphyte foraging substrate included: 1) alectorioid lichen (e.g., *Alectoria* spp., *Bryoria* spp. *Usnea* spp.), 2) fruticose lichen (other than alectorioid lichen, e.g., *Ramalina* spp.), 3) foliose lichen (other than *Lobaria* spp., e.g., *Platismatia* spp.), 4) other lichen (e.g., *Cladonia* spp.), 5) bark lichen (i.e. crustose lichens, e.g., *Physcia* spp.) , 6) cyanolichen (e.g., *Lobaria* spp.), 7) pendant bryophytes (e.g., *Isothecium myosuroides* Brid. and *Antitrichia curtipendula* (Hedw.) Brid.), 8) cushion mosses (e.g., *Dicranum fuscescens* Turn.), and 9) prostrate mosses (e.g., *Rhytidiadelphus loreus* (Hedw.) Warnst.)). The categorical variable "bark lichen" included: finely appressed crustose lichens; *Sphaerophorus globosus* (Huds.) Vain.; thin, strongly appressed strands of corticolous bryophytes, (e.g., *Hypnum circinale* Hook); and other associated corticolous lichen forms (e.g., *Cladonia* spp.). Closely appressed, corticolous, alectorioid lichens were considered unique features of the bole, and dissimilar from the pendant forms common in the outer canopy. Saxicolous species growing on logs and dead wood were considered epiphytic. Epiphytic categories were pooled into groups (McCune 1997) for data analysis: 1) alectorioid lichens, 2) cyanolichens and other lichens, 3) bryophytes, and 4) lichen/bryophyte admixture.

Non-epiphytic substrates included biotic substrates provided by the host (phorophyte) including bark, branchlets, wood, live foliage, flower, and cone. Phorophyte resources also included woody debris (large horizontal boles and associated limbs), components on the forest floor that characterize old-growth stands. The dead woody debris supports epiphytes for decades (Harmon *et al*. 1986). Although mistletoe brooms were considered a unique substrate exploitable by birds, their general use was likely underestimated. For instance, if a bird gleaned a prey item from *Lobaria* spp. located on a mistletoe broom formation, the recorded substrate was foliose lichen, and not the latter "mistletoe broom". Since many epiphyte substrates are sympatric with mistletoe brooms, the use of mistletoe broom as a contributing factor was probably underestimated. Non-epiphytic/phorophytic resources included abiotic substrates such as air and ground, and biotic substrates terrestrial herbs and mosses.

Foraging bouts were defined as any bird maneuvers or activities spent searching for, procuring and/or handling food (Post and Götmark 2006). The only exception to this definition of bout was for members of the aerial insectivore foraging guild (e.g., Tyrannidae) where only food removal from a given substrate was considered a foraging bout: determination of a specific foraging substrate inspected by flycatchers from a perch site could not be determined. A trial period was conducted to train and minimize variation between individual observers. A laser range finder was used to ensure that ocular height estimates were reliable and within 10% of true height. The major difference between Walking Transects and Tree Plots data collection protocols was that multiple observations of conspecific foraging individuals (to ensure observations were independent) could be avoided in the Walking Transects but not in the Tree Plots.

Observations were recorded using digital voice recorders and transcribed to an MS Access Database from tape playback in real time. The original voice-recorded observation data were archived in digital files.

Resource Availability

Bird selection and proportional use of epiphytic and host tree resources were analyzed by comparing epiphytic and host tree attributes with resource and tree species availability. Quantifying epiphyte availability is important because most surfaces in old-growth forests are covered by epiphytes. Therefore, bird use of epiphytes may reflect opportunism rather than specialization (Sillett 1994). Relative availability of intra-epiphytic groups was determined from biomass estimates derived from vertical transects in a 2.3 ha plot located within the southwestern portion of the RNA study area (McCune 1993, McCune *et al*. 1997, Harmon *et al*. 2004). The 2.3 ha plot comprises the Wind River Canopy Crane Research Facility (Franklin and DeBell 1988, Shaw *et al*. 2004). Although bryophyte biomass data were lacking in the 2.3 ha plot (McCune *et al*. 1997), Harmon *et al*. (2004) estimated bryophyte biomass to be equivalent to cumulative lichen biomass, because bryophytes and lichen were equally abundant. The relative proportion of each epiphyte group was calculated by dividing the biomass estimate of each group by the total (Table 4). For instance, alectorioid lichen biomass was 934 kg ha^{-1} or 14% of the total combined epiphyte group biomass. Cyanolichen & other lichen comprised 36% of total epiphyte biomass, and bryophytes comprised 50% (Table 4).

Table 4: Estimated biomass, relative proportion and ratio of epiphyte groups (source: McCune 1997 unless otherwise specified).

Epiphyte group	**Estimate kg ha^{-1}**	**Relative Proportion**
Alectorioid lichens	934	0.14
Cyanolichens and Other lichens	2382	0.36
Bryophytes* (2x lichen biomass)	3316	0.50
Total	**6632**	**1.00**
* Harmon et al. (2004)		

Estimated stores of carbon associated with live biomass as measured by Harmon *et al.* (2004) were used to calculate relative resource availability for stem bark, live and dead branches, foliage, understory vegetation, and total epiphytes (Table 5). The relative proportion of each major resource pool was calculated by dividing the biomass estimate of each respective available resource pool by the total resource pool carbon store (9,405 g C m^{-2}). For instance, foliage biomass was 941 g C m^{-1} or 10% of the total available resource pool. Following, total epiphyte biomass was 100 g C m^{-2} or 1% of the total available resource pool.

Table 5: Estimated stores of carbon from the Canopy Crane Plot (Harmon *et al.* 2004).

Major Resource Pool	**Store (g C m^{-2})**	**Relative Proportion**
Stem bark	3,337	0.35
Branches (live and dead)	4,807	0.51
Tree foliage	941	0.10
Understory shrubs and herbs	220	0.02
Epiphytes	100	0.01
Total	**9,405**	**1.00**

I used tree data from permanent monitoring plots in the TT Munger RNA (Meyers and Fredricks 1993) to calculate relative availability of individual tree species, and compare against the observed frequency of tree selection by birds. The data from each of the 20 respective Tree Plots and all permanent monitoring plots located within 400 m of the Walking Transect were averaged to calculate relative tree availability for five trees in the pooled analysis (Table 6). The category "Others" included *T. brevifolia*, *Cornus nuttallii* and vertical snags. Understory shrubs, herbs and logs were not included in the analysis. For the comparison between survey sampling procedures (Tree Plots versus Walking Transect), relative tree availability were calculated separately.

Table 6: Relative availability of tree species (Data were provided by the Permanent Study Plot program, a partnership between the H. J. Andrews Long-Term Ecological Research program and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, OR.).

Tree species	**No. Trees**	**Relative Proportion**
Pseudotsuga menziesii	66	0.17
Tsuga heterophylla	227	0.57
Abies spp.	57	0.14
Thuja plicata	12	0.03
Others	35	0.09
Total	**9,405**	**1.00**

Point Counts

Although point counts may result in an upward bias of density estimates (Buckland 2006), extensive point counts are an efficient and data rich census method for bird populations in forested and difficult terrain (Ralph *et al*. 1993). Standard 10-minute variable circular plot (VCP) point counts (Reynolds *et al*. 1980, Ralph and Michael 1981) provided an estimate of numbers of species and individuals present. One point count station was established in each of the Tree Plots and each station was located a minimum of 400 m apart and was visited once, for a total of 20 sites. Point counts began after a five-minute quiet period after the canopy-level observer climbed the tree and assumed his position on the tree seat. The two observers (upper canopy-level observer and ground-level observer) conducted the point counts simultaneously. Because of logistic constraints, the point counts at the canopy-level were performed by one person. Similarly, all ground-level point counts were performed by another individual observer. Observers participated in a week-long trial period to train and minimize variation between individual observers, and a laser range finder was used to ensure that distance estimates were reliable. The abilities of observers to identify birds by both sight and sound and estimate horizontal distances were tested.

All birds detected during the counts were recorded, and the distance from the observer to each individual detected was estimated to the nearest meter. Distances were collected to assess differences in counts recorded in three distance bands: 30 m, 75 m, and unlimited plots. No attempt was made to calculate individual species densities because only one point was sampled each day (Buckland 1993, Bibby *et al*. 1992). Rather, detection differences in relative abundances and species richness were assessed among the three distance bands between observers. Birds were identified by sight and vocalization. The location of the “first” detection of an individual was recorded, even if the individual moved closer during the count. For the point counts, coarse scale habitat variables such as tree species availability were assessed using methods of Ralph *et al.* (1993). Canopy cover was calculated from the ground-level with a spherical convex densiometer (Lemmon 1956): nine samples were taken within the 30 m-radius plots. Point counts were conducted between 07:00 and 09:00, and all bird species were recorded to generate a master species list (Appendix C).

Statistical Analysis

Sequential foraging data were collected for each individual bird observed until the individual disappeared from sight. However, data analyses were performed for only the first foraging bout and/or searching activity, to avoid problems with independence (Hejl *et al.* 1990). Nine foraging guild categories were defined by substrate exploited, following Manuwal (1991): 1) aerial insectivores (AI), 2) bark insectivores (BI), 3) aerial predators (H), 4) low understory herbivore/insectivores (LUHI), 5) nectarivores (N), 6) omnivore scavengers (OS), 7) timber-foliage insectivores (TFI), 8) timber-foliage insectivore/omnivores (TFIO), and 9) timber seed eaters (TS). The H and TFIO foraging guilds, and one TS member (Band-tailed Pigeon) were excluded from the statistical analyses.

Foraging bouts for each species and/or foraging guild were quantified as a percentage of the total foraging bouts (frequency). Frequency distributions and descriptive statistics were computed to assess:

1. Number of species and foraging guilds that used epiphyte groups,
2. Frequency of substrate used by species, foraging guilds and all observations,
3. Proportion of total foraging bouts that involved epiphyte resources, relative to phorophyte resources, by tree species, tree class, horizontal and vertical crown zone, bird position in the tree, foraging height, foraging posture, foraging behavior, and tree status.

All Tree Plot and Walking Transect data were pooled for an overall analysis, but were also analyzed separately, to compare survey procedures.

Resource Availability and Use: The log-likelihood ratio test (G-test for independence with the William's correction factor) was used to compare substrate selection and substrate availability among epiphyte and phorophyte substrates (Sokal and Rohlf 1995). The G-test was also used to determine whether species use of epiphytic groups and tree species were in proportion to their availability. Proportional use of epiphyte and host resources, relative to availability, was compared among survey procedure for five common species (e.g., Brown Creeper, Chestnut-backed Chickadee, Hairy Woodpecker, Gray Jay, and Red-breasted Nuthatch). In addition to a pooled analysis for the five species, I used log-likelihood ratio tests for each of the five species for a comparison between survey procedures. Expected frequencies were based on hypotheses extrinsic to the data (McCune *et al.*1997 for epiphytic group availability, and Harmon *et al*. 2004 for tree species). The following rule for the G-stat test was employed: no expected frequency should be less than 5.0. For expected frequencies less than 5.0, classes were pooled. Data analysis was performed using Microsoft Access and Excel (Keller 2001).

Epiphyte Specialization: Epiphyte users were considered specialists (species whose foraging activities involved epiphytic resources >75% of their total foraging bouts), regulars users (between 25 - 75 %), or occasional users/generalists (less than 25%) (Remsen and Parker 1984). Only species with a minimum sample size ≥ 10 total foraging bouts were assigned a degree of specialization (Remsen and Parker 1984).

Community Structure: Nonmetric multidimensional scaling (NMS) was performed to graphically represent the differences (and similarities) in epiphyte-related foraging strategies and extract meaningful gradients about the community structure of foraging guilds and species. NMS is an ordination procedure that provides insight into a high-dimensional space by seeking and displaying the strongest structure. NMS uses ranked distances (similarities and dissimilarities) to summarize the relationship among samples (McCune and Grace 2002). The NMS of the pooled Tree Plot and Walking Transect epiphyte foraging data was a niche-space analysis of guilds/species (objects) and the epiphyte resources they used (attributes). The distances between the points on the ordination approximate dissimilarity in foraging strategies and foraging locations, and thus provide a visual tool for examining the multiple interrelated foraging location and behavior factors, and insight into interactions among species and guilds. Two categorical foraging behaviors (foraging posture, foraging maneuver), seven environmental attributes (crown class, vertical and horizontal crown position, tree species, tree condition, substrate and tree position) and one quantitative variable (bird height) compared among guild and species use of epiphyte resources. The TFIO foraging guild and 16 outliers were excluded from the NMS analysis, due to insufficient sample sizes, and results of an outlier analysis. With the exception of the quantitative variable foraging height, all raw categorical data were ordinated for the NMS. Monte Carlo procedures (randomization tests) were conducted to assess whether the amount of variation described by the different axes was more or less than expected by chance. The

Sørensen (Bray and Curtis) similarity measure was used for calculating the similarity matrix. Random starting configurations were used for the 'autopilot (slow and thorough)' mode, 3-D solution of 250 runs with real data and random data, with 500 iterations. Stability was examined by analyzing a plot of stress versus iteration (stress value in relation to dimensionality). Stress is defined as a measure of lack of fit, or departure from monotonicity in the relationship between the dissimilarity of the original matrix and the new 3-D configuration/solution (McCune and Grace 2002). Correlation coefficients enabled a comparison of sample positions on the ordination with guild foraging strategies, and foraging location variables. The correlation coefficients express linear (Pearson's *r*) and rank (Kendall's Tau) relationships between the ordination scores and foraging height.

I used Multi-Response Permutation Procedures (MRPP) to test the null hypothesis of no difference between groups (e.g., foraging guilds in the Tree Plots and Walking Transects). MRPP is an analysis of similarity and does not require distributional assumptions (Mielke 1984, Mielke and Berry 2001). The MRPP analysis measured how similar foraging strategies were within a group, compared to similarities among groups. Among-group dissimilarity and within-group similarity occurs when groups chance-corrected within-group agreement values (A values) exceed 0.1. Among-group similarity is evident with groups whose A values are <0.1, which indicates broad overlapping, and among-group similarity. MRPPs were conducted on all pooled epiphyte foraging events using: 1) the four epiphyte functional group categorical variables (alectorioids, bryophytes, and cyanolichens & other lichens, and lichen/bryophyte admixture, hereafter referred to as "epiphyte functional groups"), and 2) eight finer scale categorical variables denoting specific epiphyte substrates (alectorioid lichen, foliose lichen, fruticose lichen, fruticose and foliose lichen, pendant bryophyte, appressed bryophyte, other lichen, and bryophyte and lichen; hereafter referred to as "finer scale epiphyte substrates"). I ran MRPP pairwise comparisons on the finer scale epiphyte substrate variables to measure differences within and among foraging behaviors and environmental attributes (e.g., pendant vs. appressed bryophyte). NMS and MRPP were performed with PC-ORD, version 5 (MjM Software Design, Gleneden Beach, Oregon, Kruskal 1964a, 1964b, Mather 1976).

Point Counts: I performed Paired Student t-tests ($\propto = 0.05$) to compare detection frequencies, species richness and relative abundance between observer location, and among distance bands: 30 m, 75 m, and unlimited, and a two-factor analysis of variance (ANOVA) with replication to compare detection frequencies and relative abundance between point count stations among distance bands and between observers for nine core species (e.g., Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, Gray Jay, Hermit Thrush, Hermit Warbler, Pacific-slope Flycatcher, Red-breasted Nuthatch and Winter Wren). I used the Wilcoxon Rank Sum test to compare the rank order of species relative abundance in the unlimited-radius plots between canopy- and ground-level observers, and the Wilcoxon Signed Rank Sum test to compare the rank order of species abundances in my 75 m radius plots with mesic old-growth forest bird abundances in Manuwal (1991). The Student t-tests, ANOVA and Rank Sum tests were performed with Excel. Because there is a dependence in counts based on subsequent increases of distance bands from a common point (i.e., the samples are not independent), the significance of the ANOVA and t-test may be liberal (Thompson and Schwalbach 1995).

Shannon's species diversity indices were generated with PC-ORD, version 5 (MjM Software Design, Gleneden Beach, Oregon, Kruskal 1964a, 1964b, Mather 1976). Although no attempt was made to calculate relative species densities or detection probabilities (Reynolds *et al.* 1980, Buckland *et al.* 1993), I compared the relative distribution of detection distances between observers for the nine core species. Calculations of densities would be imprudent because my point count methodology violated an important assumption of density measures: a multi-point count station survey assumes that bird detections in each plot are independent and the same birds are not recounted from station to station. However, since only one survey per day was conducted, birds could perceivably move from one station to another (despite a minimum distance of 400 m from each other), resulting in both population and density overestimates.

CHAPTER 4

RESULTS

This chapter is divided into five sections. In Section 1, I summarize results of the foraging observations and address whether any species are epiphyte specialists. Sections 2 through 4 report the results of spatial and substrate specialization (Section 2), use of resources in relation to availability (Section 3), and community structure and composition (Section 4). In Section 5, I compare the two sampling procedures (Subsection 1) and results of the simultaneous canopy- and ground-level variable circular plot point counts (Subsection 2).

Section 1

Bird Use of Epiphytes

A total of 71 bird species, representing 30 families, were detected during the surveys (Appendix C). Five families were well represented: the Tyrannidae (5 species), Parullidae (5 species), Hirundinidae (6 species), Emberizidae (7 species), and Fringillidae (6 species). Cumulatively for both sampling procedures (Walking Transects and Tree Plots), foraging data for 735 individuals were captured, representing 2,902 sequences from 29 species, 20 families and 9 foraging guilds. The majority of foraging data (85%) were contributed by 8 species (Table 7). The Chestnut-backed Chickadee was the most frequently detected species, followed by Gray Jay, Winter Wren, Red-breasted Nuthatch, Brown Creeper, Pacific-slope Flycatcher, Red Crossbill, and Dark-eyed Junco. Of the 735 bird observations from 29 species, 722 foraging bouts from 22 species were used for assessing relative resource use (Table 7).

Of all 722 foraging observations, 28.7% (207) involved epiphyte substrates (Table 8). Bryophytes were the most frequently used epiphyte group (44% of all epiphyte foraging bouts), followed by "cyanolichens and other lichens" (41%), and alectorioid lichens (13%). Pendant bryophytes were the most common finer-scale epiphyte substrate used, followed by foliose lichen, then appressed bryophytes. Approximately 20% of all bouts on bryophytes involved the cattail moss, *Isothecium myosuroides*. Foliose lichens were the most frequently exploited lichen substrate, accounting for over half of the bouts (48 of 85 records) on all lichen substrates. Foraging bouts on alectorioid lichens exclusively comprised less than 4% of all observations, although an additional 11 foraging bouts involved an admixture of alectorioid lichens and bryophyte/other lichens. More than 60% of the total bouts occurred on resources provided by the host (Table 8); live foliage comprised most of the phorophyte records (183 of 468 records or 25%); bark substrates were used in 23% of all observations.

Table 7: Total species observation time (s), number of foraging observations (n, number of individuals) and sequences (Tree Plot and Walking Transect data pooled).

English Name	Foraging Guild[1]	Time	n	seq.
Band-tailed Pigeon*	TS	2	1	1
Barred Owl*	H	250	2	2
Black-headed Grosbeak*	TFIO	3	1	1
Brown Creeper	BI	1416	51	186
Chestnut-backed Chickadee	TFI	4412	167	574
Common Nighthawk*	AI	2	1	1
Dark-eyed Junco	LUHI	1310	22	137
Golden-crowned Kinglet	TFI	529	21	86
Gray Jay	OS	4774	108	427
Hairy Woodpecker	BI	3378	43	254
Hammond's Flycatcher	AI	17	3	4
Hermit Thrush	LUHI	798	18	83
Hermit Warbler	TFI	50	2	10
Northern Flicker	BI	45	1	1
Northern Pygmy-Owl*	H	117	1	5
Pacific-slope Flycatcher	AI	1181	46	114
Pileated Woodpecker	BI	69	2	9
Pine Siskin	TS	16	2	2
Red Crossbill	TS	1473	43	64
Red-breasted Nuthatch	BI	2825	60	317
Red-breasted Sapsucker	BI	42	1	8
Rufous Hummingbird	N	380	21	37
Steller’s Jay	OS	601	7	49
Turkey Vulture*	H	40	1	1
Varied Thrush	LUHI	24	2	4
Vaux’s Swift*	AI	85	5	7
Western Tanager	TFI	167	3	16
Wilson’s Warbler	LUHI	1	1	1
Winter Wren	LUHI	5146	99	501
	TOTAL	29153	735	2902

[1] Foraging guild codes: AI = aerial insectivore, BI = bark insectivore, LUHI= low-understory herbivore/insectivore, N = nectarivore, OS = omnivore scavenger, TS = timber seed-eater, TFI = timber foliage insectivore, TFIO = timber foliage insectivore/omnivore, H = aerial predator (catch non-insectivorous prey); * excluded from statistical analysis

When Tree Plot and Walking Transect data were pooled, four foraging guilds comprised 83% of the foraging data, namely low-understory herbivore/insectivores (LUHI), bark insectivores (BI), timber foliage insectivores (TFI), and omnivore-scavenger (OS) foraging guilds (Table 7, Figs. 4 and 5). All seven foraging guilds used epiphytes. BI used lichen and bryophyte substrates more frequently than any of the other foraging guilds, accounting for 37% of the foraging guild's records. BI used pendant bryophytes and foliose lichen substrates more often than other epiphytic substrates, although alectorioid lichens and appressed bryophytes located on the tree boles were also important foraging substrates. Epiphytic resources were also important foraging locations for OS (35% of their foraging bouts) and LUHI (32%, Fig. 4). OS used pendant bryophytes, foliose lichens and alectorioid lichens in almost equal proportions (Fig. 5). Observations comprising the OS foraging guild reflected foraging bouts weighed heavily by the corvid, Gray Jay (45 of 48, 94%); the other sympatric corvid, Steller's Jay, comprised the remaining OS foraging bouts (Table 7). Appressed and pendant bryophytes accounted for over 75% of the foraging bouts of epiphytic substrates by LUHI (Fig. 5). Observations of Winter Wren comprised 68% of the sample data to the LUHI foraging guild, followed by Dark-eyed Junco (Table 8). TFI foraged primarily amongst live foliage, although 27% of their foraging bouts involved epiphytic resources. A third of all TFI epiphyte-related foraging bouts occurred on foliose lichen, and more than 15% of their bouts occurred on pendant bryophytes, fruticose and alectorioid lichens (Fig. 5). Nectarivores (N), aerial insectivores (AI), and timber-seed eaters (TS) used epiphytes less frequently than the other foraging guilds; approximately 10% of N, AI and TS foraging bouts occurred on epiphytes.

Fourteen species of birds used epiphyte substrates whereas phorophyte resources provided foraging substrates for an additional seven species (21 species). All fourteen bird species used lichen substrates when all lichen substrates were pooled (e.g., alectorioid, cyanolichen and other lichens), whereas three fewer species used bryophytes. Although 11 species used bryophytes, four species accounted for 79% of these data: Winter Wren (33 records), Brown Creeper (13 records), Chestnut-backed Chickadee (13 records), and Gray Jay (14 records). Fewer bird species used alectorioid lichens than the other epiphyte groups, and 77% of the foraging bouts on alectorioid lichens were done by three species: Gray Jay, Chestnut-backed Chickadee, and Brown Creeper.

Chestnut-backed Chickadees and Red-breasted Nuthatches comprised approximately 50% of the "cyanolichen and other lichens" foraging records. The 18 records involving an "admixture of foliose and fruticose lichen" included activities by seven bird species on dense, tangled mixtures of both epiphyte forms. Of the 18 "admixture of foliose and fruticose lichen" records, seven records were bouts by Chestnut-backed Chickadee: six of the seven records were alectorioid lichen twisted around foliose forms (*Lobaria* spp. and *Platismatia* spp.). Four of the 18 records involved mistletoe broom formations on *T. heterophylla*. A Pacific-slope Flycatcher, two Chestnut-backed Chickadees and one Hairy Woodpecker used an admixture of "lichen/bryophyte". Only a small proportion of the records (8 bouts) involved exclusive use of *T. heterophylla* mistletoe brooms.

Table 8: Number of species, foraging guilds, and individuals (% of all substrates) that used epiphyte, phorophyte and other substrates (Tree Plot and Walking Transect data pooled).

Substrate		**No. species**	**No. guilds**	**No. individuals**
Epiphyte	Alectorioid lichen	8	6	26
	Cyanolichen and other lichen			
	Foliose lichen	9	5	48
	Fruticose lichen	2	2	5
	Other lichen	8	5	14
	Admixture (fruticose & foliose)	7	7	18
	All cyanolichen and other lichen	**12**	**6**	**85**
	Bryophytes			
	Pendant bryophyte	10	6	53
	Appressed bryophyte	7	3	39
	All bryophytes	**11**	**6**	**92**
	Admixture (lichen & bryophyte)	3	3	4
	Epiphyte Total	**14**	**7**	**207 (28.7%)**
Phorophyte	Foliage (live and dead foliage)	18	7	183
	Bark	17	7	166
	Dead wood (includes rootwads)	11	6	73
	Cone	1	1	30
	Other (flower)	1	1	8
	Mistletoe brooms	3	3	8
	Phorophyte Total	**21**	**7**	**468 (64.8%)**
Other	Air	5	4	16
	Perched litter	4	4	4
	Ground	4	2	16
	Terrestrial herbs/mosses	4	2	10
	Other	1	1	1
	Other Total	**10**	**7**	**47 (6.5%)**
All Substrates Total		**22**	**7**	**722 (100.0%)**

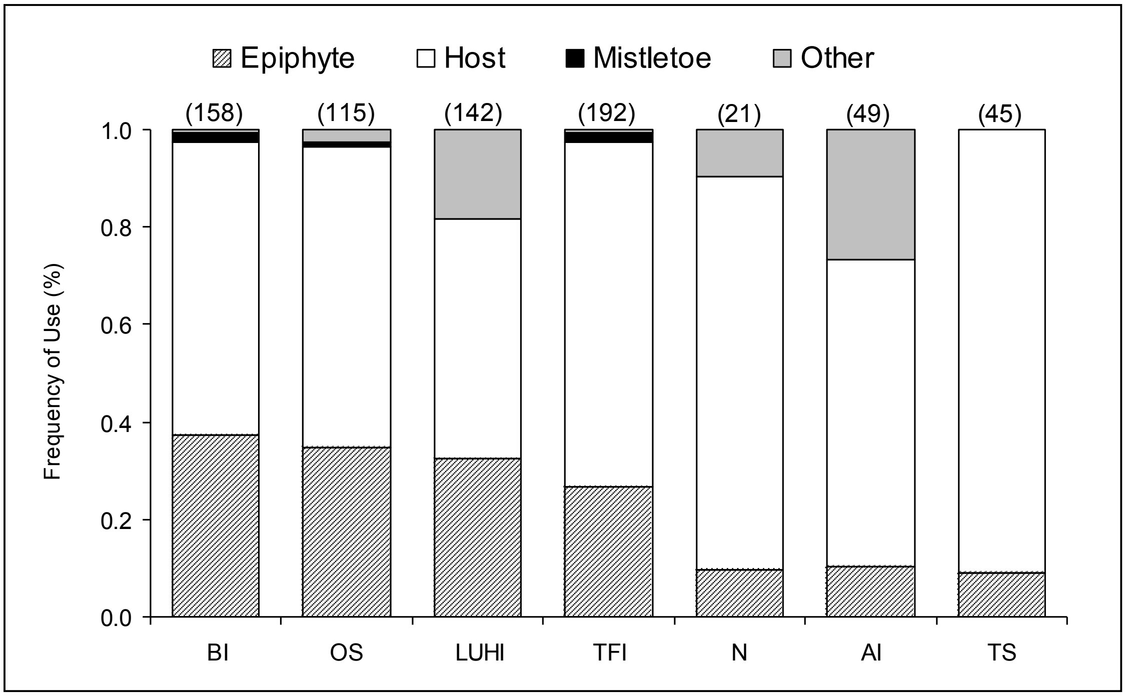

Figure 4: Major resource allocation for seven avian foraging guilds (*n* = total number of foraging bouts); Tree Plot and Walking Transect data pooled; foraging guild codes: AI = aerial insectivores, BI = bark insectivores, LUHI= low-understory herbivore/insectivores, N = nectarivores, OS = omnivore scavengers, TFI = timber foliage insectivores, TS = timber seed-eaters).

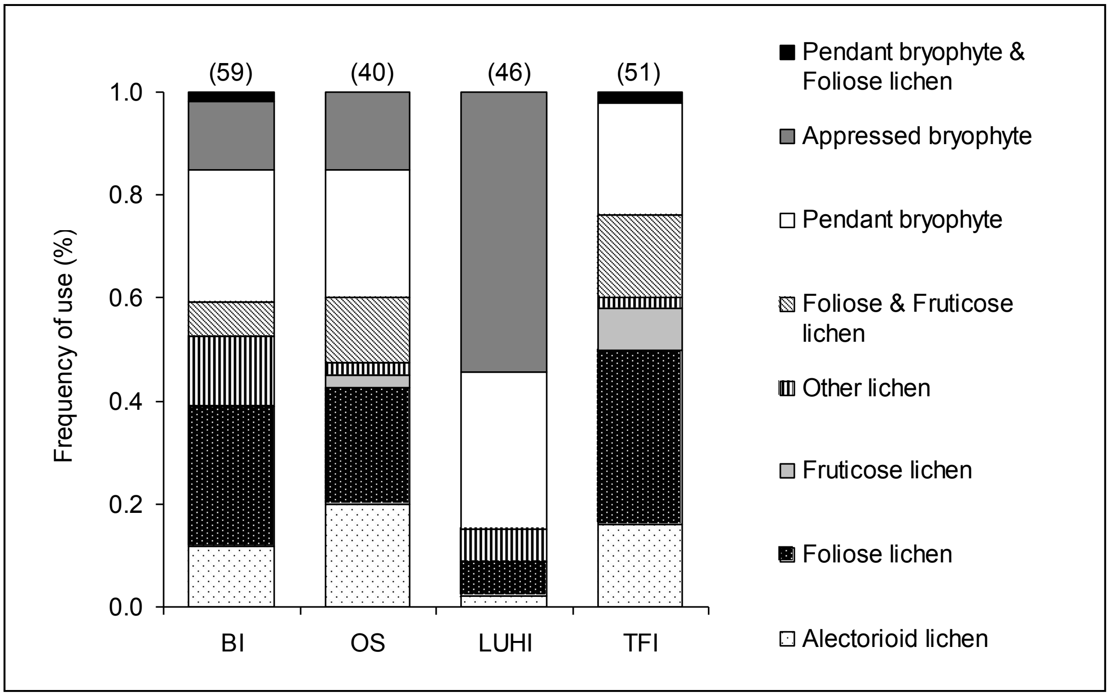

Figure 5: Epiphytic group allocation for four avian foraging guilds (*n* = total number of foraging bouts, Tree Plot and Walking Transect data pooled; foraging guild codes: BI = bark insectivores, LUHI= low-understory herbivore/insectivores, OS = omnivore scavengers, TFI = timber foliage insectivores).

Epiphyte Specialization

No species or foraging guild was an epiphyte specialist. Seven species were regular users of epiphytes, and five species were occasional users/generalists (Table 9). The BI, Brown Creeper, used epiphyte substrates during 53% its foraging bouts, more frequently than the other regular users of epiphytes. The LUHI, Winter Wren, used epiphytes during 47% if it's foraging bouts, and approximately one third of all foraging bouts by Red-breasted Nuthatch, Gray Jay and Chestnut-backed Chickadee involved epiphytes.

Alectorioid lichens were used by four regular epiphyte users (Brown Creeper, Gray Jay, Chestnut-backed Chickadee, and Red-breasted Nuthatch) and three occasional users (Dark-eyed Junco, Red Crossbill, and Rufous Hummingbird), although less than 10% of their bouts involved the pendant fruticose lichen. Five of the 12 regular and occasional users did not use alectorioid lichens as a foraging substrate. Brown Creepers and Gray Jays used alectorioid lichens slightly more often, relative to the other 12 species.

Three regular epiphyte users (Brown Creeper, Hermit Thrush and Winter Wren) used bryophyte substrates during more than 20% of their foraging bouts, which accounted for the lower mean height of their epiphyte-related foraging activities, relative to the other regular users. Although Gray Jay and Hairy Woodpecker used bryophytes during more than 10% of their bouts, both species also foraged in the upper canopy (e.g., at 60 m). Bryophytes were used by all occasional users except Golden-crowned Kinglet and Red Crossbill. Cyanolichens and other lichens were used more frequently by Red-breasted Nuthatch, Brown Creeper and Chestnut-backed Chickadee, although all regular users used these groups of epiphytic lichens. The Rufous Hummingbird did not use cyanolichens and other lichens as a foraging substrate, but searched alectorioid lichens more frequently than the other occasional users.

In general, the foraging behaviors used most frequently by regular users of epiphytes were hanging, perching, and hopping while searching, and glean or pecking food items (see Section 2 for an analysis of foraging behaviors of all observations). Members of the BI foraging guild (e.g., Brown Creeper and Hairy Woodpecker) used epiphytes primarily by hanging vertically or upside-down while probing, hammering/pecking or inspecting cyanolichen and other lichen (primarily bark lichen and prostrate mosses on the bole, e.g., *Hypnum* spp.). Red-breasted Nuthatches foraged slightly higher in the canopy than Chestnut-backed Chickadee when using epiphytic substrates, relative to host resources, and both species used "cyanolichen and other lichen" substrates regularly. Chestnut-backed Chickadees foraged with hops and short flights across splays of foliage and branchlets to pause momentarily, hang and glean food items from both phorophyte and epiphyte substrates. Gray Jays used bryophytes and cyanolichen and other lichens in equal proportions, and used a variety of postures: searching while perched, hanging vertically, reaching under, or hanging upside-down. Gray Jays obtained food items from epiphytes with gleaning, pecking/probing, pulling and hammering maneuvers. The hover-glean activities of the Pacific-slope Flycatcher occurred below and in the lower canopy, at mean heights of 14 m (host resources) and 15 m (bark lichen on the bole, and pendant bryophytes on dead branches). Comparatively, the 12 Pacific-slope Flycatcher aerial sallies and sorties (where flying insects were captured on the wing) took place at a mean height of 16 m.

Discussion

Differences in foraging strategies reflect the restrictions imposed upon the foraging bird by foraging substrates as well as the morphological characteristics of the birds themselves (Robinson and Holmes 1982). Similarly, the foraging strategies required to exploit epiphytes are restricted by the physiological constraints of the respective epiphyte substrates, which has been shown in tropical forests (Sillett 1994). In addition, the vertical zones (heights) of epiphyte foraging substrates reflect the vertical stratification of epiphyte communities (McCune *et al.* 2007), which could influence the vertical distribution of bird communities in coniferous forests (Shaw 2004, Shaw *et al.* 2002). The species and foraging guilds documented during the Tree Plots and Walking Transects are congruent with species abundance reported for the area (Shaw *et al.* 2002). Not all bird species and foraging guilds used epiphytes in similar proportions or with similar foraging strategies.

Although I found no specific epiphyte group specialists, all epiphytic lichens and bryophytes were used as foraging substrates. How the presence or absence of the epiphyte groups influences the foraging strategies of the bird communities cannot be ascertained with these data. However, epiphytic lichens have been positively correlated with increased avian species richness in boreal forests (Pettersson *et al.* 1995, Uliczka 1999). Similarly, experimental manipulation has shown that the complete removal of epiphytes in a tropical forest negatively influenced some bird communities (Cruz-Angon *et al.* 2008). Further research is needed to determine whether or how alteration of temperate coniferous forest epiphytes would influence avian communities or foraging strategies.

Table 9: Percent total foraging, postures, maneuvers and foraging height (m) of 12 bird species searching epiphyte functional groups, relative to all foraging bouts, Tree Plots and Walking Transects data pooled.

English Name (n, total observations)	Alectorioid Lichens	Cyanolichens and Other Lichens	Bryophytes	Epiphyte Foraging Posture[1]	Epiphyte Foraging Maneuver[2]	Epiphyte Foraging Height (mean, range)	Foraging Height of Non-Epiphytes (mean, range)
REGULAR USERS							
Brown Creeper (51)	7.8	19.6	25.5	HA, HG/PE	S, PK, PR, GL, PL	11.6 (1-32)	16.4 (1-41)
Chestnut backed Chickadee (167)	4.8	18.0	7.8	HA, PE, HP, HG, LE, SF,HO	S, GL, PK, PR, PL	23.1 (1.5-55)	19.7 (0.5-55)
Gray Jay (108)	7.4	13.0	13.0	PE, HA, RU LE/HG/RU	S, PK/GL, PR, PL, HA	21.5 (2-50)	26.3 (0-60)
Hairy Woodpecker (43)	0	9.5	19.0	HA, PE, HG	HA, PK, S	16.6 (1.5-40)	21.8 (2-60)
Hermit Thrush (18)	0	5.6	22.2	PE, LE, AM	S, PK	1.3 (0-2)	2.5 (0.5-5)
Red-breasted Nuthatch (60)	3.3	23.3	3.3	HA, PE, HG, HP	S, PK, PR, HA	34.2 (3-60)	34.3 (11-60)
Winter Wren (99)	0	14.1	33.3	HP, PE, HA/SD, RP, LE, AM, HO	PK, S, GL, PR	1.4 (0-8)	1.1 (0-10)
OCCASIONAL USERS/GENERALISTS							
Golden crowned Kinglet (21)	0	9.5	0	PE	S	12.0 (6-18)	17.9 (6-36)
Dark-eyed Junco (22)	4.5	4.5	9.1	LE/PE/RU/SD	PK, GL/S	11.2 (0.75-23)	1.3 (0-5)
Pacific-slope Flycatcher (46)	0	6.5	6.5	HO, PE	GL, S	15.2 (6-27)	14 (0-40)
Red Crossbill (43)	2.3	7.0	0	PE	S, PK/PR	45 (45-50)	43.9 (27-60)
Rufous Hummingbird (21)	4.8	0	4.8	HO	S	11.8 (5.5-18)	5.6 (0.5-40)

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[1] Postures: HA = hang, PE = perch, HG = hang upside-down, HP = hop, RU = reach under, LE = lean into, RP = reach up, SF = short flight (within substrate), SD = stand, AM = walk/run on ground, HO = hover; [2]Maneuvers: S = search, PR = probe, HA = hammer, PK = peck, GL = glean, PL = pluck; foraging postures and maneuvers listed in order of importance. Regular epiphyte users were those species whose foraging activities involved epiphytic resources between 25 - 75 % of their total foraging bouts, and occasional users/generalists (less than 25%) (Remsen and Parker 1984).

Section 2

Spatial and Substrate Specialization

More than 30% and 50% of all bryophyte and lichen foraging bouts, respectively, occurred on *T. heterophylla*. Approximately 80% of all foraging bouts on lichens occurred on *P. menziesii* and *T. heterophylla*, and 62% of the bouts on these two tree species were birds using foliose lichen, or an admixture of foliose and fruticose lichen (Table 10). *Thuja plicata* was rarely used during bouts on epiphytes (Tables 10 and 11). See Section 3 for an analysis of tree species use, relative to tree species availability.

Birds used all tree classes, and foraged throughout the vertical and horizontal crowns of both live and dead trees during foraging bouts on epiphyte substrates (Table 12). Dominant and suppressed trees comprised over 70% of all epiphytes foraging bouts, with 43% occurring in the inner portion of the live crown and 63% occurring in the mid and lower vertical crown. In general, the proportional use of tree classes during foraging bouts on epiphytes reflected the proportions found for host substrates, with one exception: intermediate trees were selected slightly more frequently during foraging bouts on host resources, attributed to foraging bouts on foliage (21%) and conifer seed cones (31%). Overall epiphyte use was more frequent in the inner- and mid-portion of the horizontal tree crown, relative to overall phorophyte use. Lichens were used more frequently in larger trees whereas bryophytes were used more frequently in the lower portion of the forest profile.

Birds concentrated foraging activities on alectorioid lichens in the outer, upper and mid portions of the live crown on dominant and codominant *P. menziesii* and *T. heterophylla* (Tables 10 and 12). Almost 90% of the bouts involving alectorioid lichens occurred on *P. menziesii* and *T. heterophylla* and more than half of the bouts occurred between 12 and 37 m while birds were hanging, searching, pecking or probing the pendant lichens. Both small-bodied passerines (including Chestnut-backed Chickadee, Brown Creeper, and Red-breasted Nuthatch) and a medium-sized corvid (Gray Jay) were able to hang onto or hang nearby the pendant lichens to procure or search for food items. Birds also used alectorioid lichens located on branches and the bole in the inner portion of the crown, although less frequently. Members of the BI, OS, and TFI foraging guilds used alectorioid lichens generally between 29 and 34 m, although bouts on alectorioids ranged in height from 3 to 60 m (Tables 13 through 15).

Table 10: Number of foraging bouts on lichen substrates by tree species/types, Walking Transect and Tree Plot data pooled.

Tree species/type	Lichen type[1]					
	AL	**BL**	**FR**	**FO**	**FR & FO**	**Total**
T. heterophylla	14	4	3	29	11	61
P. menziesii	9	4	1	11	5	30
Abies spp.	2	2	0	1	2	7
T. brevifolia	0	0	0	1	0	1
T. plicata	0	0	1	0	0	1
Pinus monticola	1	0	0	3	0	4
Log	0	1	0	0	0	1
Snag	0	2	0	1	0	3
Understory shrubs	0	0	0	1	0	1
Branches on ground	0	1	0	1	0	2
Total	**26**	**14**	**5**	**48**	**18**	**111**

[1] Lichen types: AL = alectorioid, BL = bark lichen, FR = fruticose, FO = foliose.

Table 11: Number of foraging bouts on bryophyte substrates by tree species/vegetation type, Walking Transect and Tree Plot data pooled.

Tree species/type	Bryophyte type		
	Pendant	**Appressed**	**Total**
T. heterophylla	24	6	30
P. menziesii	0	3	3
Abies spp.	9	2	11
T. brevifolia	13	5	18
Acer circinatum	9	6	15
T. plicata	1	0	1
Logs	1	14	15
Snags	0	1	1
Branches on ground	0	2	2
Total	**57**	**39**	**96**

Cyanolichens and other lichens were used throughout the horizontal profile of the tree crown on branches in the mid- and lower-live crowns of dominant and codominant trees (Table 12). Birds used foliose lichens with the hanging posture, although less so than by the perched position. The most frequent maneuvers used on foliose lichens included pecking, gleaning, and probing behaviors, while hanging from or leaning into the thallus. Foraging strategies used on *Lobaria* spp. included a variety of postures. For those bouts on *L. oregana* where food items were actually procured (i.e., not searching), “hanging” and “leaning into” were the most frequent postures used. Approximately half of the foraging activities on foliose, fruticose and bark lichens occurred between 12-37 m and the remaining bouts were distributed equally between the high and low height classes (Tables 13 and 15).

Foraging bouts on bryophytes occurred mostly in the inner, mid and lower portion of the live crown on live branches and boles of suppressed *T. heterophylla* and *Taxus brevifolia* (Table 12). More than 84% of these bouts occurred below 12 m, and approximately 40% of the bouts occurred on *Acer circinatum*, and appressed bryophytes on horizontal logs (Table 11). Species that foraged in the mid to upper canopy, such as Chestnut-backed Chickadee and Red-breasted Nuthatch, rarely foraged on bryophytes. Possible explanations for this is likely resource scarcity rather than resource avoidance since the critical height limit for bryophytes is 28 m (McCune *et al.* 1997) and the mean foraging heights of Chestnut-backed Chickadee (23 m) and Red-breasted Nuthatch (34 m) were at or well above this limit. Aerial insectivores used bryophytes located higher in the canopy, relative to the other foraging guilds (Table 14). During bouts on bryophytes, birds primarily hung while searching, pecking or gleaning food items from pendant and appressed mosses and liverworts (Table 12). For example, Hairy Woodpecker hung vertically while searching and procuring stationary insects from within or behind appressed bryophytes or beneath pendant bryophytes.

Chestnut-backed Chickadees and Red-breasted Nuthatches concentrated foraging activities in the outer-portions of the mid- and lower-crown, when both host and epiphytic substrates were used (Appendices D and E). Red-breasted Nuthatches used epiphytic substrates more frequently in the outer zones, and less frequently in the middle and inner zones, and showed a preference for dominant (58%) and co-dominant trees (42%) when foraging on epiphytic substrates. Red-breasted Nuthatches were observed using intermediate trees when foraging on host resources only (Appendix F). Gray Jays used epiphytes more frequently in the middle and inner portions of the mid and lower canopy. Brown Creepers used tree classes more evenly than any of the other species and used suppressed and co-dominant tree classes for the majority of their epiphytic substrate foraging bouts. Brown Creepers used the lower crown or below the live crown and the inner crown exclusively during foraging bouts on both epiphyte and phorophyte substrates. Similarly, Hairy Woodpeckers concentrated activities in the inner crown when using host resources, whereas all epiphyte-related bouts occurred in both the mid and inner portions of the lower live crown. Host substrate use by Hairy Woodpeckers was distributed throughout all vertical tree zones. Hairy Woodpeckers selected suppressed trees for more than half of their foraging bouts, and were not observed on intermediate nor co-dominant trees when using epiphytic substrates, whereas they used all tree classes when foraging on host resources. Red Crossbills concentrated foraging activities in dominant trees (67%), in the outer foliage of the mid canopy, while taking seed from *T. heterophylla* cones. Pacific-slope Flycatchers used intermediate trees more often than suppressed and dominant classes and concentrated their activities in the outer, lower portions of, and below the live tree crown.

Table 12: Number of foraging bouts on epiphyte and phorophyte groups by tree class, tree status, tree position, crown zone, posture and maneuver; data pooled.

	Epiphyte Group			**Phorophyte**	
	Alectorioid Lichens	**Cyanolichens & Other Lichens**	**Bryophytes**	**Foliage**	**Bark and Branches**
Tree Class					
Dominant	15	45	10	61	56
Codominant	7	21	10	31	26
Intermediate	2	15	6	38	27
Suppressed	1	5	66	37	46
Tree Status					
Live	25	79	70	172	135
Dead	1	8	23	1	24
Tree Position					
Bole	6	17	31	0	54
Branch	7	45	63	16	81
Branchlet	7	21	1	4	23
Foliage	6	6	1	152	2
Vertical Zone					
Above	1	8	0	0	5
Upper	12	14	4	51	16
Middle	4	25	7	62	30
Lower	4	21	25	38	35
Below	4	7	13	1	20
Horizontal Zone					
Outer	12	23	5	111	18
Middle	4	20	18	26	27
Inner	9	25	25	19	65
Posture					
Hang	18	26	23	17	57
Hang upside-down	0	6	9	18	9
Hover	1	3	6	35	4
Perch	7	32	31	61	71
Other	0	22	27	52	25
Maneuver					
Glean	1	15	17	80	18
Peck	3	15	33	14	18
Probe	3	4	9	2	4
Hammer	1	3	6	0	14
Search	18	51	29	84	104
Other	0	1	2	3	8

Table 13: Percentage of foraging bouts by substrate among three height classes.

Substrate		High (>37 m)	Mid (12-37 m)	Low (≤12 m)
Epiphyte	Alectorioid Lichen	34.6	53.8	11.5
	Cyanolichens and Other Lichen	25.8	50.6	23.6
	Bryophytes	1.0	14.6	84.4
	All Epiphytes	**15.6**	**34.6**	**49.8**
Phorophyte	Foliage	20.6	45.6	33.9
	Bark and Branches	11.5	42.4	46.1
	All Phorophyte	**18.1**	**41.4**	**40.5**
Other	Mistletoe	37.5	50.0	12.5
	Other	0	25.5	74.5
	All Substrates	**16.4**	**38.5**	**45.1**

Table 14: Mean foraging height (m ± SE) and range (m) of bird foraging guilds by substrate.

Foraging Guild	Epiphyte Group			Phorophyte	
	Alectorioid Lichens	Cyanolichens & Other Lichens	Bryophytes	Foliage	Bark and Branches
AI	---	11.3 ± 2.7 (6-15)	16.0 ± 6.1 (6-27)	15.9 ± 2.4 (3-41)	15.0 ± 2.9 (1.5-40)
BI	29.0 ± 7.9 (7-60)	26.7 ± 2.7 (1-60)	9.2 ± 1.5 (1-32)	35.1 ± 4.1 (6-55)	24.0 ± 1.7 (1-60)
LUHI	23.0	5.0 ± 2.9 (0.2-18)	1.3 ± 0.2 (0-5)	3.5 ± 1.7 (0-37)	1.2 ± 1.1 (0-5)
N	18.0	---	5.5	5.2 ± 2.5 (1-15)	19.3 ± 11.1 (2-40)
OS	34.0 ± 4.3 (12-50)	28.3 ± 3.9 (3-50)	8.9 ± 2.4 (2-40)	31.8 ± 2.5 (6-60)	22.0 ± 2.9 (0-55)
TFI	29.3 ± 5.6 (3-55)	25.9 ± 2.1 (6-45)	8.6 ± 1.2 (1.5-15)	22.0 ± 1.5 (0.5-55)	17.2 ± 1.8 (1-45)
TS	40.0	46.7 ± 3.3 (40-50)	---	51.6 ± 3.8 (32-60)	60.0

Table 15: Mean foraging height (m ± SE) and range (m) of all bird by finer-scale substrates.

Substrate		Height
Epiphyte	Alectorioid lichen	30.4 ± 3.0 (3-60)
	Cyanolichen and other lichen	
	Foliose lichen	27.5 ± 2.2 (0.2-60)
	Fruticose lichen	20.4 ± 3.2 (12-30)
	Other lichen	20.3 ± 3.7 (1-46)
	Admixture (fruticose & foliose)	31.6 ± 2.5 (9-46)
	All cyanolichen and other lichen	26.1 ± 1.6 (0.2-60)
	Bryophyte	
	Pendant bryophyte	7.3 ± 1.0 (0.1-40)
	Appressed bryophyte	3.9 ± 1.0 (0-32)
	All bryophytes	5.9 ± 0.8 (0-40)
	Admixture (lichen & bryophyte)	10.0 ± 1.9 (6-15)
	All Epiphyte Substrates	**17.4 ± 1.1 (0-60)**
Phorophyte	Foliage (live and dead foliage)	23.0 ± 1.3 (0-60)
	Bark	17.4 ± 1.1 (0-60)
	Dead wood (includes rootwads)	16.9 ± 2.2 (0-60)
	Cone	41.1 ± 2.0 (27-58)
	Other (flower)	2.2 ± 1.3 (0.5-11)
	Mistletoe brooms	32.9 ± 5.0 (7-55)
	All Phorophyte Substrates	**21.1 ± 0.8 (0-60)**
Other	Air	14.4 ± 2.4 (1-37)
	Perched litter	14.9 ± 8.0 (0.75-33)
	Terrestrial herbs/mosses	0.02 ± 0.01 (0-0.02)
	All Other Substrates	**6.0 ± 1.4 (0-37)**
All Substrates Total		**19.0 ± 0.6 (0-60)**

Discussion

Red-breasted Nuthatches, Chestnut-backed Chickadees and Gray Jays were the most commonly encountered birds and foraging strategies differed from those reported in the literature. For example, foraging observations differed from the findings of Lundquist and Manuwal (1990), in which Red-breasted Nuthatches were reported using horizontal tree zones equally in the spring. Conversely, I found Red-breasted Nuthatches using the outer-, then the mid-horizontal zones more often than the inner zone during that season. Red-breasted Nuthatches shifted foraging activities to the mid- and upper-crown in spring (Lundquist and Manuwal 1990), which was consistent with this study. However, in their study, no differentiation was made between host or epiphyte substrates exploited in the vertical and horizontal zones. My study showed that Red-breasted Nuthatches used epiphyte substrates more often in the mid canopy (vertical), relative to foraging bouts on host substrates. Similarly, my canopy-level observations showed Chestnut-backed Chickadees using the mid-vertical and outer-horizontal zones more often when both phorophyte and epiphyte substrates were used, whereas Lundquist and Manuwal (1990) reported Chestnut-backed Chickadees using the lower-vertical and mid-horizontal crown in spring.

Explanations for the discrepancy are unknown; although observer location might be an important factor as all their observations were ground-based. In addition, their study had substantially higher sample sizes than mine, and their study sites included both old-growth and second-growth forest stands, which also might be contributing factors. Second-growth forests do not contain refugia for as many organisms as do old-growth stands (Lindenmayer and Franklin 2002), which may influence foraging patterns (Weikel and Hayes 1999). Species richness and biomass of all epiphyte groups is greatest in old-growth forests (McCune 1993). Accordingly, the frequent use of lichen substrates by Gray Jays in this study may be partially explained by their generalistic foraging nature and their proclivity to cache food for the winter by placing the sticky mucilaginous stored food item behind flaking lichen, or covering the cache with pieces of lichen (Strickland and Ouellet 1993). Similarly, the relatively high use of bryophytes and lichens by Red-breasted Nuthatches may be explained by their caching behavior of storing invertebrates, nuts and seeds, and concealing their caches, located under bark and beneath branches, with pieces of bark, lichens, mosses and snow (Ghalambor *et al*. 1999). For both species, epiphyte use is likely to remain the same or increase slightly in the fall and winter, because Gray Jays cache food throughout the year, whereas Red-breasted Nuthatches cache food more frequently in the fall and winter (Ghalambor *et al*. 1999, Sibley 2001). For other forest birds, the importance of epiphytes in the non-breeding season remains unknown.

Section 3

Use of Resources and Availability

The relative frequency of epiphyte and host substrates use, and tree selection by foraging birds revealed the relative importance of each substrate and tree species for that species, so I could compare between species and foraging guilds. I compared epiphyte and host resources availability and relative resource selection for five species (Chestnut-backed Chickadee, Red-breasted Nuthatch, Brown Creeper, Hairy Woodpecker and Gray Jay), and for all foraging bouts captured in the Tree Plots and Walking Transects (data pooled). I also compared tree species availability and tree species use during foraging bouts on epiphyte substrates, relative to foraging bouts on host substrates. My null hypotheses were: species (and all foraging bouts) will use resources in the same proportions (ratios) to their availability, as follows:

H_{01}: Bird use of major resources is proportionate to resource availability:
Foliage: Branches and Stem Bark: Epiphytes is 0.12:1.00:0.01 (McCune 1997).

H_{02}: Bird use of intra-epiphyte group is proportionate relative to intra-epiphyte group availability: Alectorioid Lichens: Cyanolichens and Other Lichens: Bryophytes is: 0.28:0.72:1.00 (Harmon *et al*, 2004).

H_{03}: Bird selection of tree species is proportionate relative to tree species availability: *Abies* spp., *P. menziesii*: *T. heterophylla*: *T. plicata*: Others is: 0.25:0.29:1.00:0.05:0.15.

Epiphyte and Host Resource Use and Availability

In general, all five species used epiphytes disproportionately relative to the available resource pool. Epiphytes were used disproportionately when the data were analyzed by species, pooled across species, and pooled by survey procedure (Table 16; Appendix G). Epiphyte use among the five species ranged from 30% (Chestnut-backed Chickadee) to 53% (Brown Creeper). Epiphyte substrates were used less frequently than branch and stem bark (34% vs. 39%) and more frequently than foliage, but in all cases disproportionately relative to epiphyte and phorophyte availability. Foliage was used more frequently by Chestnut-backed Chickadee, whereas Hairy Woodpecker avoided the resource. With the exception of Brown Creeper, the bark insectivores

(Red-breasted Nuthatch, and Hairy Woodpecker) used branches and bark stem more frequently than foliage or epiphytes. When the log-likelihood ratio test was performed on pooled data of all individual foraging bouts (N = 505), the disproportionate use of epiphyte substrates, relative to non-epiphyte resources (foliage, branches, stem bark, and understory shrubs and herbs), was more apparent ($G_{adj} = 1{,}303$, $P < 0.005$).

Table 16: Relative availability of host and epiphyte resources (g Cm^{-2}) and their proportional use (%) by five species; Tree Plot and Walking Transect data pooled.

	Resource Pool					
	Foliage	**Branches and Stem Bark**	**Epiphytes**			
Available Resources[1] (%)	941 (10.2)	8144 (88.7)	100 (1.1)			
English Name[2]	**Proportionate Use**			G_{adj}	**Critical** χ^2	***P***
Chestnut-backed Chickadee	43.8	26.3	30.0	238.83	3.84	< 0.05
Red-breasted Nuthatch	19.6	48.2	32.1	54.91	5.99	< 0.01
Gray Jay	28.8	36.5	34.6	170.20	5.99	< 0.005
Brown Creeper	2.0	45.1	52.9	77.29	5.99	< 0.01
Hairy Woodpecker	0.0	69.8	30.2	23.66	5.99	< 0.025
All five species	27.1	38.6	34.3	930.13	5.99	< 0.005

[1] Estimated stores of carbon associated with live biomass (Harmon *et al*. 2004), [2] Total foraging bouts (n): Chestnut-backed Chickadee (160), Red-breasted Nuthatch (56), Gray Jay (104), Brown Creeper (51), Hairy Woodpecker (43), all species (414).

When pooled, the five species used epiphyte groups disproportionately, relative to the available epiphyte resource pool. Cyanolichens and other lichens were used disproportionately more often, whereas bryophytes were used disproportionately less often ($P < 0.005$, Table 17). When the log-likelihood ratio test was performed on pooled data of all epiphyte foraging bouts by all species (N = 172), the disproportional use of intra-epiphyte substrates was still significant ($G_{adj} = 12.3$, $P < 0.05$). Chestnut-backed Chickadees foraged disproportionately on cyanolichens and other lichens, relative to alectorioid lichens and bryophytes ($P < 0.05$, Table 17, Appendix H). Red-breasted Nuthatch foraged disproportionately on cyanolichens and other lichens, however, the variation between the expected values and the observed values were not statistically significant ($P > 0.05$). Gray Jays foraged on live foliage and epiphytic substrates in significantly greater proportions, relative to the availability of branches and stem bark ($P < 0.005$). Gray Jays used bryophytes and cyanolichens and other lichens in the same proportions (38.9% of foraging bouts), however, the expected values were not significantly different than the observed values ($P > 0.1$). Brown Creepers used epiphytic substrates during more than half of their foraging bouts, and foraged significantly more often on epiphytic resources than host resources ($P < 0.01$). Brown Creeper also frequently used bole and branch bark devoid of epiphytes, and live foliage was generally avoided. Hairy Woodpeckers did not use the major resources proportionately ($P < 0.025$), foraging primarily on stem and branch bark, whereas approximately one third of their foraging bouts included epiphytic substrates.

Table 17: Relative availability of epiphyte groups (kg ha^{-1}) and their proportionate use (%) by five species, Tree Plot and Walking Transect data pooled.

	Epiphyte Group					
	Alectorioid lichens	**Cyanolichens & Other lichens**	**Bryophytes**			
Available Resources[1] (%)	934 (14.1)	2382 (35.9)	3316 (50.0)			
English Name[2]		**Proportionate Use**		**G_{adj}**	**Critical χ^2**	***P***
Chestnut-backed Chickadee	16.7	60.4	22.9	15.53	5.99	< 0.05
Red-breasted Nuthatch	11.1	77.8	11.1	12.06	3.80	> 0.05
Gray Jay	22.2	38.9	38.9	2.44	5.99	> 0.1
Brown Creeper	14.8	37.0	48.2	0.04	5.99	> 0.1
Hairy Woodpecker	0.0	38.5	61.5	3.67	3.84	> 0.1
All five species	15.5	50.7	33.8	16.19	5.99	< 0.05

[1] McCune 1993, McCune *et a*l. 1997; [2] Sample sizes (n): Chestnut-backed Chickadee (48), Red-breasted Nuthatch (18), Gray Jay (36), Brown Creeper (27), Hairy Woodpecker (13), and All five species (142).

Tree Use and Availability

When all foraging bouts were pooled, birds used tree species proportionately, relative to their availability (N = 578, log-likelihood ratio test: $G_{adj} = 6.75 <$ critical chi square value of 9.5; $P < 0.05$). For all foraging substrates, *T. heterophylla* (the most common tree species in the forest) was used more frequently than any of the other tree species (Table 18). Birds rarely used *T. plicata*; this tree species was relatively rare in the forest. When all epiphyte-related foraging bouts were pooled, all four dominant trees were used disproportionately (N = 171, $P < 0.025$). *Pseudotsuga menziesii*, and "Other Species" were used disproportionately more frequently, whereas *T. heterophylla*, *Abies* spp., and *T. plicata* were used less frequently, relative to their availability. Approximately 73% of all epiphyte-related foraging bouts occurred on *P. menziesii* and *T. heterophylla*, proportionate to their combined availability of 74%. Foraging bouts involving bryophytes rarely occurred on *P. menziesii*, whereas *P. menziesii* was used more frequently when lichen substrates were used. Snags and Others and *Abies* spp. were used disproportionately more frequently during the bouts that involved bryophyte substrates. Birds used *P. menziesii* and *Abies* spp. disproportionately more often when they used foliage, and when phorophyte resources were pooled (N = 392, $P > 0.05$).

Three of the four dominant tree species provided epiphyte foraging substrates for all five foraging guilds (AI, BI, LUHI, OS, and TFI). *Thuja plicata* was never used during epiphyte foraging bouts except by OS (Table 19). In general, OS proportionate use of tree species during foraging bouts on epiphyte substrates mirrored their proportionate bouts on phorophyte substrates ($P < 0.05$ for both). Approximately half of all OS and TFI foraging bouts on epiphyte and phorophyte substrates occurred on *T. heterophylla*. When foraging on phorophyte substrates, *P. menziesii* and *Abies* spp. were used disproportionately more frequently by BI and TFI, respectively ($P < 0.05$ for both). Conversely, during bouts on epiphytes, BI and TFI used "Other Species" more frequently, relative to their availability, although the log likelihood ratio test statistics were not statistically significant ($P > 0.1$). Brown Creepers and Red-breasted Nuthatches used *T. heterophylla* more frequently when foraging on epiphyte substrates, relative to *T. heterophylla* availability of 57% (Appendix I). In contrast, the Hairy Woodpecker did not show a similar preference for *T. heterophylla*, and used "Other Species" and *Abies* spp. disproportionately more frequently. In general, Chestnut-backed Chickadees used tree species proportionately during bouts on epiphytes, although the Chickadees used *P. menziesii* during 25% of their bouts, relative to *P. menziesii* availability of 17%.

Table 18: Relative availability of tree species (relative %) and their proportional use (%) by all species during foraging bouts on epiphyte and host substrates, Tree Plot and Walking Transect data pooled.

	Available Resource Pool Tree Species[1]							
	PSME	**TSHE**	**ABSP**	**THPL**	**OTHERS**			
Available[2]	17	57	14	3	9			
Foraging Substrate			**Proportionate Use (%)**			**G_{adj}**	**Crit. χ^2**	***P***
Alectorioid Lichens	34.6	53.8	7.7	0	3.8	9.9*	7.8	<0.05
Cyanolichens & Other Lichens	24.7	56.5	9.4	1.2	8.2			
Bryophytes	4.7	46.9	17.2	1.6	29.7	23.0	7.8	<0.005
All Epiphytes	**19.3**	**53.2**	**10.5**	**1.2**	**15.8**	**13.1**	**9.5**	<0.025
Foliage	21.8	57.6	18.2	0.6	1.8	22.3	9.5	<0.005
Bark or Branches	19.8	52.5	17.5	4.0	6.2	4.9	9.5	<0.05
All Phorophytes	**18.4**	**55.9**	**15.6**	**2.0**	**8.2**	**2.9**	**9.5**	**>0.05**
Mistletoe	0	87.5	12.5	0	0	n/a	n/a	n/a
Other	37.5	50.0	12.5	0	0	n/a	n/a	n/a
All Substrates	**18.7**	**55.4**	**14.0**	**1.7**	**10.2**	**6.75**	**9.5**	**<0.05**

[1] ABSP = *Abies* spp., PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, Others = *Cornus nuttallii*, *Taxus brevifolia*, Snags.[2] Data were provided by the Permanent Study Plot program, a partnership between the H.J. Andrews Long-Term Ecological Research program and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, OR; *All lichen foraging bouts pooled for log-likelihood ratio test (n = 108)

Table 19: Relative availability of tree species (%) and their proportional use (%) by seven foraging guilds during foraging bouts on epiphyte and host substrates, Tree Plot and Walking Transect data pooled.

		Available Resource Pool Tree Species[1]							
		PSME	**TSHE**	**ABSP**	**THPL**	**OTHERS**			
Available[2]		17	57	14	3	9			
Foraging Guild	**Foraging Substrate (n)**	**Proportionate Use (%)**					**G_{adj}**	**Critical χ^2**	***P***
AI	Epiphytes (5)	20.0	60.0	20.0	0	0	n/a	n/a	n/a
	Host (29)	3.4	69.0	17.2	6.9	3.4	n/a	n/a	n/a
BI	Epiphytes (57)	14.0	59.6	12.3	0	14.0	1.7	7.8	>0.1
	Host (94)	25.5	44.7	11.7	1.1	17.0	9.7	7.8	<0.05
LUHI	Epiphytes (15)	20.0	40.0	20.0	0	20.0	n/a	n/a	n/a
	Host (24)	8.3	45.8	25.0	4.2	16.7	n/a	n/a	n/a
OS	Epiphytes (38)	21.1	50.0	5.3	5.3	18.4	6.9	7.8	<0.05
	Host (66)	22.7	51.5	7.6	4.5	13.6	6.0	7.8	<0.05
N	Epiphytes (2)	50.0	50.0	0	0	0	n/a	n/a	n/a
	Host (9)	12.5	50.0	25.0	0	12.5	n/a	n/a	n/a
TFI	Epiphytes (50)	24.0	56.0	10.0	0	10.0	2.3	7.8	>0.1
	Host (135)	17.8	54.1	23.7	0.7	3.7	15.5	7.8	<0.025
TS	Epiphytes (4)	0	0	0	0	100.0	n/a	n/a	n/a
	Host (40)	12.5	87.5	0	0	0	n/a	n/a	n/a
All Guilds	**Epiphytes (171)**	**19.3**	**53.2**	**10.5**	**1.2**	**15.8**	**13.1**	**9.5**	**< 0.025**
	Host (392)	**18.4**	**55.9**	**15.6**	**2.0**	**8.2**	**2.9**	**9.5**	**> 0.05**

[1] ABSP = *Abies* spp., PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*, Others = *Cornus nuttallii*, *Taxus brevifolia*, Snags.[2] Data were provided by the Permanent Study Plot program, a partnership between the H.J. Andrews Long-Term Ecological Research program and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, OR**;** AI = aerial insectivore, BI = bark insectivore, LUHI= low-understory herbivore/insectivore, N = nectarivore, OS = omnivore scavenger, TFI = timber foliage insectivore, TS = timber seed-eater.

Discussion

Chestnut-backed Chickadees, Red-breasted Nuthatches, Gray Jays, Brown Creepers, and Hairy Woodpeckers showed selectivity in use of the major foraging resources. When the five species were pooled, epiphyte-groups were used disproportionately, with cyanolichens and other lichens used disproportionately more often and bryophytes less often, whereas alectorioid lichens were used proportionately, relative to their availability. The disproportionate use of bryophytes by Chestnut-backed Chickadees was consistent with Weikel and Hayes' (1999) study that documented this species selecting live trees with relatively low bryophyte cover. In their study of young coniferous forests, Weikel and Hayes (1999) grouped all lichen and moss epiphyte forms into their categorical variable "bryophytes". The relatively low use of bryophytes by Chestnut-backed Chickadees in young and old forests may be a function of beak size. Chickadees are small passerines (<10 g), with small, short beaks. Compared with the larger and longer bills of Gray Jay and Hairy Woodpecker, Chickadee (and Red-breasted Nuthatch) beaks are less well-suited to extract invertebrates concealed within appressed bryophytes. Gray Jays probed or plucked food items while perched upon appressed bryophytes, whereas Hairy Woodpeckers hammered and pecked through densely appressed bryophytes. Although Brown Creepers also have small bills and are slightly smaller than Chickadees, Creepers used bryophytes by hanging upside-down beneath large branches while searching bryophytes, a foraging posture that is unavailable to Chickadees.

Trees were used disproportionately during bouts on epiphytes. *P. menziesii* and *T. heterophylla* were used more frequently but in proportion to their availability, accounting for 77% of all epiphyte foraging bouts on dominant and codominant trees. Foraging bouts on bryophyte substrates rarely occurred on *P. menziesii* whereas "Other Species" and *T. heterophylla* were used disproportionately more often. However, tree species and epiphyte habitats and distribution are interdependent: *P. menziesii* and *T. heterophylla* constituted the tallest components of the coniferous forest, and are associated with increased species richness and biomass of lichens (McCune *et al*. 2000). Conversely, most bryophyte-related foraging bouts occurred in the lower strata of the forest, on *T. brevifolia*, and understory shrubs, which are associated with higher species richness and biomass of bryophytes.

The paucity of foraging activities on *T. plicata* could be explained by their relative rarity in the forest: *T. plicata* accounted for only 3% of the relative tree species abundance. Alternatively, avoidance of *T. plicata* might be due to phytophagous insects avoiding the secondary compounds (tannins and oils) produced by *T. plicata,* which would in turn limit insectivorous birds. *Calocedrus decurrens* is avoided by insectivorous birds during the breeding season (Ariola and Barret 1985).

With the exception of foraging bouts on bryophytes, birds used dominant and co-dominant trees more frequently than intermediate or suppressed trees. This could be a function of survey location where most observations were recorded in the canopy and where these tree classes are more abundant. The vertical stratification and distribution of epiphyte groups is well documented, with the greatest cover of epiphytes occurring in the mid crown of large trees (McCune 1993, Lyons *et al.* 2000). Alternatively, the greater use of dominant, codominant and suppressed trees may be relative: these tree classes were the most available resource (Table 3). However, many cavity-nesting birds also show a preference for larger diameter trees as foraging locations (Weikel & Hayes 1999).

Section 4

Community Structure

Results for Epiphyte Foraging Events

The MRPP statistics indicated less heterogeneity within, and greater heterogeneity among epiphyte groups and substrates, than was expected by chance (A = 0.177 for epiphyte groups, and A = 0.215 for finer scale epiphyte substrates, $P < 0.001$) (Table 20). Similarly, overall MRPP runs of crown class, vertical canopy crown class, foraging posture, tree species and position of the bird in the tree showed within-group similarities, and among-group dissimilarities. The three-dimensional NMS solution explained 93% of the variability in the data (39.9% (Axis 1) + 33.0% (Axis 2) + 20.1% (Axis 3) (Figs. 6 and 7). Final stress for the three-dimensional solution was 14.38 (final instability = 0.061). Results of the Monte Carlo procedure with 250 randomized runs, and 250 runs of real data showed that the NMS real data runs produced a relatively stronger structure than expected by chance ($P = 0.004$). The NMS ordination (Figs. 6 and 7) supported the MRPP statistic, which indicated both less heterogeneity within foraging guild and species groups, and greater heterogeneity among groups, than expected by chance.

Foraging guilds and species: The MRPP showed strong similarities and separation among several of the foraging guilds (Table 20, Appendices K and L). MRPP indicated both less heterogeneity within foraging guilds, and greater heterogeneity between foraging guilds, than expected by chance (A = 0.178, $P < 0.001$). The overall chance-corrected within-species and within-foraging guild agreement statistics were strongly heavily influenced by the LUHI. Winter Wrens comprised the majority of the LUHI data, and showed clear separation from all other non-LUHI foraging guilds and associated species (Figs. 6 and 7, Appendices K and L). Conversely, within LUHI group comparisons indicated broad overlapping of foraging strategies (e.g., $A = 0.077$, $P < 0.001$ for WIWR vs. DEJU; and $A = 0.006$, $P = 0.282$ for WIWR vs. HETH). The high P-value reflects the low sample size of Hermit Thrush epiphyte foraging activities. As guild members, the foraging behaviors and strategies of Winter Wren, Dark-eyed Junco, and Hermit Thrush using epiphytic substrates differed significantly from those strategies employed by most members of the other foraging guilds (Appendices M and N). Strong among-group patterns were observed among LUHI and five foraging guilds, namely the AI, BI, OS, TFI, and TS. Nectarivores was the only foraging guild that showed weak patterns with LUHI. Strong among-group patterns were also observed among TS and two foraging guilds, namely AI and N. The

OS, BI, and TFI guilds showed weak within-group patterns among their foraging behaviors, suggesting these guilds used similar foraging strategies.

Table 20: Comparison of differences in epiphyte related foraging strategies with non-metric Multi-Response Permutation Procedures, based on Sørensen distances; g = number of groups; A = chance-corrected within-group agreement; P = probability of Type I error for H_o: no difference between groups. Bonferroni-adjusted significant P-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups	***g***	**Pooled Data (N = 191)**	
		***A* value**	***P***
Major epiphyte groups[1]	4	**0.177**	**< 0.001**
Finer scale epiphyte groups[2]	8	**0.215**	**< 0.001**
Foraging Guilds[3]	7	**0.178**	**< 0.001**
Species[4]	13	**0.231**	**< 0.001**
Crown class[5]	4	**0.225**	**< 0.001**
Horizontal Crown[6]	3	0.063	0.001
Vertical Crown[7]	5	**0.149**	**< 0.001**
Foraging Maneuver[8]	6	0.038	< 0.001
Foraging Posture[9]	10	**0.105**	**< 0.001**
Tree Species[10]	6	**0.215**	**< 0.001**
Tree Condition[11]	2	0.081	< 0.001
Tree Position[12]	5	**0.108**	**< 0.001**

[1] alectorioid lichen, cyanolichen and other lichen, bryophyte, lichen/bryophyte admixture; [2] alectorioid lichen, foliose lichen, fruticose lichen, fruticose and foliose lichen, pendant bryophyte, appressed bryophyte, other lichen, bryophyte and lichen; [3] aerial insectivores, bark insectivores, nectarivores, low-understory herbivore/insectivores, omnivore-scavengers, timber foliage insectivores, timber seed-eaters; [4] Brown Creeper, Chestnut-backed Chickadee; Dark-eyed Junco, Golden-crowned Kinglet, Gray Jay, Hairy Woodpecker, Hermit Thrush, Pacific-slope Flycatcher, Red-breasted Nuthatch, Red Crossbill, Rufous Hummingbird, Steller's Jay, Winter Wren; [5] dominant, codominant, intermediate, suppressed; [6] inner, middle, outer live crown; [7] above, upper, middle, lower, below live crown; [8] hammer, glean, probe, peck, pluck, search;[9] hang, hang upside-down, hop, hover, lean over/into, perch, reach under, short flight, stand, walk/run; [10] *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Abies* spp., "*Pinus monticola*, *Thuja plicata* and Snags", "*Acer circinatum* and *Taxus brevifolia*", others; [11] live, dead; [12] bole, branch, branchlet, dead branch/lets, foliage.

The NMS graphical representation also indicated that LUHI used different foraging strategies when using epiphytes, relative to the other foraging guilds (Figs. 6 and 7). Although widely spaced along Axis 2, LUHI showed a clear separation from all other guilds and species. However, there was considerable overlap with several points, including OS, BI, and AI. For example, the OS point that scored lowest on both Axes 2 and 3 was an individual Gray Jay that was observed hammering a food item located in a pendant bryophyte on the branch of *A.*

circinatum at 2.25 m. Similarly, the low-scoring AI point was a Pacific-slope Flycatcher that hover-gleaned at pendant bryophyte and fruticose lichen admixture at 6 m. This AI event reflected the sole bryophyte-associated foraging bout on *Abies* spp., and the lowest epiphyte foraging event by Pacific-slope Flycatcher, hence the separation on the ordination. The four Red Crossbill points (Fig. 7) showed a tight clustering pattern, reflecting their specialized foraging behavior. Conversely, Gray Jay points were widely distributed along both axes reflecting the generalist nature of the scavengers' foraging behaviors on epiphytes coupled with their ubiquitous distribution throughout the vertical forest profile. In general, the points representing both the TFI and BI foraging guild scored higher on both axes, reflecting similar foraging strategies. This was also evident in the statistics from the multiple MRPP comparisons between the two guilds (and species that represent the bulk of these data) that indicated extremely broad overlapping (A = 0.026 for guild comparison; and A = 0.018 for species comparison of Red-breasted Nuthatch and Chestnut-backed Chickadee) (Appendices K and L).

Finer-scale epiphyte substrates: Finer-scale epiphyte substrates showed stronger and more statistically significant patterns than obtained from the MRPP run with the coarser scale, epiphyte functional groups (A = 0.215, $P < 0.001$) (Table 20). Foraging activities on epiphyte substrates indicated similar within-group foraging behaviors, and among-group dissimilarities between bryophyte groups and both lichen groups (Appendix J). Foraging activities on appressed and pendant bryophyte groups differed considerably when compared with the lichen groups. The strongest among-group patterns observed were among appressed bryophytes and three lichen finer-scale substrates, namely alectorioid lichen, foliose and the foliose and fruticose admixture (Appendix J). In addition, foraging behaviors for alectorioid lichens showed some separation from the other lichen substrates. The strongest patterns were found between alectorioid lichens and pendant bryophytes (A = 0.168, $P < 0.001$). The majority of the pairwise comparisons of among-lichen and bryophyte finer scale substrates indicated dissimilar foraging strategies (Appendix J). Conversely, most pairwise comparisons of within-lichen and within-bryophyte finer scale substrates groups yielded statistics that indicated similar foraging strategies (Appendix J). Pairwise comparisons of the remaining finer scale epiphyte substrate groups showed broad overlap suggesting similar foraging strategies, or otherwise smaller sample sizes (Appendix J).

Epiphyte functional groups: There was both more homogeneity within epiphyte groups, and greater heterogeneity between epiphyte groups, than expected by chance (A = 0.177, $P < 0.001$, Table 20). The comparisons of bryophyte and both lichen functional groups generated statistics comparable to the overall comparison, with the strongest differences in foraging strategies observed among bryophytes and lichens (Appendix J). The strongest among-group pattern was observed among bryophytes and cyanolichens and others lichens (A = 0.169, $P < 0.001$), and then between "bryophytes" and "alectorioid lichens" (A = 0.155, $P < 0.001$).

Tree species: Use of tree species groups showed a strong pattern (A = 0.215, $P < 0.001$; Table 20). The strongest patterns were among *P. menziesii* and two groups, namely *A. circinatum* and *T. brevifolia* (A = 0.333, $P < 0.001$), and "ground, logs or other species" (A = 0.333, $P < 0.001$). *Tsuga heterophylla* showed similar but weaker patterns with these latter two groups (Appendix J). These patterns implied that the foraging strategies used on epiphytes located on *P. menziesii* and *T. heterophylla* were different than those strategies and behaviors used for the other tree groups.

Crown class: The comparisons of crown classes indicated significantly different foraging strategies (A = 0.225, $P < 0.001$), with the strongest patterns observed between suppressed trees and all other crown classes (Table 20, Appendix J). Broad overlapping was observed within and between dominant and codominant classes, and codominant and intermediate crown classes (A = 0.01, $P < 0.05$ for both). Bird use of epiphyte substrates was significantly different when suppressed trees were used, relative to dominant, codominant and intermediate trees.

Vertical and horizontal crown use: No strong patterns were observed when comparing overall use of the three horizontal tree zones (inner, middle, and outer zones, A = 0.063, $P < 0.001$). Conversely, use of the vertical crown zones showed significantly different foraging strategies in these zones. Comparisons of above- and upper live crown versus lower and below live crown categories generated statistics similar to the overall comparison (A = 0.103, $P = 0.024$; A = 0.145, $P = 0.052$, respectively) (Appendix J).

Foraging maneuvers and postures: Overall comparisons of all foraging behaviors indicated commonality in foraging maneuvers, but dissimilarities in foraging postures when using epiphyte groups (A = 0.038 for maneuvers, A = 0.105 for postures, $P < 0.105$ for both). Comparisons of foraging postures showed broad overlapping and all results were statistically insignificant, save one: the comparison between "reach under" and "hopping" (A = 0.113, $P = 0.037$) (Table 20, Appendix J). Foraging strategies used by LUHI on all substrates and by all guilds on bryophytes accounted for most of the differences in foraging strategies between the guilds and epiphyte groups. Five foraging postures (hopping, hovering, standing, walking/running and reaching-up) showed among group dissimilarity and within group similarity. These five postures were used more frequently by the LUHI and AI guilds, respectively, which contributed to among-foraging guild differences.

Tree position and condition: Overall comparison of tree positions was statistically significant, and stronger agreement than from the comparisons of tree condition ($A = 0.108$, $P < 0.001$). Statistically significant strong patterns were obtained from comparisons of two tree position pairs: branchlet versus bole groups ($A = 0.178$, $P < 0.001$), foliage versus bole groups ($A = 0.142$, $P < 0.001$). No strong patterns were observed when comparing overall use of live versus dead trees.

Foraging Height: Both the correlation coefficients and scatterplots indicated an environmental gradient, with the vertical stratification of foraging guilds, where foraging height maintained a positive relationship with guild foraging strategies and behaviors. Axis 2 showed a strong positive correlation with height, where specific foraging guilds showed distinct linear and rank relationships. When the ordination was rotated -135 degrees, the linear correlation coefficients between foraging height and the ordination represented by Axes 1, 2 and 3 were 0.528, 0.956, and -0.107, respectively, which explained 27.9, 91.4 and 1.1 percent of the variation (R^2), respectively. R-squared denoted the proportion of variation expressed by the ordinated position on each respective axis that was explained by the variable (McCune and Grace 2002). The rank correlation coefficients represented by Axes 1, 2 and 3 were 0.472, 0.820, and -0.051, respectively.

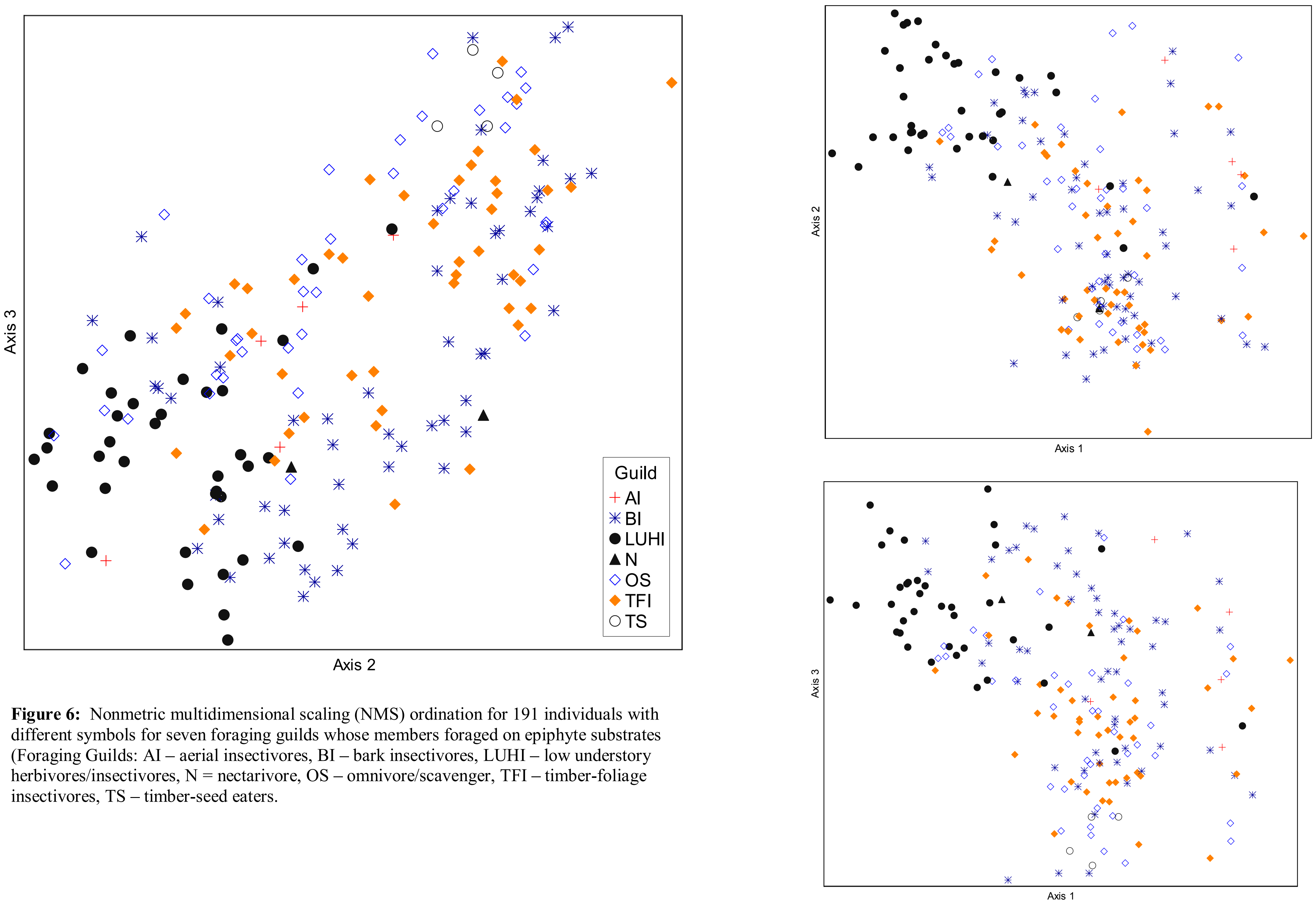
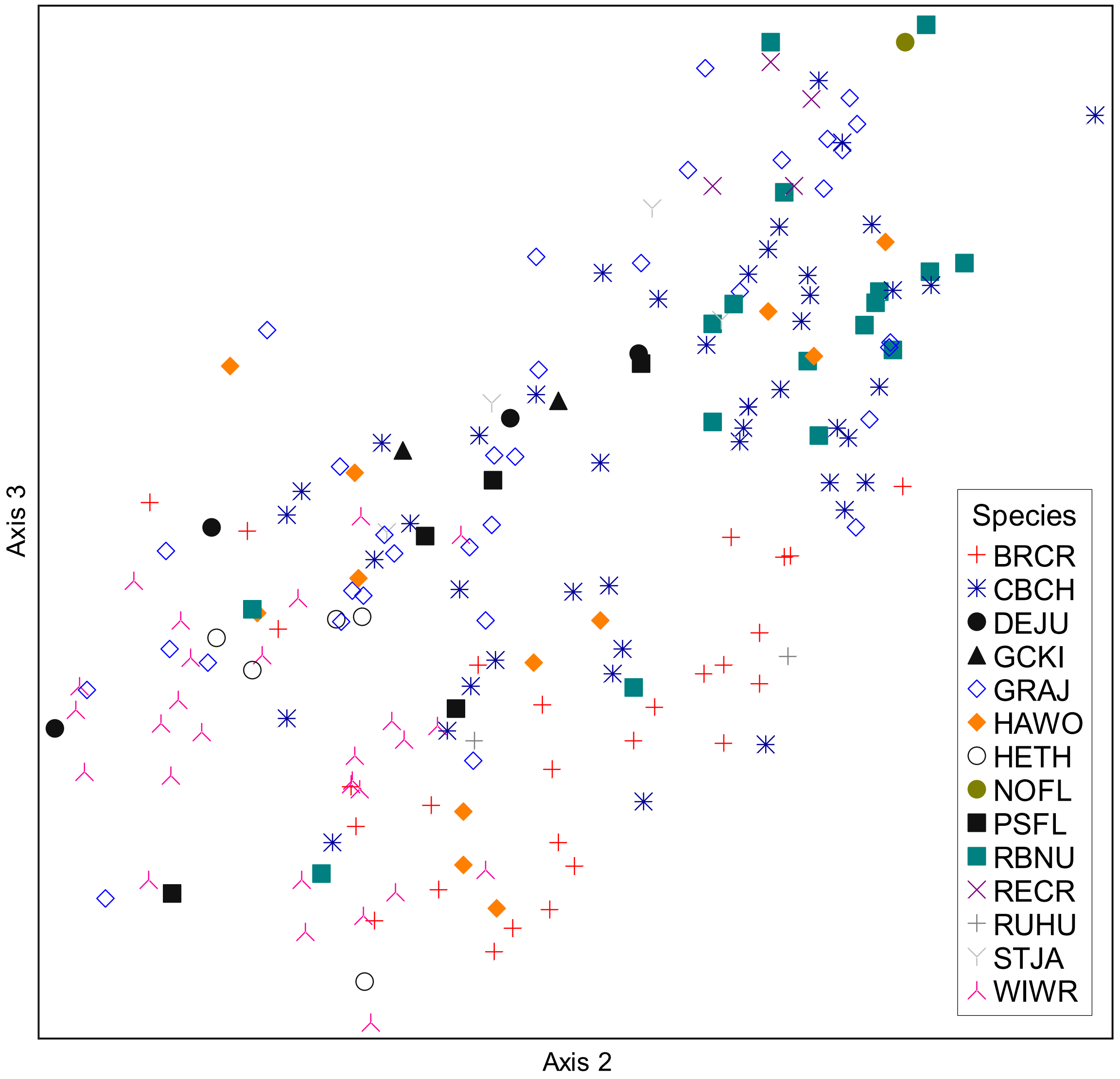


Figure 6: Nonmetric multidimensional scaling (NMS) ordination for 191 individuals with different symbols for seven foraging guilds whose members foraged on epiphyte substrates (Foraging Guilds: AI – aerial insectivores, BI – bark insectivores, LUHI – low understory herbivores/insectivores, N = nectarivore, OS – omnivore/scavenger, TFI – timber-foliage insectivores, TS – timber-seed eaters.



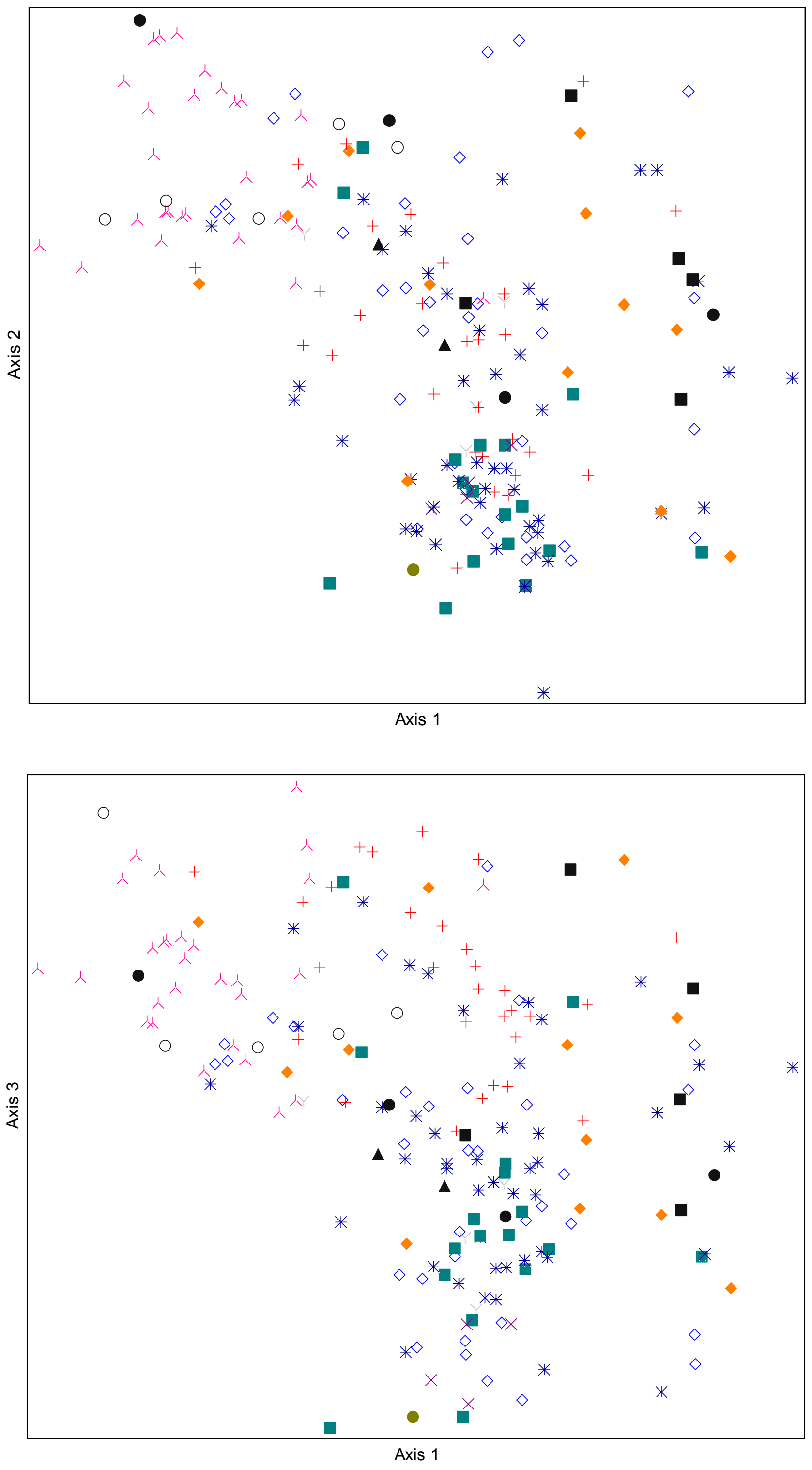


Figure 7: Nonmetric multidimensional scaling (NMS) ordination for 191 individuals with different symbols for fourteen species observed using epiphyte substrates in the Tree Plots (Species: BRCR = Brown Creeper, CBCH = Chestnut-backed Chickadee, DEJU = Dark-eyed Junco, GCKI = Golden-crowned Kinglet, GRAJ = Gray Jay, HAWO = Hairy Woodpecker, HETH = Hermit Thrush, NOFL = Northern Flicker, PSFL = Pacific-slope Flycatcher, RBNU = Red-breasted Nuthatch, RECR = Red Crossbill, RUHU = Rufous Hummingbird, STJA = Steller's Jay, WIWR = Winter Wren.

Discussion

The NMS and MRPP differentiated the overall species and foraging guild groups based on foraging locations and foraging strategies by which birds used epiphytes. The species contributing to the separation of foraging guilds were Winter Wren, Dark-eyed Junco, Rufous Hummingbird, and Red-Crossbill, and the most important epiphyte substrates that contributed to the separation of foraging guilds and species were appressed and pendant bryophytes and the admixture of fruticose and foliose lichens. To a lesser degree, tree species, crown class and vertical crown location were also important factors.

Evaluating and interpreting the quality of any ordination requires both statistical considerations as well as *a posteriori* knowledge (McCune and Grace 2002). The cluster of bird activity between 20 and 30 m is not unlike the vertical profile of surface area density and distribution of foliage characteristic of forest stands (Nadkarni *et al.* 2004, see Fig. 1-2; Ishii *et al.* 2004, see Fig. 5-3). This cluster of bird activity coincides with the unimodal vertical distribution of foliage in mature and old-growth forests (at least for closed canopy forests), with the greatest values occurring in the 20 to 30 m profile of *T. heterophylla* and *P. menziesii* old-growth forests (Ishii *et al* 2004). Broad overlapping of foraging strategies and behaviors among alectorioid lichen and cyanolichen and other lichen groups may be explained by the tendency for alectorioid lichens to occur both in the upper outer canopy as well as on the bole in the interior and lower canopy, sympatric with cyanolichens and other lichens.

Among the five foraging guilds, LUHI and TS showed the strongest pattern of dissimilarity among all other guilds. Strong patterns implied a gradient in the foraging strategies among these foraging guilds, representing similar foraging strategies within groups, and dissimilarities among groups. These strong patterns and the ordination suggested a vertical gradient (or structure) in foraging guild use of epiphyte substrates which encompassed the height variable. The stratification of foraging guilds in the vertical profile of the old-growth forest stand is consistent with the vertical stratification of bird assemblages found by others (Lundquist and Manuwal 1990, Shaw *et al.* 2002). Although the majority of the sample units were clustered in the mid canopy, the graphical ordination reflected a gradient in foraging guild structure, as follows (listed in decreasing foraging height): TS: BI: OS: TFI: AI: LUHI. The relatively tight cluster of larger symbols from four foraging guilds (OS, TFI, BI, and TS) reflects a pattern of similarity among the individuals which concentrated activity in the mid to upper canopy. Timber-foliage insectivores and BI often foraged together in mixed-flocks and used epiphytes in the same vicinity of the canopy where they used phorophyte resources. This gradient also reflects the rank order of mean foraging heights for each foraging guild (Table 14).

The variables foraging height, crown class, and tree species are confounded. Phorophyte and epiphyte abundance are interdependent: larger trees with large branches support more epiphytes throughout the vertical profile of the forest (Clement and Shaw 1999). Tree species and epiphyte habitats and distribution are interdependent: *P. menziesii* and *T.heterophylla* constituted the tallest components of the coniferous forest, and are associated with increased species richness and biomass of lichens (McCune *et al*. 2000). Epiphytes are stratified vertically: understory shrubs, suppressed and small trees (e.g., *A. circinatum* and *T. brevifolia*) support more abundant bryophyte communities, relative to lichens which are more abundant with increasing height (i.e., larger trees). Thus, the dissimilarities among lichens and bryophytes may be explained by the prevalence of bryophytes in the lower forest strata which necessitate different foraging strategies than those used on lichens.

Although TFI, OS and BI concentrated their activities in portions of the canopy that support the most foliage and cover of epiphyte groups, their wide-ranging distribution on the ordination illustrates their opportunistic foraging nature and propensity to forage throughout the vertical and horizontal profile of the forest, while using a wide variety of postures and maneuvers. TS used the mid and upper canopy more often, and their close proximity in the graphic can be explained by similar foraging strategies used when probing or searching lichens when they perched at 40 m and 50 m. The low foraging profile and use of substrates unique to the ground level by LUHI explain their scattered distribution along Axis 3 and lower scores on Axis 2, contrasting with OS, BI and TFI, which used epiphytes throughout the vertical forest profile.

Possible explanations for the among-group heterogeneity in tree position might be that only one species (Brown Creeper) used appressed bryophytes and bark lichens on the bole of the tree, whereas branchlet and dead branch tree positions were each used by species from four different foraging guilds. Fruticose, foliose and alectorioid lichens located on branchlets were used by four species (Chestnut-backed Chickadee, Red-breasted Nuthatch, Steller's Jay, and Red Crossbill). Epiphytes located on dead branches were used by all four aforementioned species and two others (Gray Jay and Hairy Woodpecker).

MRPP indicated that use of epiphyte substrates differed among suppressed trees and the other tree classes (e.g., dominant, codominant and intermediate trees). The vertical stratification of epiphytes is a likely explanation for the strong patterns observed among tree classes and vertical canopy zones. The relative cover of lichen epiphyte groups generally increase with increasing height above 20 m (Lyons *et al.* 2000). This height clustering is also associated with the critical height limit for bryophytes, 28 m (McCune *et al.* 1997). Bryophytes are located in the lower forest profile, and birds are using the resources accordingly. The NMS ordination showed a clustering of foraging guilds (e.g., OS, TFI, and BI). These guilds also used similar foraging strategies on phorophyte resources, which suggests that birds may optimize foraging opportunities if they concentrate their foraging activities in portions of the canopy that yield the majority of the available resources. In addition, sympatry in the mid to upper canopy by OS, TFI, and BI is consistent with the notion that PNW birds are generalists (Sharpe 1996).

It appears that observer location is a good predictor of epiphyte group and tree species use. Most canopy-level observations captured foraging activity at greater heights, and since epiphytes are vertically stratified in the forest, the canopy-level observations captured birds using bryophytes less frequently than lichens, relative to those observations gathered in the ground-based Walking Transects. Thus, resource availability and proportionate resource use by birds is influenced by the field method used to capture such foraging and habitat preferences. Hence, a more accurate assessment of resource use should include a combination of canopy-level and ground-based field methods.

Section 5

Comparison of Methods

This section is divided into two subsections. Subsection 1 is a comparison between foraging data captured in the two sampling procedures (Tree Plots and Walking Transects). A comparison is necessary since most ornithological field work is conducted at the ground level, and rarely has behavioral activity been recorded from the canopy level in temperate forests. Subsection 2 is the results of the comparative point count assessment between ground and canopy-level observers in the Tree Plots.

Subsection 1

Comparison between Tree Plot and Walking Transect Sampling Procedures

Duration of all bird observations (including all foraging and non-foraging observations) from all Walking Transects and Tree Plot sequences tallied 14.2 hrs, from 862 individuals of 32 species (Table 21). Compared with the Tree Plots, the Walking Transects yielded a greater number of behavioral observations per hour (2.8 vs. 2.1) and sequences per hour (11.9 vs. 6.9), relative to the total survey time of each sampling procedure. Similarly, the cumulative number of foraging bouts (735) was not equally distributed amongst species or sampling procedure (Table 22).

The 237 foraging bouts captured in the Tree Plots represented 18 species from eight foraging guilds, whereas the 498 bouts recorded during the Walking Transects included 25 species from nine foraging guilds. Foraging data obtained from the Walking Transects yielded more than twice the number of species and individuals per day, relative to the Tree Plots ($t = 2.55$, $P = 0.016$, $df = 30$, Table 23). The Walking Transects captured more observations per hour (2.3 vs. 1.9) and a greater number of behavioral sequences per hour (10.1 vs. 6.0) when calculated as a function of total survey time. Members of the low understory herbivore/insectivore foraging guild (LUHI), namely Hermit Thrush, Dark-eyed Junco, and Winter Wren, were poorly represented in the Tree Plots, relative to the Walking Transects (Fig. 8, Table 24). The vast majority of behavioral activities collected in the Tree Plots were captured from the canopy level (80%), and no sequence data in the Tree Plots were recorded at ground level for 3 of the 20 days.

The Chestnut-backed Chickadee was the most frequently detected species during both survey procedures (Fig. 8). Gray Jay, Red Crossbill and Red-breasted Nuthatch were the next most frequently detected species in the Tree Plots, and these four species accounted for approximately 75% of all Tree Plot foraging data. The numbers of Red Crossbill individuals observed per day in the Tree Plots were significantly higher than those observed during the Walking Transects. At the canopy level, Red Crossbills were easily observed, and individuals within large flocks could be differentiated due to sexual dimorphism in plumage. Foraging data for Winter Wren were obtained each day of the Walking Transects and were the second most frequently detected species. Chestnut-backed Chickadee and another five species (Winter Wren, Gray Jay, Pacific-slope Flycatcher, Hairy Woodpecker, and Brown Creeper) accounted for approximately 75% of the Walking Transect data (Table 25).

The Tree Plots recorded foraging data for four species that were never encountered during the Walking Transects (Fig. 8, Table 24). Two of the four species, Hermit Warbler and Pine Siskin, typically use upper canopy foliage and seed resources, and the remaining two species (Vaux's Swift and the Turkey Vulture) forage while flying above the canopy. The Walking Transects captured foraging data for 11 species that were never detected in the Tree Plots (Fig. 8).

Table 21: Behavioral activity (foraging and non-foraging activity) data summary by survey procedure.

Survey Procedure	**Time (hrs)**	**Number of Individuals**	**# Species**	**# Sequences**
Walking Transects	11.13	601	30	2,549
Tree Plots				
Canopy Location Only	2.15	211	17	710
Ground Location Only	0.91	50	10	137
Tree Plots subtotal	3.06	261	19	847
Total	**14.19**	**862**	**32**	**3,396**

Table 22: Searching and foraging bout survey effort summary by survey procedure.

Survey Procedure	**Time (hrs)**	**Number of Individuals**	**# Species**	**# Sequences**
Walking Transects	5.94	498	25	2,162
Tree Plots				
Canopy Location Only	1.78	195	16	642
Ground Location Only	0.38	42	8	98
Tree Plots subtotal	2.16	237	18	740
Total	**8.10**	**735**	**29**	**2,902**

Table 23: Number of foraging species, individuals and foraging guilds (mean ± SE) detected per day and by survey procedure.

Category	Survey Procedure		Comparison[1]
	Tree Plots	Walking Transects	
Species per day	3.90 ± 0.41	9.55 ± 0.41	$t = 9.49, P < 0.001$
Individuals per day	11.85 ± 2.18	24.90 ± 1.79	$t = 4.087, P < 0.001$
Foraging guilds per day	3.25 ± 0.29	5.70 ± 0.21	$t = 7.123, P < 0.001$

[1] Student's t-test comparison between survey procedures, $df = 19$, $\propto = 0.05$

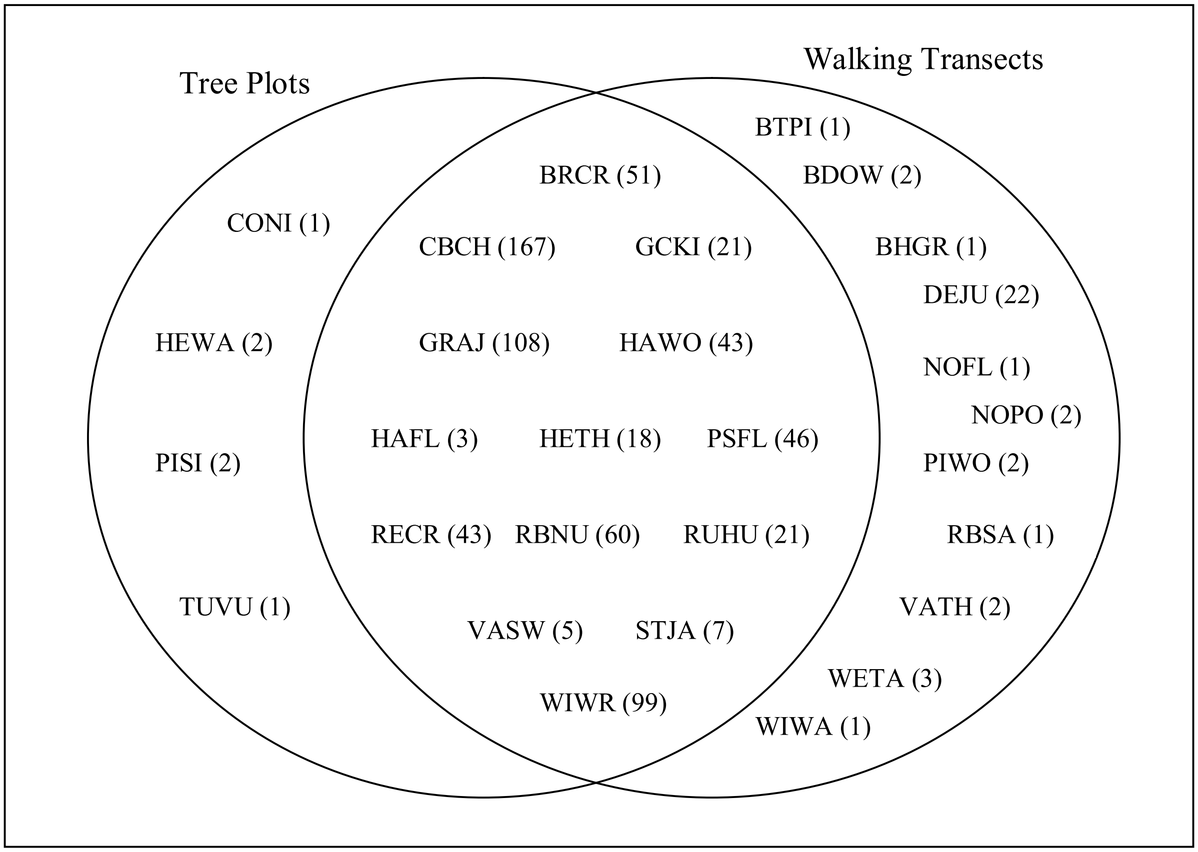


Figure 8: Venn diagram of species and foraging bouts (n) captured by survey procedure. Species codes: BDOW = Barred Owl, BHGR = Black-headed Grosbeak, BRCR = Brown Creeper, BTPI = Band-tailed Pigeon, CBCH = Chestnut-backed Chickadee, CONI = Common Nighthawk, DEJU = Dark-eyed Junco, GCKI = Golden-crowned Kinglet, GRAJ = Gray Jay, HAFL = Hammond's Flycatcher, HAWO = Hairy Woodpecker, HETH = Hermit Thrush, HEWA = Hermit Warbler, NOFL = Northern Flicker, NOPO = Northern Pygmy-Owl, PISI = Pine Siskin, PIWO = Pileated Woodpecker, PSFL = Pacific-slope Flycatcher, RBNU = Red-breasted Nuthatch, RBSA = Red-breasted Sapsucker, RECR = Red Crossbill, RUHU = Rufous Hummingbird, STJA = Steller's Jay, TUVU = Turkey Vulture, VATH = Varied Thrush, VASW = Vaux's Swift, WETA = Western Tanager, WIWA = Wilson's Warbler, WIWR = Winter Wren

Table 24: Total observation time (s), number of individuals (n) and sequences by survey type for each bird species.

English Name	Foraging Guild[1]	Tree Plots			Walking Transects		
		Time	n	seq.	Time	n	seq.
Band-tailed Pigeon	TS		-		2	1	1
Barred Owl	H		-		250	2	2
Black-headed Grosbeak	TFIO		-		3	1	1
Brown Creeper	BI	137	10	21	1279	41	165
Chestnut-backed Chickadee	TFI	1396	63	183	3016	104	391
Common Nighthawk	AI	2	1	1		-	
Dark-eyed Junco	LUHI		-		1310	22	137
Golden-crowned Kinglet	TFI	71	3	10	458	18	76
Gray Jay	OS	1756	48	173	3018	60	254
Hairy Woodpecker	BI	148	5	19	3230	38	235
Hammond's Flycatcher	AI	4	1	2	13	2	2
Hermit Thrush	LUHI	5	1	1	793	17	82
Hermit Warbler	TFI	50	2	10		-	
Northern Flicker	BI		-		45	1	1
Northern Pygmy-Owl	H		-		117	1	5
Pacific-slope Flycatcher	AI	101	3	6	1080	43	108
Pileated Woodpecker	BI		-		69	2	9
Pine Siskin	TS	16	2	2		-	
Red Crossbill	TS	1194	35	54	279	8	10
Red-breasted Nuthatch	BI	1696	33	164	1129	27	153
Red-breasted Sapsucker	BI		-		42	1	8
Rufous Hummingbird	N	90	7	10	290	14	27
Steller's Jay	OS	402	4	33	199	3	16
Turkey Vulture	H	40	1	1		-	
Varied Thrush	LUHI		-		24	2	4
Vaux's Swift	AI	82	4	6	3	1	1
Western Tanager	TFI		-		167	3	16
Wilson's Warbler	LUHI		-		1	1	1
Winter Wren	LUHI	588	14	44	4558	85	457
	TOTAL	**7778**	**237**	**740**	**21375**	**498**	**2162**

[1] Foraging guild codes: AI = aerial insectivore, BI = bark insectivore, LUHI= low-understory herbivore/insectivore, N = nectarivore, OS = omnivore scavenger, TS = timber seed-eater, TFI = timber foliage insectivore, TFIO = timber foliage insectivore/omnivore, H = aerial predator (catch non-insectivorous prey).

Table 25: Number of foraging individuals (mean ± SE) detected per survey day, frequency of detection, by survey procedure (frequency is the proportion of survey days that the species was detected).

English Name	**Tree Plots**		**Walking Transects**	
	Individuals/day (min/max)	**Freq.**	**Individuals/day (min/max)**	**Freq.**
Band-tailed Pigeon	---	---	0.05 ± 0.05 (0/1)	0.05
Barred Owl	---	---	0.1 ± 0.07 (0/1)	0.1
Black-headed Grosbeak	---	---	0.05 ± 0.05 (0/1)	0.05
Brown Creeper	0.5 ± 0.22 (0/4)	0.3	2.05 ± 0.37 (0/6)	0.85
Chestnut-backed Chickadee	3.15 ± 0.94 (15/0)	0.65	5.2 ± 0.76 (1/14)	1
Common Nighthawk	0.05 ± 0.05 (0/1)	0.05	---	---
Dark-eyed Junco	---	---	1.1 ± 0.24 (0/4)	0.7
Golden-crowned Kinglet	0.15 ± 0.08 (0/1)	0.15	0.9 ± 0.27 (0/4)	0.55
Gray Jay	2.4 ± 0.61 (0/7)	0.55	3 ± 0.42 (0/7)	0.9
Hairy Woodpecker	0.25 ± 0.01 (0/1)	0.25	1.9 ± 0.35 (0/6)	0.9
Hammond's Flycatcher	0.05 ± 0.05 (0/1)	0.05	0.1 ± 0.07 (0/1)	0.1
Hermit Thrush	0.05 ± 0.05 (0/1)	0.05	0.85 ± 0.27 (0/3)	0.4
Hermit Warbler	0.1 ± 0.10 (0/2)	0.05	---	---
Northern Flicker	---	---	0.05 ± 0.05 (0/1)	0.05
Northern Pygmy-Owl	---	---	0.05 ± 0.05 (0/1)	0.05
Pacific-slope Flycatcher	0.15 ± 0.11 (0/2)	0.1	2.15 ± 0.22 (0/4)	0.95
Pileated Woodpecker	---	---	0.1 ± 0.07 (0/1)	0.1
Pine Siskin	0.1 ± 0.07 (0/1)	0.1	---	---
Red Crossbill	1.75 ± 1.31 (0/26)	0.15	0.4 ± 0.27 (0/5)	0.15
Red-breasted Nuthatch	1.65 ± 0.67 (0/11)	0.45	1.35 ± 0.30 (0/4)	0.65
Red-breasted Sapsucker	---	---	0.05 ± 0.05 (0/1)	0.05
Rufous Hummingbird	0.35 ± 0.15 (0/2)	0.25	0.7 ± 0.19 (0/3)	0.5
Steller’s Jay	0.2 ± 0.12 (0/2)	0.15	0.15 ± 0.08 (0/1)	0.15
Turkey Vulture	0.05 ± 0.05 (0/1)	0.05	---	---
Varied Thrush	---	---	0.1 ± 0.07 (0/1)	0.1
Vaux’s Swift	0.2 ± 0.12 (0/2)	0.15	0.05 ± 0.05 (0/1)	0.05
Western Tanager	---	---	0.15 ± 0.11 (0/2)	0.1
Wilson’s Warbler	---	---	0.05 ± 0.05 (0/1)	0.05
Winter Wren	0.7 ± 0.25 (0/4)	0.4	4.25 ± 0.48 (2/11)	1.0
TOTAL	**11.85 ± 2.18 (1/39)**		**24.9 ± 1.79 (13/44)**	

Comparison between Sampling Procedures for Epiphyte Use

For both sampling procedures, approximately 28% of the foraging bouts involved epiphyte substrates, and more than 60% of these records reflected individuals foraging on resources provided by the host (Appendix M). Likewise, the relative proportion of species recorded using epiphyte substrates was similar for both survey procedures (9 of 18 species, or 50% in the Tree Plots, and 13 of 25 species, or 56% in the Walking Transects). However, the use of epiphyte groups was not equally distributed among sampling procedures. For instance, 73% of Tree Plot epiphyte foraging bouts involved cyanolichen and other lichens substrates; foliose lichens were the most frequently exploited epiphyte substrate. In comparison, 60% of all epiphyte foraging bouts captured in the Walking Transects involved bryophyte substrates. Although 11 species (from seven foraging guilds) were recorded using bryophytes in the Walking Transect, four species accounted for 63% of these data (in decreasing order of abundance: Winter Wren, Brown Creeper, Chestnut-backed Chickadee, and Gray Jay). In contrast, the Tree Plots captured only eight foraging bouts on bryophyte substrates by three species, Winter Wren, Gray Jay and Brown Creeper. Foraging bouts on alectorioid lichens comprised less than 5% and 3% of all Tree Plot and Walking Transect observations, respectively. Although more species were recorded using cyanolichen and other lichen substrates in the Walking Transects, the proportion of individual records on these substrates in the Tree Plots was generally higher than those recorded for the Walking Transects (Appendix M).

In the Tree Plots, five of the six species assigned a degree of epiphyte specialization were considered regular users of epiphyte substrates (e.g., Brown Creeper, Chestnut-backed Chickadees, Gray Jay, Red-breasted Nuthatch and Winter Wren) (Appendix N). The sixth species, Red Crossbill, used epiphytes occasionally. In the Walking Transects, 12 species were assigned a degree of epiphyte specialization (Appendix O). Brown Creeper, Hairy Woodpecker, Gray Jay, Winter Wren and Hermit Thrush used epiphytes regularly whereas the seven other species (e.g., Red-breasted Nuthatch, Chestnut-backed Chickadee, Golden-crowned Kinglet, Dark-eyed Junco, Pacific-slope Flycatcher, Red Crossbill and Rufous Hummingbird) were occasional users.

Comparison between Sampling Procedures for Spatial and Substrate Specialization

The mean height of all foraging birds detected during the Walking Transects was significantly lower than in the Tree Plots (Student T-test, $t = -15.6$, $P < 0.001$) (Table 26). When LUHI observations were excluded, the Tree Plots captured birds foraging considerably higher than the Walking Transects (34.2 m ± 0.9 for Tree Plots, as compared with 17.5 m ± 0.8 for the Walking Transects; $t = -13.31$, $P < 0.001$). For both Tree Plots and Walking Transects, birds used bryophytes lower in the canopy than lichen substrates (Table 26). Foraging activities on lichen substrates were captured generally between 21 and 35 m in the Tree Plots, and between 14 and 31 m in the Walking Transects. The mean height of all Tree Plot foraging bouts on epiphytes was almost three times higher than the Walking Transects (30 m vs. 12 m), whereas foraging bout locations on phorophyte substrates was only twice as high (32 m vs.15 m).

In the Walking Transects, members of the BI foraging guild foraged significantly higher in the canopy when using phorophyte resources, relative to epiphyte substrates (Table 27). Observations in the Tree Plots showed no differences between epiphyte or host substrate foraging heights but the Tree Plots did capture BI foraging activities generally higher in the canopy than records obtained from the Walking Transects. For both survey methods, BI used bryophytes lower in the canopy than lichen substrates. Red-breasted Nuthatches, which accounted for 69% of the Tree Plot BI data, were captured foraging in the mid canopy and were never observed using bryophytes. Conversely, Red-breasted Nuthatches comprised 38% of the Walking Transect BI foraging data and were observed foraging on bryophytes.

For TFI, no within-survey method differences were found between the foraging heights on epiphyte and phorophyte substrates (Table 28). However, the Tree Plot surveys appear to facilitate a more reliable assessment of TFI foraging activity in the upper canopy. Among-survey mean height comparisons showed that all recorded heights of all substrates used by TFI were higher in the Tree Plots than the Walking Transects. For example, Chestnut-backed Chickadees, which accounted for 93% and 83% of Tree Plot and Walking Transect TFI foraging activities, respectively, were captured foraging significantly lower in the Walking Transects (16 m) as compared to the Tree Plots (29 m) ($t = 7.65$, $df = 152$, $P < 0.001$). Similarly, the Tree Plots captured Chestnut-backed Chickadees using epiphytic substrates at a mean height of 32 m, compared with 15 m in the Walking Transects. This difference between survey procedures held true on a finer scale when epiphyte groups were considered. For instance, in the Tree Plots, Chestnut-backed Chickadees foraged higher on alectorioid lichen and “other lichen” substrates at 32 m and 32 m, respectively, as compared with 21 m and 24 m, respectively, in the Walking

Transects. In the Tree Plots, Chestnut-backed Chickadees foraged on epiphytic substrates at a similar height, relative to host resource, whereas there was greater variation in foraging heights when documented from the ground level during the Walking Transects.

Table 26: Mean foraging height (m ± SE) of all bird records by substrate and survey procedure.

Substrate		**Tree Plots**	**Walking Transects**
		Height	**Height**
Epiphyte	Alectorioid lichen	33.2 ± 1.6	28.6 ± 4.8
	Cyanolichen and other lichen		
	Foliose lichen	34.6 ± 2.1	15.7 ± 2.9
	Fruticose lichen	21.5 ± 3.5	21.0 ± 12.7
	Other lichen	24.0 ± 11.0	14.4 ± 4.4
	Admixture (fruticose & foliose)	31.9 ± 3.0	30.6 ± 4.9
	All cyanolichen and other lichen	32.7 ± 1.7	17.7 ± 2.3
	Bryophyte		
	Pendant bryophyte	4.9 ± 4.1	7.5 ± 7.7
	Appressed bryophyte	10.6 ± 5.7	3.4 ± 0.9
	All bryophytes	9.0 ± 4.1	5.8 ± 0.8
	Admixture (lichen & bryophyte)	---	10.0 ± 1.9
	All Epiphyte Substrates	30.2 ± 1.6	11.6 ± 1.1
Phorophyte	Foliage (live and dead foliage)	34.1 ± 1.7	16.3 ± 1.4
	Bark	28.3 ± 2.1	13.7 ± 1.2
	Dead wood (includes rootwads)	22.4 ± 4.6	14.9 ± 2.5
	Cone	42.7 ± 2.4	35.7 ± 2.7
	Other (flower)	0.5	2.4 ± 1.4
	Mistletoe brooms	32.3 ± 2.2	33.2 ± 8.2
	All Phorophyte Substrates	32.1 ± 1.2	15.4 ± 0.9
Other	Air	61.4 ± 11.6	17.6 ± 3.9
	Perched litter	28.5 ± 4.5	2.0
	Ground	0	0.05 ± 0.05
	Terrestrial herbs/mosses	---	0.02 ± 0.01
	Other	---	1.0
	All Other Substrates	48.7 ± 10.5	6.4 ± 1.8
All Substrates Total		32.2 ± 1.1	13.5 ± 0.7

Table 27: Mean bark insectivore foraging heights (m ± SE), and sample size (n) by substrate and survey procedure (* includes non phorophyte and non-epiphyte substrates).

Substrate		Tree Plots		Walking Transects	
		Height	**n**	**Height**	**n**
Epiphyte	Alectorioid lichen	31.0	1	28.7 ± 0.8	6
	Cyanolichen and other lichen	34.0 ± 0.2	15	19.0 ± 0.3	14
	Bryophyte	32.0	1	7.9 ± 0.1	22
	All Epiphyte Substrates	33.7 ± 0.2	17	14.6 ± 0.1	42
Phorophyte	Foliage (live and dead foliage)	36.4 ± 0.5	5	34.1 ± 0.6	7
	Bark	33.7 ± 0.1	20	17.3 ± 0.1	46
	Wood	42.3 ± 1.3	3	29.4 ± 0.3	14
	All Phorophyte Substrates	35.1 ± 0.1	28	21.6 ± 0.1	67
All Substrates*		34.2 ± 0.1	48	19.1 ± 0	110
Comparison[1]		$t = -0.44$, $df = 43$, $P = 0.33$		$t = -2.35$, $df = 107$, $P = 0.02$	

[1] Student's t-test, cumulative epiphyte and phorophyte comparison by survey type, ∝ = 0.05

Table 28: Mean timber-foliage insectivore foraging heights (m ± SE), and sample size (n) by substrate and survey procedure (* includes non phorophyte and non-epiphyte substrates).

Substrate		Tree Plots		Walking Transects	
		Height	**n**	**Height**	**n**
Epiphyte	Alectorioid lichen	32.4 ± 0.5	5	24 ± 1.7	3
	Cyanolichen and other lichen	31.8 ± 0.2	19	18.4 ± 0.3	12
	Bryophyte	---	---	8.5 ± 0.2	11
	All Epiphyte Substrates	31.9 ± 0.1	24	14.3 ± 0.1	26
Phorophyte	Foliage (live and dead foliage)	30.5 ± 0.1	27	18 ± 0.1	57
	Bark	27.4 ± 0.4	9	10.9 ± 0.1	28
	Dead Wood	27.3 ± 0.7	4	21.3 ± 1	4
	All Phorophyte Substrates	28.9 ± 0.1	42	15.7 ± 0	94
All Substrates*		29.9 ± 0	67	16 ± 0	125
Comparison[1]		$t = 1.22$, $df = 65$, $P = 0.27$		$t = -0.71$, $df = 116$, $P = 0.48$	

[1] Student's t-test, cumulative "epiphyte" and "phorophyte" comparison by survey type, ∝ = 0.05

In the Tree Plots, OS generally foraged higher in the tree canopy when using phorophyte substrates, relative to epiphytes, although the difference was not statistically significant ($P = 0.08$). Similarly, the Walking Transects captured OS foraging at similar heights during bouts on both epiphyte (18 m) and phorophyte substrates (19 m, Table 29). Tree Plot and Walking Transect differences were apparent: heights recorded for foliage, bark, and all epiphyte substrates (except “bryophyte” substrates) were higher in the Tree Plots. Gray Jays, which accounted for 94% of all OS foraging activities in the Tree Plots, used the mid canopy when foraging on both epiphytic and host resources but showed a shift to the lower canopy when using bryophytes. This trend was consistent in the Walking Transects. Gray Jays were documented foraging significantly higher on host resources in the Tree Plots, as compared with foraging data from the Walking Transects (t = 4.06, df = 70, $P < 0.001$). However, no between-survey procedure differences were found when epiphyte resources were used (t = 1.59, df = 34, P = 0.06).

Although the Winter Wren was observed foraging on other lichens at 3.3 m above the ground, the LUHI foraged exclusively in the understory. Dark-eyed Juncos concentrated most foraging activity in the low understory but were detected higher in the canopy when searching and gleaning prey items from lichen substrates, namely alectorioid lichens and the foliose lichen, *L. oregana*, at 23 m and 18 m, respectively. The two pecking records of Dark-eyed Juncos foraging on *Dicranum* and *Isothecium* mosses occurred on a horizontal bole, and branch of a suppressed *T. heterophylla* at 0.7 m and 3 m, respectively.

Table 29: Mean omnivore scavenger foraging heights (m ± SE), and sample size (n) by substrate and survey procedure (* includes non phorophyte and non-epiphyte substrates).

Substrate		**Tree Plots**		**Walking Transects**	
		Height	**n**	**Height**	**n**
Epiphyte	Alectorioid lichen	33 ± 0.5	3	34.6 ± 0.8	5
	Cyanolichen and other lichen	33.3 ± 0.4	9	21.9 ± 0.6	7
	Bryophyte	7.1 ± 0.5	4	9.5 ± 0.3	12
	All Epiphyte Substrates	**26.7 ± 0.2**	**16**	**18.4 ± 0.2**	**24**
Phorophyte	Foliage (live and dead foliage)	37 ± 0.2	21	23.3 ± 0.3	13
	Bark	31 ± 0.6	3	8.8 ± 0.3	11
	Dead Wood	30.1 ± 0.4	**9**	23 ± 0.4	11
	All Phorophyte Substrates	**33.9 ± 0.1**	**36**	**18.7 ± 0.1**	**35**
All Substrates*		**31.7 ± 0.1**	**52**	**18.3 ± 0.1**	**63**
Comparison[1]		t = -1.78, df = 50, P = 0.08		t = -0.07, df = 57, P = 0.94	

[1] Student’s t-test, cumulative “epiphyte” and “phorophyte” comparison by survey type, ∝ = 0.05

When all tree classes were considered for five bird species (e.g., Brown Creeper, Chestnut-backed Chickadee, Red-breasted Nuthatch, Hairy Woodpecker and Gray Jay), *P. menziesii* and *T. heterophylla* accounted for 93% of all foraging bouts in the Tree Plots, whereas these two tree species comprised only 63% of the foraging activities in the Walking Transects. More than 75% of all Gray Jay foraging activities in the Tree Plots occurred in the inner and mid portions of the lower and upper live crown, although the mid-crown (vertical zone) was used. Gray Jays shifted to the outer portions of the mid- live crown when using host resources (Appendix D). This shift was not observed in the Walking Transects: Gray Jays used the horizontal zones equally when foraging on host resources (Appendix E), but used the upper and lower crown more frequently. In the Tree Plots, Gray Jays used dominant trees more often than the other tree classes when foraging on epiphytic substrates (79% of all epiphytic foraging bouts), and 43% of these bouts on epiphytes occurred on *P. menziesii* (Appendices F and I). In the Walking Transects, Gray Jays used suppressed trees more frequently, when using both host and epiphytic resources. In the Walking Transects, Chestnut-backed Chickadees were observed more frequently in the lower live crown when foraging on both host and epiphytic resources (Appendix E). The Tree Plots captured Chestnut-backed Chickadees using intermediate trees slightly more frequently (38%) when foraging on epiphytic substrates than any of the other classes (Appendix F). In the Walking Transects, Chestnut-backed Chickadees used dominant trees more often during their foraging bouts on epiphytes, and more than 30% of their bouts involved co-dominant and intermediate classes. When foraging on phorophyte resources in the Tree Plots Chestnut-backed Chickadees used dominant trees more frequently, whereas they used suppressed trees more frequently in the Walking Transects.

Comparison between Sampling Procedures for Resource Use and Availability

Proportional use of epiphyte and host resources, relative to availability, was compared among survey procedure for five species (Brown Creeper, Chestnut-backed Chickadees, Hairy Woodpecker, Gray Jay, and Red-breasted Nuthatch). Epiphyte use ranged from 23% (Red-breasted Nuthatch in the Walking Transects) to 59% (Brown Creeper in the Walking Transects) (Appendix G). Both sampling procedures showed the five pooled species using epiphytes disproportionately, relative to the available resource pool, although, the test statistic was greater with the Walking Transect data (Table 30, Appendix G). The Tree Plots captured the five species using epiphyte group disproportionately, compared to the Walking Transects (Table 31, Appendix H). Both sampling procedures showed Chestnut-backed Chickadee and Gray Jay using epiphytes disproportionately (Appendix G). The Walking Transects captured only two of the three BI members (e.g., Brown Creeper and Hairy Woodpecker) using epiphytes disproportionately (Appendix G). The third BI member, Red-breasted Nuthatch, showed disproportionate use of epiphytes in the Tree Plot, but the differences were not statistically significant. Separate analyses of intra-epiphyte groups by survey procedure showed disproportional use of epiphyte substrates, but differences were not statistically significant for any of the five species for either sampling procedure (Appendix H).

Table 30: Relative availability of host and epiphyte resources (g Cm^{-2}) and their proportionate use (%) by five species by survey procedure.

	Resource Pool					
	Foliage	**Branches and Stem Bark**	**Epiphytes**			
Available Resources[1] (%)	941 (10.2)	8144 (88.7)	100 (1.1)			
Survey Procedure[2]		**Proportionate Use**		G_{adj}	**Critical** χ^2	***P***
Tree Plots	29.9	34.4	35.7	380.40	5.99	< 0.005
Walking Transects	25.4	41.2	33.5	551.10	5.99	< 0.005
Pooled for five species	27.1	38.6	34.3	930.13	5.99	< 0.005

[1] Estimated stores of carbon associated with live biomass (Harmon et al. 2004), [2] Total foraging bouts (n): Tree Plots (154), Walking Transects (260) pooled species (414).

Table 31: Relative availability of epiphyte groups (kg ha^{-1}) and their proportionate use (%) by five species by survey procedure.

	Epiphyte Group					
	Alectorioid lichens	**Cyanolichens & Other lichens**	**Bryophytes**			
Available Resources[1] (%)	934 (14.1)	2382 (35.9)	3316 (50.0)			
English Name (n)		**Proportionate Use**		G_{adj}	**Critical** χ^2	***P***
Tree Plots	16.4	74.5	9.1	44.98	5.99	< 0.025
Walking Transects	14.9	35.6	49.4	0.05	5.99	> 0.1
Pooled for five species	15.5	50.7	33.8	16.19	5.99	< 0.05

[1] McCune 1993, McCune et al. 1997; [2] Total foraging bouts (n): Tree Plots (55), Walking Transects (57) pooled species (142).

Comparison between Sampling Procedures for Community Structure

The MRPP statistics for each run of both survey procedures indicated less heterogeneity within, and greater heterogeneity between epiphyte groups and substrates, than expected by chance (Table 32, Appendix P). For both procedures, overall MRPP runs of foraging guilds, species, crown class, and vertical canopy crown showed within-group similarities, and among-group dissimilarities. Between survey procedures differences were evident in the MRPP runs of tree species, tree condition and foraging posture.

Foraging guilds and species: The overall chance-corrected within-species and within-foraging guild agreement statistics for both survey procedures were heavily influenced by LUHI (Appendix Q). The strongest among-group patterns were observed between LUHI and three foraging guilds (BI, TFI, and OS). In the Tree Plots, TS showed stronger dissimilarities with LUHI (A = 0.579, $P = 0.009$), whereas TFI showed strong dissimilarities with LUHI in the Walking Transects (A = 0.162, $P < 0.001$). The OS, BI, and TFI foraging guilds in both survey procedures showed weak within-group patterns among their foraging behaviors.

Epiphyte groups and finer-scale substrates: Foraging activities on epiphyte substrates obtained from both survey procedures indicated similar within-group foraging behaviors, and among-group dissimilarities between bryophyte groups and both lichen groups (Appendix P). Stronger among-epiphyte group patterns were observed in the Tree Plot data, relative to the Walking Transects, although relative group comparison ranks were similar. For both survey methods, the strongest among-group pattern was observed between bryophytes and alectorioid lichens (A = 0.331 for Tree Plots, A = 0.094 for Walking Transects, $P < 0.001$), and then between bryophytes and cyanolichens and other lichens (A = 0.103 for Tree Plots, A = 0.069 for Walking Transects, $P < 0.001$). For both survey procedures, foraging activities used on appressed and pendant bryophyte groups differed considerably when compared with the lichen groups. For instance, foraging strategies used on foliose and fruticose lichen and appressed bryophytes were different in the Tree Plots (A = 0.099, $P = 0.014$); and between foliose lichen and appressed bryophytes in the Walking Transects (A = 0.147, $P < 0.001$).

The strongest patterns were found between alectorioid lichens and pendant bryophytes in the Tree Plots. In the Walking Transects, the strongest patterns were found between foliose and fruticose lichen and an admixture of lichen and bryophytes. Analogous patterns were obtained from both survey methods for the comparison with alectorioid lichens and appressed bryophytes (A

= 0.222 for Tree Plots, and A = 0.201 for the Walking Transects, $P = 0.001$). The majority of the pairwise comparisons of among-lichen and bryophyte finer scale substrates indicated dissimilar foraging strategies. Conversely, most pairwise comparisons of within-lichen and within-bryophyte finer scale substrates groups yielded statistics that indicated similar foraging strategies. Pairwise comparisons of the remaining finer scale epiphyte substrate groups showed broad overlap suggesting similar foraging strategies employed, or otherwise smaller sample sizes.

Tree species and Crown Class: Use of tree species showed among-survey procedure differences (Table 32). Use of tree species groups showed a weak pattern in the Tree Plots, whereas use of tree species in the Walking Transects showed among-tree species differences (A = 0.114, $P < 0.001$). For both survey procedures, the comparisons of crown classes showed strong patterns between suppressed trees and all other crown classes. Broad overlapping was observed within and between dominant, codominant, and intermediate crown classes.

Foraging maneuvers and postures: Comparisons of all foraging maneuvers and postures indicated commonality in foraging behaviors in both the Tree Plots and Walking Transects (Table 32). Comparisons of foraging postures showed broad overlapping and all results were statistically insignificant, except one: the comparison between “reach under” and “hopping” (A = 0.113, $P = 0.037$). Foraging strategies used by LUHI on all substrates and by all guilds on bryophytes accounted for most of the differences in foraging strategies between the guilds and epiphyte groups. In the Walking Transects, three foraging postures (hopping, hovering and reaching-up) showed among group dissimilarity and within group similarity. Reaching up and hovering postures were used more frequently by the LUHI and AI guilds, respectively, which contributed to among-foraging guild differences.

Tree position and condition: Use of tree position groups showed a stronger pattern in the Tree Plots, relative to the Walking Transects (Table 32). Statistically significant strong patterns were obtained from comparisons of two tree position pairs: branchlet versus bole groups (A = 0.129, $P < 0.001$), dead branch versus bole groups (A = 0.148, $P < 0.001$).

Table 32: Comparison of differences in epiphyte-related foraging strategies by survey procedure with non-metric Multi-Response Permutation Procedures, based on Sørensen distances; g = number of groups; A = chance-corrected within-group agreement; P = probability of Type I error for H_o: no difference between groups. Bonferroni-adjusted significant P-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups		Tree Plots		Walking Transects	
	g	*A* value	*P*	A value	*P*
Major epiphyte groups[1]	3	**0.124**	**< 0.001**	**0.102**	**< 0.001**
Finer scale epiphyte groups[2]	8	**0.111**	**< 0.001**	**0.151**	**< 0.001**
Foraging Guilds (major groups)[3]	7	**0.166**	**< 0.001**	**0.152**	**< 0.001**
Foraging Guilds (finer scale groups)[3]	7	**0.159**	**< 0.001**	**0.144**	**< 0.001**
Species (major groups)[4]	13	**0.193**	**< 0.001**	**0.183**	**< 0.001**
Species (finer scale groups)[4]	13	**0.194**	**< 0.001**	**0.167**	**< 0.001**
Crown class[5]	4	**0.164**	**< 0.001**	**0.193**	**< 0.001**
Horizontal Crown[6]	3	0.059	0.001	0.049	< 0.001
Vertical Crown[7]	5	**0.099**	**0.001**	**0.096**	**< 0.001**
Foraging Maneuver[8]	6	0.022	0.109	0.025	0.017
Foraging Posture[9]	9	0.043	0.038	**0.090**	**< 0.001**
Tree Species[10]	4	0.053	0.004	**0.114**	**< 0.001**
Tree Condition[11]	2	0.023	0.022	**0.092**	**< 0.001**
Tree Position[12]	5	0.073	< 0.001	0.054	< 0.001

[1] alectorioid lichens, cyanolichens and other lichens, bryophytes; [2] alectorioid lichen, foliose lichen, fruticose lichen, fruticose and foliose lichen, pendant bryophyte, appressed bryophyte, other lichen, bryophyte and lichen; [3] aerial insectivores, bark insectivores, nectarivores, low-understory herbivore/insectivores, omnivore-scavengers, timber foliage insectivores, timber seed-eaters; [4] Brown Creeper, Chestnut-backed Chickadee; Dark-eyed Junco, Golden-crowned Kinglet, Gray Jay, Hairy Woodpecker, Hermit Thrush, Pacific-slope Flycatcher, Red-breasted Nuthatch, Red Crossbill, Rufous Hummingbird, Steller's Jay, Winter Wren; [5] dominant, codominant, intermediate, suppressed; [6] inner, middle, outer live crown; [7] above, upper, middle, lower, below live crown; [8] hammer, glean, probe, peck, pluck, search;[9] hop, reach under, short flight, perch, hanging, hang upside-down, lean over/into, reach up, hovering;[10] *Tsuga heterophylla*, *Pseudotsuga menziesii*, *Abies* spp., Others; [11] live, dead; [12] bole, branch, branchlet, foliage, dead foliage.

Discussion

Foraging data among species and foraging guilds were not equally represented in both the Tree Plot and Walking Transect surveys. Although neither survey procedure considered any species or foraging guild as epiphyte specialists and both designated five species as "regular users", only three of the five species were in common (Brown Creeper, Gray Jay and Winter Wren). The Tree Plots showed that Chestnut-backed Chickadees and Red-breasted Nuthatch were "regular users" of epiphyte groups, whereas the Walking Transects classified both species as "occasional users/generalist". The Tree Plots captured Chestnut-backed Chickadee and Red-breasted Nuthatch using lichens frequently but failed to capture either species using bryophytes. In comparison, the

Walking Transects captured both species using bryophytes. The differences between the survey procedures suggest that observer location influences the determination of foraging substrates. Sturman's (1968) study of Chestnut-backed Chickadees concluded that while foraging in conifers and hardwood forests they selected bare bark surfaces over moss or lichen covered bark. Similarly, Weikel and Hayes (1999) found Chestnut-backed Chickadees (and Hairy Woodpeckers) selecting substrates with relatively low epiphyte cover. Despite the differences in stand age, both Sturman's (1968) and Weikel and Hayes (1999) studies were ground-based foraging observations, which might have underestimated the importance of lichens as foraging sites.

Eighty percent of the Tree Plot data were obtained from the canopy level and no sequence data within the plots were recorded at ground level for 3 of the 20 days. Although the reason for this was untested, this suggests that the presence of the ground-level observer might have had a negative influence on lower-canopy and understory bird activity in the Tree Plot viewing arena. Alternatively, the tree climbing activity might have flushed LUHIs from the viewing arena. Yet, non-invasive tree climbing techniques allowed the researcher to conduct foraging observations from the canopy level and capture foraging activities in the mid and upper live crown. Because the upper 50 to 60% of the crown contains the greatest number of biodiversity elements due to the increased number of biological niches (Lindenmayer and Franklin 2002), bird foraging activity is most likely concentrated in the canopy, attributable to more opportunities to procure food items – an optimized foraging strategy.

The mean height of all foraging birds detected in the Walking Transects was significantly lower than those recorded in the Tree Plots. The differences in foraging heights captured among the two sampling procedures raises the question of whether the observed height differences between procedures might be a function of the person in the canopy thinking they were taller based on being high versus ground observers thinking the same height was lower. However, this is unlikely because the mean height of all Tree Plot observations was almost double the mean height of observations in the Walking Transects. Furthermore, during the training period prior to data collection, observers were trained with a laser range finder to ensure that ocular height estimates were within 10% of true height. Likely explanations for height differences among sampling procedures include the tendency for Walking Transect observers to concentrate on bird activity occurring in the lower canopy and understory, coupled with the fact that ground-level observers found it difficult to observe activity and determine the substrate exploited in the mid to upper canopy due to dense overstory and general obstruction of view. Dense mid-canopy and sometimes understory foliage limited ground based observers' ability to see birds or distinguish substrates used in the mid and upper crowns of larger trees. High-powered binoculars cannot counteract the visual barriers that face the ground-level observer, and with the height of many dominant trees in the RNA reaching 60 m, it is virtually impossible for the ground-based observer to detect bird activity and substrate selection in the upper crown.

Foraging data obtained from the Walking Transects indicated that birds used epiphyte groups in proportion to the epiphyte groups' availability, whereas data obtained from the Tree Plots showed that lichens were used more frequently than bryophytes, relative to their availability. I consider the observed relationships in the Tree Plots to be confounded; explained partially by the height of the observer (canopy versus ground level), and that epiphytes are vertically stratified in the forest profile. Canopy height and light transmittance influences the distribution of epiphytes (Parker 1997, McCune *et al.* 1997). Bryophytes occur in the lower profile; cyanolichens occur in the light transition zone, between 15 and 35 m, whereas other lichens are spread throughout the vertical profile (McCune *et al.* 1997). The vast majority of behavioral activities collected in the Tree Plots were obtained by the canopy-level observer (located at a mean height of 31 m), where bryophytes reach their upper height limit (McCune *et al.* 1997). The Walking Transect observers collected foraging data in the lower profile of the forest, where bryophytes are concentrated. This might explain differences between survey procedures. For example, although the proportionate use of alectorioid lichens by birds was similar between sampling procedures, the proportionate use of bryophyte was five times greater in the Walking Transects than the Tree Plots. Conversely, the Tree Plots recorded birds using cyanolichens and other lichens more frequently than the Walking Transects. Thus, use of epiphyte substrates for foraging appears to be a function of observer location, rather than actual resource selection. Similarly, the location of the observer was an important determinant for recording the height of bird foraging activity.

In summary, surveys from the canopy facilitated foraging observations of bird species in the mid to upper canopy, but underestimated bird use of bryophytes. Conversely, the Walking Transects were important for determining which resources were used in the mid to low canopy and understory, and allowed observers to access a greater proportion of the RNA, and capture foraging data for more species and individuals, relative to the Tree Plots. Thus, a combination of canopy- and ground-level survey procedures facilitated a more comprehensive assessment of species richness, increased sample sizes necessary for statistical vigor, and provided a more comprehensive assessment of epiphyte use throughout the forest's vertical profile.

Subsection 2

Comparison between Canopy- and Ground-Level Point Counts

Thirty-six species were detected during the 20 point counts. When all detections (including flyovers) were considered, the canopy-level observer detected one more species than the ground level, although both locations recorded 27 species in common (Appendices R and S). Of 33 total species detected by the canopy-level observer, five species were not detected by the ground-level observer (Common Raven, Western Tanager, Olive-sided Flycatcher, Purple Finch and Western Wood-Pewee) (Appendices R and S). Conversely, four of the 32 total species recorded by the ground-level observer, were undetected by the canopy-level observer (American Goldfinch, Common Nighthawk, Pileated Woodpecker, and Song Sparrow).

Multiple comparisons of alpha diversity measures in the unlimited-radius plots showed increased species diversity when counts were conducted at the canopy level, relative to the ground level (Table 33). Species diversity indices, calculated by plot and survey location in the unlimited-radius plots, showed that the canopy-level observer detected a more species diverse bird community, and the differences between the ground and canopy species diversity measures were statistically significant (Shannon's diversity index: $t = 3.67$, $P = 0.001$). Species richness was greatest with the canopy-level point count data ($t = 4.38$, $P < 0.001$). However, both survey locations showed that the bird community was evenly distributed (Evenness: $t = 0.05$, $P = 0.96$). The rank order of species relative abundance in the unlimited-radius plots was similar between canopy and ground locations (Wilcoxon Rank Sum Test, $z = 0.774$, $P = 0.44$). Similarly, there was no significant difference in the rank order of species detection between canopy and ground locations within 75 m ($z = -0.523$, $P = 0.60$) and 30 m ($z = -0.33$, $P = 0.74$).

Table 33: Species diversity by point count observer location in unlimited-radius plots (all detections, S = Species richness, E = evenness (H / ln (Richness)), H = Shannon`s diversity index).

Observer Location	**Mean ± SE**	**S (total)**	**E**	**H**
Canopy	0.4 ± 0.23	8.45 (33)	0.92	1.9
Ground	0.27 ± 0.18	6.4 (32)	0.92	1.61

For both survey locations in the unlimited-radius-plots, the most frequently detected species was Winter Wren, which occurred in all but two stations. Red-breasted Nuthatch, Pacific-slope Flycatcher and Chestnut-backed Chickadee were next most frequently detected species in the unlimited-radius counts. Winter Wren, followed by Vaux's Swift (*Chaetura vauxi*), were the most frequently detected species in the 30 m-fixed radii plots when maximum counts were calculated. However, the canopy-level location detected more individuals of Vaux's Swift more often than the ground-level location. For both survey locations in the unlimited-radius plots, the most abundant species were Red Crossbill, followed by Winter Wren, whereas the latter species was less abundant in the 30 m-plots.

Core Species

Relative Abundance: When the nine core species were pooled, the ground-level observer detected 10 more individuals than the canopy-level observer within 30 m (ANOVA, F = 3.10, df = 19, $P < 0.001$, Table 34). However, when plot band-width increased from 30 m to 75 m, the canopy-level observer recorded 93 more individuals (an increase of 258%), compared with the ground-level observer who detected only 61 more birds (an increase of 133%). The difference between observers was statistically significant (F = 4.14, $P < 0.001$). Beyond 75 m, 81 and 49 more birds were detected by canopy and ground-level observers, respectively. The differences in relative abundance between observers were proportionate when band-width increased from 30 m to 75 m and when band-width increased from 75 m to unlimited: for both increases in band-width, the canopy-level observer detected significantly more individuals (32) than the ground-level observer (F = 5.79, $P < 0.001$). Variability between observers in relative abundance, as measured by the differences in the mean number of birds detected within 30 m, was greatest for Chestnut-backed Chickadee and Golden-crowned Kinglet (Table 34). In 75 m plots, between-observer differences in relative abundance were greatest for Brown Creeper, Chestnut-backed Chickadee, Pacific-slope Flycatcher, and Red-breasted Nuthatch, and smallest for Hermit Warbler and Hermit Thrush. In unlimited VCPs, variability between observers was greatest for Pacific-slope Flycatcher and Red-breasted Nuthatch and smallest for Golden-crowned Kinglet and Hermit Thrush.

Table 34: Mean number of birds per plot for nine species by observer location (flyovers excluded).

English Name	Plot Radius 30 m Canopy	 Ground	 75 m Canopy	 Ground	 Unlimited Canopy	 Ground
Brown Creeper	0.15	0.25	0.60	0.4	0.65	0.50
Chestnut-backed Chickadee	0.40	0.55	1.00	0.75	1.00	0.75
Golden-crowned Kinglet	0.10	0.25	0.35	0.25	0.35	0.25
Gray Jay	0	0.10	0.20	0.35	0.50	0.35
Hermit Thrush	0.05	0.15	0.55	0.5	0.75	0.65
Hermit Warbler	0.05	0.05	0.15	0.15	0.45	0.15
Pacific-slope Flycatcher	0.30	0.2	1.20	0.9	1.30	0.90
Red-breasted Nuthatch	0.15	0.15	0.90	0.7	1.30	0.75
Winter Wren	0.60	0.6	1.50	1.35	1.65	1.35
Total birds	**1.80**	**2.30**	**6.45**	**5.35**	**7.95**	**5.65**
Total species	**1.55**	**1.75**	**4.35**	**3.90**	**5.20**	**4.10**

Detection Frequency: The ground-level observer detected five of nine species more frequently within 30 m, relative to the canopy-level observer (Table 35). When band width increased to 75 m from 30 m, mean detection frequency of the nine species increased 30% and 22% for the canopy-level and ground-level observers, respectively. Mean detection frequency for the nine species beyond 75 m increased 9% for the canopy-level observer compared to an increase of only 2% for the ground-level observer. Variability between observers in species detection frequencies, as measured by the differences in the percentage of VCP in which the species was recorded, was greatest for Chestnut-backed Chickadee, Gray Jay, and Hermit Thrush within 30 m. Comparatively, variability between observers in detection frequencies was greatest for Brown Creeper, Chestnut-backed Chickadee, and Golden-crowned Kinglet in 75 m plots, with each of these species detected 15% more often by the canopy-level observer. Between-observer differences in detection frequencies in unlimited plots were greatest for Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, Gray Jay, Pacific-slope Flycatcher and Red-breasted Nuthatch. No differences among-plot radii or between observer differences in detection frequencies were found for Winter Wren. For the canopy-level observer, Gray Jay, Red-breasted Nuthatch, and then Hermit Warbler were detected more frequently when plot radii exceeded 75 m. For both ground and canopy-level observers, Pacific-slope Flycatcher and Red-breasted Nuthatch were detected more frequently within 75 m radius plots, relative to 30 m radius plots. Detections of Red-breasted Nuthatch by the canopy-level observer continued to increase beyond 75 m.

Table 35: Frequency of occurrence of nine bird species by observer location (flyovers excluded).

English Name	**Percentage of VCP in which species was recorded**					
	30 m		**75 m**		**Unlimited**	
	Canopy	**Ground**	**Canopy**	**Ground**	**Canopy**	**Ground**
Brown Creeper	15	20	50	35	55	40
Chestnut-backed Chickadee	30	40	65	50	65	50
Golden-crowned Kinglet	10	15	30	15	30	15
Gray Jay	0	10	20	30	45	30
Hermit Thrush	5	15	40	30	50	40
Hermit Warbler	5	5	15	15	30	15
Pacific-slope Flycatcher	20	15	65	60	70	60
Red-breasted Nuthatch	15	15	60	65	85	70
Winter Wren	60	60	90	90	90	90

Detection Distances: I pooled the data for the nine core species and compared the relative distribution of detection distances between the canopy- and ground-level observers. When detection frequencies were truncated at 10-m intervals, the canopy-level observer detected significantly more birds than the ground-level observer (Paired Student t-test, $t = 2.20$, $df = 10$, $P = 0.02$). The pooled data shows that 40% and 91% of all birds detected were within 30 m and 70 m of the ground-level observer (Fig. 9). In comparison, only 22% and 79% of birds detected were within 30 m and 70 m of the canopy-level observer. The smoothed polynomial regression lines and corresponding R^2 values were a good fit for the data and showed that detectability declined with distance more rapidly with the observer on the ground, than it did with the observer in the canopy, as noted by the bimodal and right-skewed distribution of canopy-level detections (Fig. 9). The canopy-level detection distances averaged 16 m more than the ground-level observer (Table 36). With the exception of Winter Wren, the mode detection distance of all nine species was greater at the canopy-level than the ground-level (Appendix T).

Table 36: Comparison of detection distances (m) for nine species by observer location.

English Name	**Observer Location**	**Mean ± SE**	**Mode**
Brown Creeper	Canopy	46.8 ± 6.5	35
	Ground	38.0 ± 7.6	20
Chestnut-backed Chickadee	Canopy	36.8 ± 4.6	40
	Ground	25.0 ± 3.4	15
Golden-crowned Kinglet	Canopy	36.4 ± 5.6	35
	Ground	21.3 ± 2.4	25
Gray Jay	Canopy	96.5 ± 14.8	60
	Ground	41.1 ± 6.6	50
Hermit Thrush	Canopy	64.4 ± 5.8	100
	Ground	57.0 ± 9.0	60
Hermit Warbler	Canopy	92.0 ± 20.6	200
	Ground	41.7 ± 17.6	---
Pacific-slope Flycatcher	Canopy	49.8 ± 3.6	70
	Ground	49.5 ± 3.2	50
Red-breasted Nuthatch	Canopy	63.9 ± 5.0	100
	Ground	50.5 ± 4.7	60
Winter Wren	Canopy	47.0 ± 4.8	40
	Ground	33.7 ± 2.4	40
Total	Canopy	56.4 ± 2.6	60
	Ground	40.6 ± 2.0	35

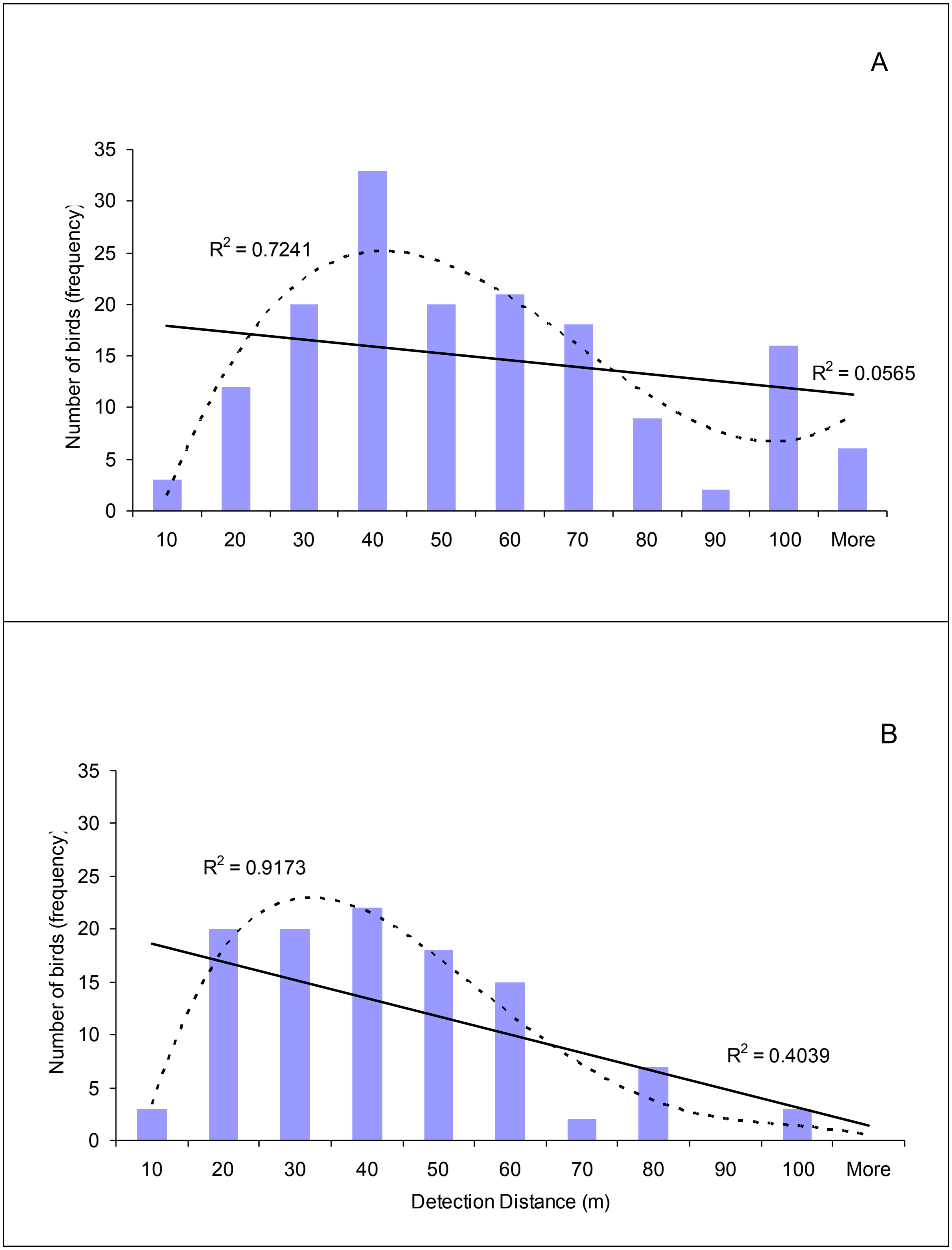


Figure 9: Histogram of A) canopy-level and B) ground-level observer detection distances (m) for nine species (Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, Gray Jay, Hermit Thrush, Hermit Warbler, Pacific-slope Flycatcher, Red-breasted Nuthatch and Winter Wren).

Discussion

The results of the VCP point counts are generally consistent with the findings of Shaw *et al.* (2002) where more species and individuals were detected in the upper canopy than lower in the canopy. I recorded a total of 23 species combining the canopy- and ground-level detections within a 30 m radius. The three year study by Shaw *et al.* (2002) recorded 29 species from their 30 m fixed radius point counts which were conducted at three vertical zones while suspended from a canopy crane's gondola on the Wind River Canopy Crane Research Facility. Although simultaneous canopy- and ground-based counts were not conducted from the crane, and are thus not directly comparable with the methods I describe, the vertical stratification of bird assemblages is similar to the results from this study. With the exception of Vaux's Swift and European Starling, the relative abundance of species detected at the upper and lower levels was similar to my findings. Winter Wren, Chestnut-backed Chickadee, Brown Creeper, Gray Jay, Golden-crowned Kinglet, and Pacific-slope Flycatcher comprised the most frequently detected species in their study, and all were within the top ten most frequently encountered species in this study. An explanation for the decreased detections of Vaux's Swift from the crane gondola, relative to the Tree Plot point counts, might be avoidance of the canopy crane.

Although ground-level based observations resulted in an underestimate of species diversity and density, and paired observers in closed-canopy forests are more likely to obtain precise density estimates (Kissling and Garton 2006), the incorporation of canopy- and ground-level observers for multiple point count stations is logistically restrictive. Where assessments of abundance estimates among observers have been conducted, most studies have only considered differences in ground-based observers. In open habitats, for instance, observers are known to overestimate up to 122% the number of birds present in fixed-radius point counts, whereas bird abundances were underestimated in unlimited-radius counts (Simons *et al*. 2007). Vocalizing birds are less likely to be heard when background noises are present (e.g., other singing birds, wind), and when habitat structure and vegetation are complex. Among-observer estimates of bird abundance in forested landscapes with complex vegetation structure and background noises are subject to error (DeSante 1986) and estimates may be as low as 3% of the total birds present (Pacifici *et al*. 2008).

As the ground-level observer must cope with a complex forest structure above him, so too must a canopy observer cope with a complex forest structure below. Yet, species richness, detection frequencies and bird abundance of the nine core species were significantly greater for the canopy-level observer location and between-observer location differences were more pronounced as distance bands increased in size. That more individuals and species were detected by both canopy- and ground-level observers in subsequent increasing distance band widths is consistent with Thompson and Schwalbach (1995) who showed that unlimited-radius plots resulted in more individuals detected than on 70 m than 50 m radius plots. Thompson and Schwalbach (1995) data were collected by ground-level observers. This suggests that species richness and abundance estimates (and foraging behaviors) could be better assessed by sampling a higher percentage of the habitat. Because the vertical distribution of foliage biomass (Van Pelt *et al.* 2004) and crown volume (Ishii *et al*. 2004) in temperate coniferous forests is greatest between 20 and 40 m, data collection (e.g., point count and foraging data) from within the canopy results in more habitat being sampled, as compared to ground-based sampling procedures.

Another explanation for the canopy-level observer detecting more birds and more species is the tendency for observers to detect more birds that vocalize at a similar height of the observer (Waide and Narins 1988). For instance, ground-level observers in a tropical forest (with a closed canopy at 22 m) underestimated the population of canopy birds by as much as 46%, and observers more readily detected species at their mean singing height (Waide and Narins 1988). Although species mean singing height was not recorded in my study with a closed forest canopy between 50 and 60 m, the canopy-level observer likely detected more birds because bird abundance is greatest in the forest canopy, relative to the lower forest profile (Shaw *et al*. 2002). Ground-level observers recorded 30% fewer species than canopy-level observers in a tropical forest with an average tree canopy height of 35 to 40 m (Anderson 2009). Intervening foliage prohibits both visual and auditory detection from the ground level and upper canopy obligate species occurring at 50 m or higher are beyond the effective detection distance (Reynolds *et al.* 1980). For example, a Hermit Warbler vocalizing from the top of the canopy at 50 m above the ground is only 22 m away from an observer located in the canopy at 40 m. This same Hermit Warbler would be 54 m from a ground-level observer located directly below the canopy-observer. Following, the canopy-level observer has a greater probability of detecting this bird, relative to the ground observer. Thus, the canopy-level observer detected more Hermit Warblers as distance bands increased because Hermit Warblers males sing exclusively from the canopy and subcanopy (Pearson 1997). Similarly, Chestnut-backed Chickadees and Red-breasted Nuthatches, which foraged at mean heights of 21 m and 34 m, respectively, were detected more frequently by the canopy-level observer.

Other possible explanations for between-observer location differences include the variable detectibility of bird vocalizations and inter-observer variability. Bird song frequencies vary among species and attenuate differentially according habitat and weather conditions (Waide and Narins 1988, Pacifici *et al.* 2008). Vegetation and observers (ground-level) have significant effects on auditory detection probabilities (Pacifici *et al.* 2008) and low frequency songs attenuate less rapidly than birds with high frequency songs (Waide and Narins 1988). Low frequency song attenuation could explain among-species detection distance differences. For example, as band widths increased for both observers, the increase in bird abundance was greatest for Hermit Thrush and Red-breasted Nuthatch, which have lower frequency songs, relative to the other core species. Conversely, detection frequencies between observers were similar for Pacific-slope Flycatcher and Winter Wren which have high frequency songs.

Although 80-90% of bird detections in coniferous forests are by vocalizations (Waide and Narins 1988), it remains unknown to what extent detection differences between observer location for the nine core species were due to visual or auditory detection. For instance, I do not know whether the canopy-level observer recorded more individuals of these nine species because he observed them more, or heard them more. However, for some species this was evident. The canopy observer often recorded aerial insectivores and some upper canopy obligate species as flyovers prior to the ground-level flyover. For this reason, Red Crossbills were not included the core group because of the initial detection variability between observers. The canopy-level observer frequently detected Red Crossbills flocks visually flying over the plot before the ground level-observer detected the same flock by ear once they settled in the fixed plot.

Mean species richness detected from the canopy- and ground-level locations in this study is less than the mean reported from three old-growth stands surveyed in Douglas-fir forests in the southern Washington Cascades (Manuwal 1991). My unlimited radius-plots yielded mean species richness of 8.5 and 6.4, from the canopy and ground levels, respectively. With ground-based point counts, Manuwal (1991) surveyed three old growth forests with different moisture regimes and calculated the mean species richness to be 15.0. The cumulative number of species recorded in our unlimited radius plots was 33 and 32 species, from the canopy- and ground-level locations, respectively. Manuwal (1991) reported total species richness for the three sites ranging from 22 to 26. That study also consisted of six visits to the same forest stands over a two year period, which may account for differences between the studies. The size of their point count plots (75 m) does not lend a direct comparison with our unlimited-radius plots, although distinguishing detection distances of songbirds accurately at 75 m and beyond is difficult in dense old-growth stands (Reynolds *et al.* 1980). Nonetheless, the five most abundant bird species in Manuwal (1991) were also within the top nine most abundant species detected by both canopy- and ground-level observers in my study (e.g., Chestnut-backed Chickadee, Golden-crowned Kinglet, Hermit/Townsend Warbler, Western Flycatcher and Winter Wren). The rank order of the top 20 most abundant species detected within 75 m of the canopy observer was not different from the species complex in Manuwal's study (Wilcoxon Signed Rank Sum Test, $z = 1.499$, $P = 0.07$). Conversely, the rank order of the top 20 most abundant species detected within 75 m of the ground observer was statistically different from Manuwal's species complex ($z = 2.012$, $P = 0.02$). These data suggest that the canopy-level observer captured a more comprehensive species complex.

CHAPTER 5

DISCUSSION

Ecological Roles of Epiphytes for the Bird Community

Epiphytes may add to the available pool of ecological niches provided by the host plant by increasing the surface area of temperate forest canopies. The foraging rewards offered to birds by temperate forest epiphytes are not readily observable, compared with the rewards of nectar, pollen or fruit offered by their vascular epiphyte tropical counterparts (Stiles 1978, Nadkarni and Matelson 1988, Sillett 1994). However, temperate forest epiphytes, composed almost entirely of non-vascular plants, do provide insectivorous birds with indirect rewards. Bryophytes and lichens provide opportunities for arthropods to find refuge, forage, rest, aestivate, and or thermoregulate, which offer a forage base for foraging birds, which in turn exert a strong selective pressure that results in the evolution of cryptic coloration and camouflage among invertebrates (Richardson and Young 1977). Arthropods comprise the vast majority of food items for coniferous forest insectivores (Marshall *et al.* 2003) and subsequently other higher trophic levels, which implies that the functional role of epiphytes is an important component affecting canopy biodiversity (Schowalter 1989, McCune 1993, Lindenmayer and Franklin 2002). These lichens and bryophytes also conceal these rewards, requiring specific foraging tactics to capture prey items located within or alighting upon them. Each epiphyte functional group provides additional strata that increase the structural and functional diversity of canopy resources, and foraging opportunities for insectivorous birds. Below I discuss the relationships of each epiphyte functional group and the resources they provide for insectivorous birds.

Foliose lichens including cyanolichens such as *Lobaria oregana* and other conspecifics increase the surface area of the canopy branches and boles and form refugia for arthropods (Behan-Pelletier and Eamer 2001). The appressed and often curled margins of foliose lichens are morphologically similar to peeling bark (Figs. 10 - 12). The broad foliose thallus of *L. oregana* reaches 20 to 30 cm (McCune and Geiser 1997), and functions as a “catcher’s mitt” in the canopy, capturing various potential food items, conifer seed and litterfall that might be lost to granivores and other consumers on the forest floor. Considering the seed rain from *T. heterophylla*, *T. plicata*, and *P. menziesii*, a considerable amount of seed is likely captured by the tree canopy, either deposited on branches or dense splays of foliage. I observed these broad foliose thalli of macrolichens and prostrate bryophytes contributing to the maintenance of perched litter in the canopy (Fig. 11).

Dead, curled leaves suspended above the forest floor form refugia for insects and are important bird foraging habitat (Remsen and Parker 1984). Similarly, the broad, lobed thalli of pendant *L. oregana* and other broad foliose lichens are morphologically analogous to these curled, dead leaves of the tropics. The curled thalli margins likely provide refugia for arthropods. Carpenter ants (*Camponotus* spp.) were often observed beneath the foliose lichen. Nine of all foraging bouts (1%) captured birds gleaning, pecking or searching *Lobaria* spp.

Zygodactylous (two toes facing forward and two facing backward) bark insectivores, such as Brown Creeper and Hairy Woodpecker, are well suited to use these microsites, and inspect *Lobaria* spp. thalli which become pendant when large (Fig. 10). Extracting arthropods from these refugia entails specific foraging behaviors: the bird must hang upside-down or hang sideways on either the cyanolichen itself or the supporting branch while probing these cavities. This niche is unavailable to most anisodactylous (three toes facing forward and one facing backward) songbirds, with the exception of Red-breasted Nuthatch and Chestnut-backed Chickadee. However, some songbirds (e.g., Gray Jay) with larger bills are able to use the upper portions of the *Lobaria* curtains, by extending their heads and reaching under while perched upon a branch. The body weights of some smaller passerines, such as Chestnut-backed Chickadee and Golden-crowned Kinglet, enable them to inspect or capture prey from these pendant epiphytic resources by hovering or hanging briefly.

Alectorioid lichens are known to harbor a species-rich array of arthropods, particularly in the subclass Oribatida (Behan-Pelletier and Eamer 2001). These alectorioid lichens increase the number of ecological niches in the upper canopy, and provide suitable prey items for foraging passerines (Figs. 13 and 14). Alectorioid lichens drape the outer foliage and crowns of old-growth trees. *Alectoria* spp., and *Bryoria* spp. reach lengths of 40 cm, dangling from foliage or branches. They hang in single strands, in dense mats, or may cloak the outer foliage of *T. heterophylla*, and *P. menziesii* (Fig. 14). It is the latter two conditions that allowed Gray Jay to more readily use this resource. Unsupported single strands of the weak-stemmed fruticose alectorioid lichens are unable to sustain the weight of a hanging Gray Jay (70 g), since the cross-section of one *Alectoria sarmentosa* strand is approximately 2.5 mm wide (McCune and Geiser 1997). However, several strands of alectorioid lichens bear the weight of Chestnut-backed Chickadees (9.7 g), enabling birds to hang, inspect and procure food items from the lichens. Both adult and juvenile Gray Jay were observed hanging on lichen cloaked foliage in the upper canopy, although observers were unable to determine whether the individuals procured prey located on the lichens or the tree foliage. Rufous hummingbirds were also observed actively searching alectorioid lichens either for nest material or for prey such as ticks and mites, which inhabit alectorioid lichens in the canopy (Behan-Pelletier and Eamer 2001).

Bryophytes: Appressed and pendant mosses, liverworts, and hornworts provide important community relations offering cryptic opportunities for adult arthropods and their instar larvae (Rhoades 1995, Shaw 2004). Soil accumulates beneath these dense mats, which provides habitat for microorganisms and arthropods (Winchester and Ring 1996). In addition to the complex physical canopy structure provided for by the phorophyte, bryophytes and other epiphytic material ameliorate microclimate, offering thermal protection from inclement weather, providing arthropods refuge sites, and suitable aestivation sites for overwintering arthropod adults or larvae (Fig. 15). Thus, the epiphytes harbor and secure canopy soils, and contribute detritus that provides micro-habitat for microorganisms and other smaller arthropods, which in turn provides a forage base for larger arthropods and other higher trophic levels. Winchester and Ring (1996) reported that these moss mats support a unique assemblage of arthropods, relative to the forest floor, and they speculated that disruption or deterioration of these canopy habitats could decrease the biological diversity of these rich canopy environments. Although specific prey items were not identified in this study, birds were observed taking larger arthropods that inhabit and forage in and beneath appressed bryophytes.

Appressed bryophytes on tree limbs might also offer birds opportunities to bathe in the canopy. One adult Winter Wren male was observed along the Walking Transect perched on appressed moss (*Dicranum* spp.) cloaking the bole of a horizontal log that extended over an ephemeral creek. It was apparently bathing, repeatedly dipping and rubbing his head and plumage body into the appressed moss, and thereafter preening his flight feathers. After the male left the area, I discovered that the *Dicranum* spp. was wet to the touch, saturated by the heavy morning fog. Although this activity occurred approximately 1.5 meters above the ground, it is likely that moist bryophytes in the mid upper canopy also provide bathing opportunities for canopy birds. Winter Wrens are also known to bathe in dew-covered vegetation (Armstrong 1955) and Conures in Amazonia are known to bathe communally in wet moss mats at 23 m above the forest floor (Brightsmith 1999). These bryophytes may be considered the temperate counterparts to the water tanks of tropical bromeliads.

Pendant bryophytes provide some protection against larger-bodied canopy predators and insectivores, by providing arthropods locations to alight some distance below the supporting branch where many birds forage and launch their foraging strikes. The pendant and flimsy bryophytes do not provide stable sites for birds to perch, as do branches or foliage. Thus, arthropods might alight on these pendant bryophytes to avoid predation. However, several bird species can capture these insects with aerial maneuvers. The Pacific-slope Flycatcher was the most frequently observed species taking stationary insects from these pendant bryophytes using their characteristic sally, hover and glean foraging behavior. Another species observed using these pendant bryophytes was Chestnut-backed Chickadee. They searched the foliage and branches primarily with short-flights and hops, and occasionally gleaned stationary insects from pendant bryophytes by hovering or hanging from the bryophytes themselves. Larger bodied birds such as Gray Jay were never observed hanging on pendant bryophytes, presumably because the bryophytes are unable to sustain their weight.

In summary, all epiphyte groups appear to increase the surface area of the canopy crown, increasing the structural diversity and rugosity of the forest canopy. Rugosity is considered a measure of complexity, or in ecological terms, an indicator of the amount of available habitat available for colonization by organisms. Thus, with increased shelter and habitat available for lower trophic levels, these epiphytes provide additional foraging areas for birds. With increased available surfaces provided by epiphytes, structural diversity increases, and a forest canopy replete with epiphytes (mature and old-growth stands) has a greater rumple-factor than a young stand devoid of such arboreal plants. Increased rugosity of forest canopies enables birds to defend spherical territories, due to the complex forest structure (Sharpe 1996). Simplify the forest structure, and birds' territories may have to increase to maintain the same foraging opportunities.

Vertical and horizontal stratification of epiphyte groups in the canopy provide invertebrates with specific microhabitats and microniches in each strata, dictated by the epiphyte group present: alectorioid forage lichens in the inner, mid and outer upper crown; bryophytes in the mid and lower live crown; cyanolichens in the lower canopy; crustose lichens and finely appressed bryophytes in the interior crown, along the bole; and other lichens in the upper outer crown. These lichens and other canopy cryptogams increase the number of ecological niches in the upper canopy, and provide suitable prey items for foraging passerines.

Epiphytes as food: Whether epiphytic mosses or lichens provide PNW forest birds with high quality food in times of food shortages is unknown. However, these epiphytes provide an important food source and egg laying sites for invertebrates, on which many birds depend (Gerson and Seaward 1977). Many lichens contain acids and other anti-herbivory compounds, yet many invertebrates are lichenophagous, feeding on lichen (Gerson and Seaward 1977). Although birds rarely consume canopy lichens directly (except during food shortages), birds may play an important role in keeping these lichenophagous invertebrates in check. Modification or disruption of these coniferous canopy lichen assemblages and communities could alter arthropod and bird communities, and higher trophic levels (Pettersson *et al.* 1995, Uliczka 1999). Similar ecological roles might exist between birds and invertebrates in canopy bryophyte communities.

Epiphyte dispersal limitations and ecological interactions with birds: Factors responsible for lichen and bryophyte reproduction and dispersal in forest canopies are poorly known, although epiphytes may be dispersal limited (Rhoades 1995, Peck and McCune 1997, Sillet and Goslin 1999, Lindemeyer and Franklin 2002). In general, canopy cryptogams reproduce in the tree crowns, either by spore production or asexual fragmentation. Catastrophic storm events and associated winds facilitate horizontal and upward vertical movements of epiphyte propagules and spores. For instance, alectorioid and other pendant fruticose lichens disperse mostly by wind where fragments are cast off and become entangled in nearby limbs. However, canopy lichens and bryophytes in tropical forests rely on biotic mechanisms for spore and propagule dispersal, particularly in still-air environments of inner and mid canopy of middle and lower canopy (Rhoades 1995). Invertebrates (including ants, springtails and mites) disperse lichen soredia (Gerson and Seaward 1977).

Temperate forest canopy vertebrates, including resident and neotropical migratory birds, likely function as important agents of dispersal, particularly during inter-catastrophic weather events. This occurs passively; soredia, spores, and asexual vegetative propagules stick to bird feet, feathers and beaks, when birds perch, brush by or initiate a foraging strike on lichen or bryophyte substrates. Alternatively, some birds may use specific strands and fragments (with propagules attached) from particular species of bryophyte and lichen for nesting substrate. For example, a study of 50 Chestnut-backed Chickadee nests in British Columbia found that 70% of the nests contained bryophytes (Dahlsten *et al.* 2002). For Hutton Vireo, the epiphytic lichen, *Ramalina menziesii* was the most abundant material used in 71% of nests studied in California (Davis 1995). The predominance of the epiphytic lichen was an important factor in the breeding distribution of Hutton's vireos.

In this study, I found a Pacific-slope Flycatcher nest on a fractured piece of bark located on the bole of a *P. menziesii* at approximately 4 m. The rim of the nest was comprised of tightly woven strands of a bryophyte, *Isothecium* spp., and the exterior was decorated with fragments of *Sphaerophorus globosus*. *Isothecium* spp. was prolific on surrounding understory vegetation and suppressed trees. However none was apparent on the bole of the nest host, besides the nest itself. Thus, the flycatcher was involved in relocating these fragments of epiphytes and thus acting as direct dispersal agent. Bryophyte and lichen propagules collected as nesting material might be moved considerable distances, both horizontally and vertically in the forest profile. Approximately 100 bird species that breed in coniferous forests of Oregon and Washington use either lichen or moss for nesting substrate, which implies that substantial non-vascular plant material biomass is relocated and redistributed by birds every nesting season. Because birds are able to move greater distances, relative to their invertebrate counterparts, they are probably more efficient dispersal vectors aiding in both lichen and bryophyte sexual and asexual reproduction. For example, Gray Jays defend breeding territories ranging from 41 to 146 ha (Strickland and Ouellet 2002). Biotic dispersal vectors are also likely more a reliable means for ensuring that propagules are relocated to suitable substrate, relative to catastrophic events brought about by abiotic elements such as storms and high winds. Birds move from one branch to another, which increases the likelihood of "hitchhiking" soredia or propagules finding suitable substrates when the bird next perches. The epiphytes benefit from having the birds transport their propagules and the birds benefit from nest concealment and thermal insulation. Following, maximizing or at least maintaining a certain level of avian diversity in temperate forested landscapes may be a critical component for epiphytes and birds themselves.

Birds may also provide an increasingly critical ecological service, given the current stand age distribution of Washington and Oregon forestlands. Many forestlands are matrix lands which no longer support interconnected canopies. Most non-vascular epiphyte dispersal systems are adapted to a forested landscape of connected canopies, so canopy epiphyte species may be vulnerable to landscape changes (Lindemeyer and Franklin 2002). Could birds then ameliorate the deleterious effects of local or even regional habitat alteration for several dispersal limited epiphytes? Research in managed boreal forests of northern Europe shows otherwise; Petterson *et al*. (1995) suggested that a decline of avian residents is due to diminished foraging habitat quality through reduced lichen availability. Natural forests harbor greater invertebrate diversity than managed forests, supporting more complex and diverse higher trophic levels. Thus, managed forests in North America could suffer similar effects. In addition, large scale disturbances such as global climate change could potentially have significant effects on both tropical canopy epiphytes (Nadkarni and Solano 2002), and temperate forest epiphytes, and it is unlikely that birds could adequately compensate for such dramatic changes.

Figure 10: *Lobaria oregana* at 30 m provide refugia for canopy arthropods, prey items for canopy birds.

Figure 11: The broad thallus of *Lobaria oregana*, at 30 m capture seed rain and litterfall.

Figure 12: *Platismatia glauca*, a foliose lichen provides habitat for a dipteran at 30 m.

Figure 13: Alectorioid lichens on the bole of *Pseudotsuga menziesii* at 26 m.

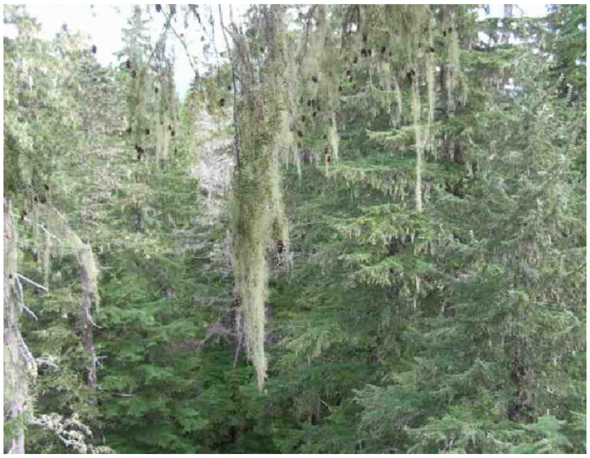


Figure 14: At 30 m, *Alectoria sarmentosa* cloaks the foliage on *Tsuga heterophylla.*

Figure 15: Appressed and pendant bryophytes cover the limbs of *Taxus brevifolia*.

Contribution of epiphytes and birds to the nutrient cycles: The contribution of epiphytes to the nutrient cycle and hydrological regime in forest ecosystems has received much attention (Pike 1978, Coxson and Nadkarni 1995). Formerly considered "nutrient pirates" (Benzing 1981), epiphytes are now known to significantly alter throughfall, "fertilizing" the forest with additional minerals that would not be deposited through normal processes of decay. Nutrients for the biological needs of most canopy epiphytes are allochthonous, derived primarily from atmospheric inputs of nitrogen. These canopy cryptogams release nutrients through decay, litterfall, and leachate. In some productive rainforest systems, epiphyte litterfall and leachate may contribute nitrogen and biomass greater or equal to that provided by the phorophyte (Nadkarni 1983, Rhoades 1995). Furthermore, these releases of water and minerals typically occur during dry periods, which supplement both the canopy environment and forest floor, long after the last rain (Nadkarni 1984, 1985).

Considering the community interactions of forest fauna with canopy epiphytes lends even more complexity to the nutrient cycle. Consumption and subsequent excretion of canopy prey items are redistributed throughout the canopy by birds, which are either retained in the canopy for use by bacteria, microepiphytes and other microorganisms, or sent to the forest floor by throughfall and litterfall. Yet, models showing nitrogen fluxes within old-growth conifer canopies of the PNW fail to include the contribution of nitrogen by birds in these mineral fluxes (Carroll 1980, Rhoades 1995). Birds move constantly either in search of food, nest sites, plucking locations, or to avoid predators, and in the process deposit fecal matter throughout the canopy. These fecal deposits are rich in phosphorus, nitrogen, and other trace minerals, which may be sequestered by canopy cryptogams and perhaps the phorophyte, through specialized mechanisms such as arboreal roots (Nadkarni 1983).

It appears that birds might play a role in the fertilization process of forest systems, and the magnitude of such role for each forest would be moderated by bird abundance, site productivity, and habitat type. Increased stand age alone and associated epiphyte loads might not be the only important variables responsible for maintaining ecosystem biochemical function. Further study is needed to measure and quantify fecal input for temperate coniferous forest birds to contribute to our understanding of birds' role in the nutrient cycle.

Study Limitations

This study documented that forest birds use epiphyte resources during the breeding season but did not address annual or temporal differences (Brennan *et al.* 2000). Since canopy arthropod activity is affected by weather extremes and moisture fluctuations, which occur in the canopy organic matter (Coxson and Nadkarni 1995), so too will the composition and foraging activities of higher trophic levels that depend on these resources. Although Grubb (1975) reported inclement weather affecting bird activity downward vertically, winter at the RNA coincides with snowfall and cooler conditions in the understory, and bird activity shifts to the upper canopy (Shaw et al. 2002). The interaction of epiphytes and birds in the winter remains unknown.

There was likely some effect of the canopy- and ground-level observers in the Tree Plots, although this was not quantified. The presence of the ground-level observer walking around the perimeter of the viewing arena in the Tree Plot could have affected understory and lower canopy bird activity within the Plot. Perhaps if the ground-level observer remained stationary, and recorded activities in the viewing arena from one location, more birds might have moved into the arena. Also, the climbing activity and the "shadow" of the canopy observer could have also suppressed bird activity in the understory and lower-canopy levels. More birds were observed at the canopy level than ground level, although this could also be a function of vertical stratification of bird assemblages in these forests (Shaw *et al.* 2002). A similar canopy study in the tropics speculated no effects of the canopy observers due to the close proximity of the observer to several foraging individuals (Nadkarni and Matelson 1989). This study documented similar accounts of foraging activities within several meters of the canopy observer (e.g., both adult and fledgling individuals of Chestnut-backed Chickadee, Red-breasted Nuthatch, and Gray Jay). However, these bird species are more tolerant of human presence. Thus, the data might bias the foraging records of these "kulturfolgers", culture followers (Rosenzweig 2003). Larger-bodied bird species were never or rarely detected in the Tree Plots. Examples of such skittish birds include Pileated Woodpecker, Hairy Woodpecker, and Hermit Thrush. Foraging events were recorded for these species along the Walking Transect but never in the Tree Plots. The majority of the foraging activities in the Tree Plots and along the Walking Transects did not seem to be affected by the observers.

CHAPTER 6

CONCLUSION AND IMPLEMENTATIONS FOR FOREST MANAGEMENT

Epiphytes as Foraging Habitat

Epiphytes were used as foraging resources by forest birds in an old-growth *Pseudotsuga menziesii*/*Tsuga heterophylla* forest in the southern Washington Cascades. Determining the ecological roles between birds and epiphytes and the relative use of epiphytes as compared to other forest structural components (e.g., foliage, bark) lends new insights into the use of a complex forest canopy. An abundant epiphyte community contributes to bird diversity because it increases the canopy rugosity, and adds to the structural complexity of the forest canopy, offering non-tree resources for harboring prey, and providing opportunities for resource specialization.

Understanding both the biotic and abiotic roles of canopy epiphytes and their importance for forest ecosystems will allow forest managers to implement ecologically sound management. Quantifying the importance of epiphytes for birds provides scientific justification for implementing these recommendations. Documenting ecological interactions in the canopy, and understanding the foraging opportunities afforded by epiphytes is vital for forest managers to manage for maximizing biodiversity elements. The importance of understanding the roles of bird and canopy epiphytes include the ability to predict and mitigate impacts to forest structures and functions that result from loss of epiphytic species, harvesting effects, or alterations in bird or epiphyte communities. For instance, current forest management objectives in the State of Washington enforce policies that facilitate a sustainable harvest. Most forests stands in Washington state lands are either selectively harvested or clear cut around the time that wood production peaks (40 to 80 years of age). However, epiphyte diversity peaks at forest ages of more than 200 years (McCune 1993). Therefore, since forests are harvested at a relatively young age where epiphyte communities are unable to mature, and since birds use these diverse epiphytic communities hosted by old growth, the ability to maximize species diversity may be compromised.

Another important component of understanding bird and canopy epiphyte interactions is having the ability to determine seasonal variations and identify their ecological roles with other trophic levels. For instance, epiphytes may play an important part in providing auxiliary resources not only during the breeding season, but perhaps during the non-breeding season. Some epiphytes (such as canopy moss mats) support unique arthropod communities (Winchester & Ring 1996), and birds may rely on these auxiliary resources when their primary food sources are no longer available. Schowalter and Ganio (1998) showed that four old-growth forest tree species had distinct arthropod communities and concluded that forests managed for fewer trees reduce arthropod diversity.

Understanding these roles also has important management implications for restoration performance standards. An important conservation tenet for forest managers regulating timber harvest is protecting biodiversity and also sustaining healthy forests. Integrated and comprehensive ecosystem management programs are necessary to conserve the entire suite of species associated with particular habitats. Except for the Northwest Forest Plan (USDA and USDI 1994), few conservation programs have considered the ecological role of epiphytes in their conservation strategies. Rather, most plans focus on conserving specific habitat important for the target species (e.g., old-growth forest for the Northern Spotted Owl and Marbled Murrelet). These fine-scale approaches to conserving "indicator species" assume that preserving target species habitat often extends preservation to habitat of species other than the target species. However, there are few mechanisms other than adaptive management procedures associated with the target species that evaluate whether these assumptions are valid.

Point Counts

Ground-based point counts are considered the best method to calculate and compare relative abundance and species richness between sites (Ralph *et al*. 1995). However point counts are subject to error in complex three-dimensional habitats (DeSante 1986). These counts are used to calculate species diversity indices, and although these ground-based assessments may sufficiently account for all bird species present, they may underestimate the true number of individuals that use the uppermost portions of the canopy, including upper canopy obligate species which forage at or above the canopy level. Variable circular plot point counts from the canopy level facilitated a more comprehensive assessment of species abundances and richness, and canopy-level point counts in unlimited- and fixed-radius plots also accounted for more flyovers, which are equally as important components of forest bird assemblages as the canopy-dependent songbirds. Observer location is an important determinant for recording bird foraging height and activity. This study does not show that point count observers need to access the forest canopy, but managers should recognize that species richness and bird abundances are likely underestimated when counts are conducted from the ground-level. Furthermore, ground-based point count assessments may not provide an adequate assessment of occupancy or presence for canopy-dependent songbirds. I suggest that point counts conducted by paired ground-based observers in closed-canopy forests are used to obtain precise density estimates (e.g., Kissling and Garton 2006) because the incorporation of canopy- and ground-level observers for multiple point count stations is logistically restrictive. The use of remote acoustic equipment located at fixed height intervals throughout the forest's vertical profile could also be used to detect forest birds.

Future Research

In some PNW coastal temperate rainforests, every square meter on every tree is occupied by an epiphyte. These rainforests harbor tremendous epiphyte biomass in the canopy, which may exceed the leaf biomass of the phorophyte (Coxson and Nadkarni 1995). Canopy mist-netting studies (Holbrook 2006) with the use of emetics to analyze stomach contents (Sillett 1994) offer opportunities to determine what prey are being taken by canopy birds. Since epiphyte communities harbor unique arthropod assemblages, a study that incorporates: 1) foraging observations, 2) canopy mist netting and use of an emetic, and 3) correlates arthropod abundances by epiphyte habitat could shed light on the relative contributions of epiphyte-related prey items for the bird community. Furthermore, forest habitats are dynamic systems which rely on natural disturbance regimes that alter epiphyte communities, and the interactions between birds and their habitats. If birds respond positively to silviculture practices that develop and retain structural integrity and their epiphyte communities, this knowledge of the interactions between these communities would assist forest managers charged with managing forests for biodiversity or target species.

Conclusions

The literature search increased the geographical range and number of birds known to use lichens in their nests. In Washington and Oregon, 100 bird species that breed in coniferous forest use either bryophyte, lichen or mistletoe in their nests. Furthermore, my canopy- and ground-based field surveys showed that almost 30% of all foraging activities involved epiphyte substrates. Epiphytes significantly increase the inner canopy rugosity and provide important ecological functions for birds and higher trophic levels. Because macrolichen and bryophyte species richness in PNW temperate forests is considered high relative to tropical forests (Rhoades 1995), conservation and maintenance of epiphyte forms and habitats is essential in maintaining total biodiversity of our forest systems. Approximately 65% of the world's terrestrial taxa occur in forest ecosystems (Lindenmayer and Franklin 2002). Yet, the vast majority (between 90 and 95%) of the world's forests have no formal protection and preservation of coniferous evergreen forests is relatively low, relative to other habitats in non-tropical forests (Lindenmeyer and Franklin 2002).

The Northwest Forest Plan (USDA and USDI 1994) mandated that forests be managed for biodiversity. However, establishing reserves does not fully guarantee the long-term viability and biodiversity of a forest stand. Buffers, connectivity, and provisions of ecological services are considerations that need to be addressed, particularly if epiphyte peak distributions and abundances are sought. To provide prime foraging habitat for forest birds, land managers should consider the epiphyte vegetative community structure within foraging habitat.

In my study, birds used all tree species proportionately as foraging locations, but used tree species disproportionately when foraging on epiphytes. Thus, forest managers should retain a diversity of leave tree species and understory trees and shrubs that maximize epiphyte loads and maintain canopy connections. Aggregate or dispersed tree retention is known to benefit old-growth dependent lichens (Sillett *et al*. 2000), and other epiphyte species with dispersal limitations. Forest practices may include:

1. retaining large live trees with large branches (associated with lichens and bryophytes);
2. retaining dead, decayed snags and logs because these have rich bryophyte communities;
3. retaining hardwoods such as big-leaf maple (*Acer macrophyllum*) which support rich bryophyte communities; and
4. retaining or enhancing diversity of understory vegetation.

Because greater structural complexity supports more invertebrate habitats and epiphyte communities and because epiphyte communities change with succession and reach their climax in old-growth stands (McCune 1993), forest managers should implement practices that maintain old-growth structural characteristics to enhance bird species communities.

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APPENDICES

Appendix A: North American and Oregon/Washington breeding birds that use non-vascular plants, Spanish Moss, epiphytic rootlets, or mistletoe as nesting substrates.

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
ANSERIFORMES	**SCREAMERS, DUCKS & RELATIVES**						
ANATIDAE	**SWANS, GEESE & DUCKS**						
Anser brachyrhynchus	Pink-footed Goose	X	X				no
Anser albifrons	Greater White-fronted Goose	X	X				no
Branta bernicla	Brant	X	X				no
Branta canadensis	Canada Goose	X	X				no
Cygnus columbianus	Tundra Swan	X					no
Cygnus cygnus	Whooper Swan	X					no
Aythya collaris	Ring-Necked Duck	X					no
Clangula hyemalis	Long-Tailed Duck	X					no
Mergus merganser	Common Merganser	X					yes
Somateria fischeri	Spectacled Eider	X					no
Somateria mollissima	Common Eider	X					no
PHASIANIDAE	**QUAIL, PHEASANTS & RELATIVES**						
Falcipennis canadensis	Spruce Grouse	X					yes
Lagopus lagopus	Willow Ptarmigan	X					no
Lagopus muta	Rock Ptarmigan	X					no
Lagopus leucura	White-Tailed Ptarmigan		X				no
Dendragapus obscurus	Blue Grouse	X					yes
Tympanuchus phasianellus	Sharp-Tailed Grouse	X					no
GAVIIFORMES	**LOONS**						
GAVIIDAE	**LOONS**						
Gavia stellata	Red-Throated Loon	X					no

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
Gavia pacifica	Pacific Loon	X					no
Gavia immer	Common Loon	X					no
PELECANIFORMES	**TROPICBIRDS, PELICANS & RELATIVES**						
PHALACROCORACIDAE	**CORMORANTS**						
Phalacrocorax penicillatus	Brandt's Cormorant	X					no
Phalacrocorax pelagicus	Pelagic Cormorant	X					no
FALCONIFORMES	**VULTURES, HAWKS & FALCONS**						
ACCIPITRIDAE	**HAWKS, OLD WORLD VULTURES & HARRIERS**						
Accipiter cooperii	Cooper's Hawk					X	yes
Aquila chrysaetos	Golden Eagle	X	X				yes
Buteo brachyurus	Short-Tailed Hawk	X	X	X			no
Buteo lagopus	Rough-Legged Hawk	X					no
Buteo lineatus	Red-Shouldered Hawk	X	X				yes
Buteo platypterus	Broad-Winged Hawk		X				no
Buteo swainsoni	Swainson's Hawk		X				no
Buteogallus anthracinus	Common Black-Hawk					X	no
Elanoides forficatus	Swallow-Tailed Kite	X	X	X			no
Elanus leucurus	White-tailed Kite	X		X			no
Haliaeetus leucocephalus	Bald Eagle	X					yes
Parabuteo unicinctus	Harris's Hawk			X			no
GRUIFORMES	**CRANES, RAILS & RELATIVES**						
ARAMIDAE	**LIMPKIN**						
Aramus guarauna	Limpkin			X			no
GRUIDAE	**CRANES**						
Grus canadensis	Sandhill Crane	X					no
CHARADRIIDAE	**PLOVERS & RELATIVES**						
Charadrius semipalmatus	Semipalmated Plover	X					no

Standard Name	**English Name**	**Substrate**					**OR/WA Coniferous Forest Breeder**
		Bryophyte	**Lichen**	**Spanish Moss**	**Epiphytic Rootlet**	**Mistletoe**	
Pluvialis apricaria	European Golden-Plover	X					no
Pluvialis dominica	American Golden-Plover	X	X				no
Pluvialis squatarola	Black-bellied Plover	X	X				no
SCOLOPACIDAE	**SANDPIPERS & RELATIVES**						
Tringa melanoleuca	Greater Yellowlegs	X					no
Tringa flavipes	Lesser Yellowlegs	X					no
Actitis macularius	Spotted Sandpiper	X					no
Numenius phaeopus	Whimbrel	X	X				no
Numenius tahitiensis	Bristle-Thighed Curlew	X	X				no
Limosa lapponica	Bar-Tailed Godwit	X	X				no
Arenaria interpres	Ruddy Turnstone	X					no
Aphriza virgata	Surfbird	X	X				no
Calidris canutus	Red Knot		X				no
Calidris alba	Sanderling		X				no
Calidris mauri	Western Sandpiper	X	X				no
Calidris minutilla	Least Sandpiper	X					no
Calidris fuscicollis	White-Rumped Sandpiper	X					no
Calidris bairdii	Baird’s Sandpiper		X				no
Calidris maritima	Purple Sandpiper		X				no
Calidris ptilocnemis	Rock Sandpiper	X	X				no
Calidris alpina	Dunlin		X				no
Tryngites subruficollis	Buff-Breasted Sandpiper	X					no
Limnodromus scolopaceus	Long-Billed Dowitcher	X					no
Gallinago gallinago	Common Snipe	X					no
Phalaropus tricolor	Wilson’s Phalarope	X					no
Phalaropus lobatus	Red-Necked Phalarope	X					no
Phalaropus fulicarius	Red Phalarope	X	X				no
LARIDAE	**SKUAS, GULLS, TERNS & SKIMMERS**						
Stercorarius pomarinus	Pomarine Jaeger	X					no

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	**Lichen**	**Spanish Moss**	**Epiphytic Rootlet**	**Mistletoe**	
Stercorarius parasiticus	Parasitic Jaeger	X	X				no
Stercorarius longicaudus	Long-Tailed Jaeger	X					no
Larus philadelphia	Bonaparte's Gull	X	X				no
Larus canus	Mew Gull	X	X				no
Larus argentatus	Herring Gull	X					no
Larus thayeri	Thayer's Gull	X					no
Larus glaucoides	Iceland Gull	X	X				no
Larus hyperboreus	Glaucous Gull	X					no
LARIDAE	**SKUAS, GULLS, TERNS & SKIMMERS**						
Larus marinus	Great Black-Backed Gull	X					no
Rissa tridactyla	Black-Legged Kittiwake	X					no
Rissa brevirostris	Red-Legged Kittiwake	X					no
Rhodostethia rosea	Ross's Gull	X	X				no
Pagophila eburnea	Ivory Gull	X	X				no
Sterna caspia	Caspian Tern	X					no
Sterna paradisaea	Arctic Tern	X					no
Sterna aleutica	Aleutian Tern	X					no
ALCIDAE	**AUKS, MURRES & PUFFINS**						
Brachyramphus marmoratus	Marbled Murrelet	X	X				yes
Brachyramphus brevirostris	Kittlitz's Murrelet	X					no
Ptychoramphus aleuticus	Cassin's Auklet	X					yes
Cerorhinca monocerata	Rhinoceros Auklet	X					no
COLUMBIFORMES	**PIGEONS & DOVES**						
COLUMBIDAE	**PIGEONS & DOVES**						
Patagioenas fasciata	Band-Tailed Pigeon	X					yes
CUCULIFORMES	**CUCKOOS & RELATIVES**						
CUCULIDAE	**TYPICAL CUCKOOS**						
Coccyzus americanus	Yellow-Billed Cuckoo	X					no

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
STRIGIFORMES	**OWLS**						
STRIGIDAE	**TYPICAL OWLS**						
Bubo virginianus	Great Horned Owl	X					yes
Bubo scandiacus	Snowy Owl	X	X				no
Glaucidium gnoma	Northern Pygmy-Owl	X					yes
Strix occidentalis	Spotted Owl					X	yes
Strix varia	Barred Owl		X				yes
Strix nebulosa	Great Gray Owl	X					yes
Aegolius acadicus	Northern Saw-Whet Owl	X					yes
CAPRIMULGIFORMES	**GOATSUCKERS & RELATIVES**						
CAPRIMULGIDAE	**GOATSUCKERS**						
Chordeiles minor	Common Nighthawk	X	X				yes
APODIFORMES	**SWIFTS & HUMMINGBIRDS**						
APODIDAE	**SWIFTS**						
Cypseloides niger	Black Swift	X					yes
Aeronautes saxatalis	White-Throated Swift	X					yes
TROCHILIDAE	**HUMMINGBIRDS**						
Cynanthus latirostris	Broad-Billed Hummingbird		X				no
Hylocharis leucotis	White-Eared Hummingbird	X	X				no
Amazilia beryllina	Berylline Hummingbird		X				no
Amazilia yucatanensis	Buff-Bellied Hummingbird		X				no
Amazilia violiceps	Violet-Crowned Hummingbird		X				no
Lampornis clemenciae	Blue-Throated Hummingbird	X					no
Eugenes fulgens	Magnificent Hummingbird	X	X				no
Calothorax lucifer	Lucifer Hummingbird		X				no
Archilochus colubris	Ruby-Throated Hummingbird		X				no
Archilochus alexandri	Black-Chinned Hummingbird	X	X				yes

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
Calypte anna	Anna’s Hummingbird	X	X				yes
Calypte costae	Costa’s Hummingbird		X				no
Stellula calliope	Calliope Hummingbird	X	X				yes
Selasphorus platycercus	Broad-Tailed Hummingbird	X	X				yes
Selasphorus rufus	Rufous Hummingbird	X	X				yes
Selasphorus sasin	Allen’s Hummingbird	X	X				yes
TROGONIFORMES							
TROGONIDAE	**TROGONS**						
Trogon elegans	Elegant Trogon	X					no
PASSERIFORMES	**PERCHING BIRDS**						
TYRANNIDAE	**TYRANT FLYCATCHERS**						
Camptostoma imberbe	Northern Beardless-Tyrannulet					X	no
Contopus cooperi	Olive-Sided Flycatcher	X	X				yes
Contopus pertinax	Greater Pewee		X				no
Contopus sordidulus	Western Wood-Pewee	X	X				yes
Contopus virens	Eastern Wood-Pewee		X				no
Empidonax flaviventris	Yellow-Bellied Flycatcher	X					no
Empidonax alnorum	Alder Flycatcher	X					no
Empidonax traillii	Willow Flycatcher		X				yes
Empidonax minimus	Least Flycatcher	X	X				yes
Empidonax hammondii	Hammond's Flycatcher	X	X				yes
Empidonax oberholseri	Dusky Flycatcher		X				yes
Empidonax difficilis	Pacific-Slope Flycatcher	X	X				yes
Empidonax occidentalis	Cordilleran Flycatcher	X					no
Empidonax fulvifrons	Buff-Breasted Flycatcher		X				no
Sayornis nigricans	Black Phoebe	X					no
Sayornis phoebe	Eastern Phoebe	X					no

Standard Name	**English Name**	**Substrate**					**OR/WA Coniferous Forest Breeder**
		Bryophyte	**Lichen**	**Spanish Moss**	**Epiphytic Rootlet**	**Mistletoe**	
Sayornis saya	Say's Phoebe	X					yes
Pyrocephalus rubinus	Vermilion Flycatcher		X				no
Pitangus sulphuratus	Great Kiskadee	X		X			no
Tyrannus melancholicus	Tropical Kingbird	X					no
Tyrannus couchii	Couch's Kingbird	X		X			no
Tyrannus forficatus	Scissor-Tailed Flycatcher	X		X			no
Pachyramphus aglaiae	Rose-Throated Becard	X	X				no
LANIIDAE	**SHRIKES**						
Lanius ludovicianus	Loggerhead Shrike	X	X				no
Lanius excubitor	Northern Shrike	X					no
VIREONIDAE	**TYPICAL VIREOS**						
Vireo griseus	White-Eyed Vireo	X	X				no
Vireo flavifrons	Yellow-Throated Vireo		X				no
Vireo cassinii	Cassin's Vireo	X	X				yes
Vireo huttoni	Hutton’s Vireo	X	X	X			yes
Vireo gilvus	Warbling Vireo		X				yes
Vireo philadelphicus	Philadelphia Vireo		X				no
Vireo olivaceus	Red-Eyed Vireo		X				yes
Vireo altiloquus	Black-Whiskered Vireo		X				no
CORVIDAE	**JAYS, MAGPIES & CROWS**						
Perisoreus canadensis	Gray Jay	X	X				yes
Cyanocitta stelleri	Steller’s Jay	X					yes
Cyanocitta cristata	Blue Jay	X	X	X			yes
Cyanocorax yncas	Green Jay	X					no
Aphelocoma californica	Western Scrub-Jay	X					yes
Gymnorhinus cyanocephalus	Pinyon Jay	X					yes
Nucifraga columbiana	Clark’s Nutcracker	X					yes
Corvus brachyrhynchos	American Crow	X					yes
Corvus caurinus	Northwestern Crow	X					yes

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
Corvus corax	Common Raven	X					yes
HIRUNDINIDAE	**SWALLOWS**						
Tachycineta bicolor	Tree Swallow	X					yes
Stelgidopteryx serripennis	Northern Rough-Winged Swallow	X					yes
PARIDAE	**TRUE TITS**						
Poecile carolinensis	Carolina Chickadee	X					no
Poecile atricapillus	Black-Capped Chickadee	X					yes
Poecile gambeli	Mountain Chickadee	X	X				yes
Poecile rufescens	Chestnut-Backed Chickadee	X					yes
Poecile hudsonica	Boreal Chickadee	X	X				yes
Poecile cincta	Gray-Headed Chickadee	X					no
Baeolophus inornatus	Oak Titmouse	X					yes
Baeolophus ridgwayi	Juniper Titmouse	X					yes
Baeolophus bicolor	Tufted Titmouse	X					no
AEGITHALIDAE	**LONG-TAILED TITS**						
Psaltriparus minimus	Bushtit	X	X			X	yes
SITTIDAE	**NUTHATCHES**						
Sitta carolinensis	White-Breasted Nuthatch	X					yes
Sitta pygmaea	Pygmy Nuthatch	X	X				yes
CERTHIIDAE	**HOLARCTIC TREECREEPERS**						
Certhia americana	Brown Creeper	X	X				yes
TROGLODYTIDAE	**WRENS**						
Salpinctes obsoletus	Rock Wren	X					yes
Catherpes mexicanus	Canyon Wren	X	X				yes
Thryothorus ludovicianus	Carolina Wren	X					no
Thryomanes bewickii	Bewick's Wren	X					yes
Troglodytes troglodytes	Winter Wren	X					yes

Standard Name	English Name	Substrate Bryophyte	 Lichen	 Spanish Moss	 Epiphytic Rootlet	 Mistletoe	OR/WA Coniferous Forest Breeder
CINCLIDAE	**DIPPERS**						
Cinclus mexicanus	American Dipper	X					yes
REGULIDAE	**KINGLETS**						
Regulus satrapa	Golden-Crowned Kinglet	X	X				yes
Regulus calendula	Ruby-Crowned Kinglet	X	X				yes
SYLVIIDAE	**OLD-WORLD WARBLERS & GNATCATCHERS**						
Phylloscopus borealis	Arctic Warbler	X					no
Polioptila caerulea	Blue-Gray Gnatcatcher		X				yes
Polioptila melanura	Black-Tailed Gnatcatcher		X				no
TURDIDAE	**THRUSHES**						
Luscinia svecica	Bluethroat	X					no
Oenanthe oenanthe	Northern Wheatear	X					no
Sialia mexicana	Western Bluebird	X					yes
Myadestes townsendi	Townsend's Solitaire	X	X				yes
Catharus fuscescens	Veery	X					yes
Catharus minimus	Gray-Cheeked Thrush	X	X				no
Catharus bicknelli	Bicknell's Thrush	X	X				no
Catharus ustulatus	Swainson's Thrush	X	X				yes
Catharus guttatus	Hermit Thrush	X	X				yes
Turdus pilaris	Fieldfare	X					no
Turdus iliacus	Redwing	X	X				no
Turdus migratorius	American Robin	X					yes
Ixoreus naevius	Varied Thrush	X	X				yes
TIMALIIDAE	**BABBLERS**						
Chamaea fasciata	Wrentit		X				yes
STURNIDAE	**STARLINGS & ALLIES**						
Sturnus vulgaris	European Starling	X	X				yes

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
MOTACILLIDAE	**WAGTAILS & PIPITS**						
Motacilla alba	White Wagtail	X	X				no
Anthus cervinus	Red-Throated Pipit	X					no
Anthus rubescens	American Pipit	X					no
BOMBYCILLIDAE	**WAXWINGS**						
Bombycilla garrulus	Bohemian Waxwing	X	X				no
Bombycilla cedrorum	Cedar Waxwing	X					yes
PTILOGONATIDAE	**SILKY-FLYCATHERS**						
Ptilogony spp.	Silky Flycatcher		X				no
Phainopepla nitens	Phainopepla					X	no
PEUCEDRAMIDAE	**OLIVER WARBLER**						
Peucedramus taeniatus	Olive Warbler	X	X				no
PARULIDAE	**WOOD WARBLERS & RELATIVES**						
Vermivora bachmanii	Bachman’s Warbler		X	X			no
Vermivora celata	Orange-Crowned Warbler	X					yes
Vermivora ruficapilla	Nashville Warbler	X	X				yes
Vermivora virginiae	Virginia’s Warbler	X	X				no
Parula americana	Northern Parula		X	X			no
Parula pitiayumi	Tropical Parula	X		X			no
Dendroica magnolia	Magnolia Warbler	X					no
Dendroica tigrina	Cape May Warbler	X					no
Dendroica caerulescens	Black-Throated Blue Warbler	X					no
Dendroica coronata	Yellow-Rumped Warbler	X	X				yes
Dendroica nigrescens	Black-Throated Gray Warbler	X					yes
Dendroica virens	Black-Throated Green Warbler	X					no
Dendroica townsendi	Townsend’s Warbler	X	X				yes
Dendroica occidentalis	Hermit Warbler	X	X				yes
Dendroica fusca	Blackburnian Warbler		X				no

Standard Name	**English Name**	**Substrate**					**OR/WA Coniferous Forest Breeder**
		Bryophyte	**Lichen**	**Spanish Moss**	**Epiphytic Rootlet**	**Mistletoe**	
Dendroica dominica	Yellow-Throated Warbler			X			no
Dendroica kirtlandii	Kirtland’s Warbler	X					no
Dendroica striata	Blackpoll Warbler	X	X				no
Dendroica cerulea	Cerulean Warbler	X	X				no
Setophaga ruticilla	American Redstart	X	X				no
Protonotaria citrea	Prothonotary Warbler	X	X				no
Helmitheros vermivorum	Worm-Eating Warbler	X					no
Limnothlypis swainsonii	Swainson’s Warbler	X					no
Seiurus aurocapilla	Ovenbird	X					no
Seiurus noveboracensis	Northern Waterthrush	X					no
Seiurus motacilla	Louisiana Waterthrush	X					no
Oporornis agilis	Connecticut Warbler	X					no
Geothlypis trichas	Common Yellowthroat	X					yes
Wilsonia citrina	Hooded Warbler	X					no
Wilsonia pusilla	Wilson’s Warbler	X					yes
Wilsonia canadensis	Canada Warbler	X					no
THRAUPIDAE	**TANAGERS & HONEYCREEPERS**						
Piranga rubra	Summer Tanager			X			no
Piranga ludoviciana	Western Tanager	X	X				yes
EMBERIZIDAE	**EMBERIZINES**						
Pipilo aberti	Abert’s Towhee					X	no
Spizella arborea	American Tree Sparrow	X	X				no
Pooecetes gramineus	Vesper Sparrow	X					no
Amphispiza bilineata	Black-Throated Sparrow					X	no
Ammodramus savannarum	Grasshopper Sparrow	X					no
Passerella iliaca	Fox Sparrow	X	X				yes
Melospiza lincolnii	Lincoln’s Sparrow	X					no
Zonotrichia albicollis	White-Throated Sparrow	X					no
Zonotrichia querula	Harris’s Sparrow	X					no

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
Zonotrichia leucophrys	White-Crowned Sparrow	X					yes
Zonotrichia atricapilla	Golden-Crowned Sparrow	X					no
Junco hyemalis	Dark-Eyed Junco	X					yes
Junco phaeonotus	Yellow-Eyed Junco	X					no
Calcarius mccownii	McCown's Longspur		X				no
Calcarius lapponicus	Lapland Longspur	X					no
Plectrophenax nivalis	Snow Bunting	X	X				no
CARDINALIDAE	**CARDINALS, GROSBEAKS & ALLIES**						
Cardinalis cardinalis	Northern Cardinal			X			no
Passerina cyanea	Indigo Bunting		X	X			no
ICTERIDAE	**BLACKBIRDS, ORIOLES & ALLIES**						
Euphagus carolinus	Rusty Blackbird	X	X				no
Euphagus cyanocephalus	Brewer's Blackbird	X					yes
Quiscalus quiscula	Common Grackle		X	X			no
Quiscalus mexicanus	Great-Tailed Grackle			X			no
Icterus cucullatus	Hooded Oriole			X			no
Icterus bullockii	Bullock's Oriole	X				X	yes
Icterus pectoralis	Spot-Breasted Oriole				X		no
Icterus gularis	Altamira Oriole				X		no
Icterus galbula	Baltimore Oriole			X			no
FRINGILLIDAE	**FRINGILLINE FINCHES**						
Fringilla montifringilla	Brambling	X	X				no
Leucosticte tephrocotis	Gray-Crowned Rosy-Finch	X	X				yes
Leucosticte atrata	Black Rosy-Finch	X					yes
Leucosticte australis	Brown-Capped Rosy-Finch	X					no
Pinicola enucleator	Pine Grosbeak	X	X				yes
Carpodacus purpureus	Purple Finch	X					yes
Carpodacus cassinii	Cassin's Finch		X				yes
Loxia curvirostra	Red Crossbill	X	X				yes

Standard Name	English Name	Substrate					OR/WA Coniferous Forest Breeder
		Bryophyte	Lichen	Spanish Moss	Epiphytic Rootlet	Mistletoe	
Loxia leucoptera	White-Winged Crossbill	X	X				yes
Carduelis flammea	Common Redpoll	X	X				no
Carduelis pinus	Pine Siskin	X	X				yes
Carduelis psaltria	Lesser Goldfinch	X	X				yes
Carduelis lawrencei	Lawrence's Goldfinch		X			X	no
Coccothraustes vespertinus	Evening Grosbeak	X	X				yes

Sources: Davie, O. (1898), Headstrom, R. (1970), Gabrielson and Jewett (1970); Seward (1977), Ehrlich *et a*l. (1988); Sibley (2000); Marshall *et al*. (2003), Baicich and Harrison (2005); Wahl *et al*. (2005); Cornell Lab of Ornithology (2009); Taxonomy according to American Ornithologists' Union Checklist of North American Birds - 7th Edition (2005): http://www.aou.org/checklist/index.php3

Appendix B: Description of canopy observer height, climbing tree specifics and other associated environmental variables within the Tree Plots' 30m-radius viewing arenas (DBH = diameter at breast height, cm; canopy cover (%) calculated with nine spherical densiometer readings per plot).

Plot no.[a]	Canopy Observer Height (m)	Tree Species Climbed (DBH)	MUNA/2 Tag # [b]	Maximum DBH (sp)	Maximum Height (sp)	Aspect (degrees)	Slope (%)	Elev. (m)	Water Present[c]	Canopy Cover	Survey Date
7	32.0	PSME (84)	M7-30	96 (PSME)	55 (TSHE)	210	3	329	no	92	26-Apr
11	36.0	ABGR (71)	538	134 (PSME)	45 (ABGR)	150	0.2	347	yes	93	27-Apr
15	31.8	TSHE (105)	M15-2	113 (TSHE)	50 (PIMO)	70	0.6	366	no	92	1-Jun
19	33.9	TSHE (69)	M19-5	181 (PSME)	40 (PSME)	50	12	390	no	94	30-May
25	26.1	TSHE (66)	758	182 (PSME)	40 (THPL)	130	0.1	323	yes	87	27-May
29	28.0	TSHE (79)	946	107 (TSHE)	49 (TSHE)	120	6	335	no	92	23-May
33	31.0	PSME (102)	M33-7	136 (PSME)	60 (PSME)	75	3	347	yes	92	3-May
37	28.0	TSHE (73)	M37-2	125 (PSME)	44 (PSME)	100	5	372	yes	91	5-May
41	25.0	TSHE (79)	M41-1	113 (TSHE)	48 (TSHE)	130	6	396	no	90	11-May
45	30.0	TSHE (72)	1541	107 (PSME)	43 (TSHE)	120	11	433	no	95	12-May
49	31.5	TSHE (71)	M49-13	151 (PSME)	56 (THPL)	140	10	396	yes	89	14-Jun
53	26.0	TSHE (81)	M53-5	139 (PSME)	45 (TSHE)	80	16	433	no	94	7-Jun
57	32.0	TSHE (83)	2037	98 (TSHE)	53 (TSHE)	140	6	475	yes	92	8-Jun
61	42.6	PSME (93)	M61-8	156 (PSME)	69 (PSME)	100	16	408	no	94	15-Jun
65	37.4	TSHE (84)	2342	128 (PSME)	47 (TSHE)	100	17	457	no	92	20-Jun
73	35.3	TSHE (92)	2619	159 (PSME)	43 (TSHE)	100	12	439	yes	89	16-Jun
77	33.5	TSHE (82)	none	137 (PSME)	34 (PSME)	60	11	488	no	93	22-Jun
85	30.5	PSME (93)	none	175 (PSME)	64 (PSME)	110	25	427	no	91	30-Jun
89	31.0	TSHE (77)	M89-6	127 (PSME)	51 (PSME)	115	20	488	no	87	29-Jun
93	26.1	PSME (92)	3587	114 (PSME)	46 (PSME)	80	24	536	no	75	6-Jul
Mean (SD)	**31.4 (4.4)**	**82.4 (10.9)**		**134.9 (2.8)**	**48.9 (8.6)**					**91 (4)**	
Min, Max	**25.0, 42.6**	**66.0, 105.0**		**107, 182**	**40, 69**					**75, 95**	

[a] These plot numbers correspond to the permanent growth and mortality plots (MUN2 and M UNA of the RNA); [b] tagged trees within permanent growth plots.; [c] water present in ephemeral stream

Appendix C: List of bird species detected in the T. T. Munger Research Natural Area.

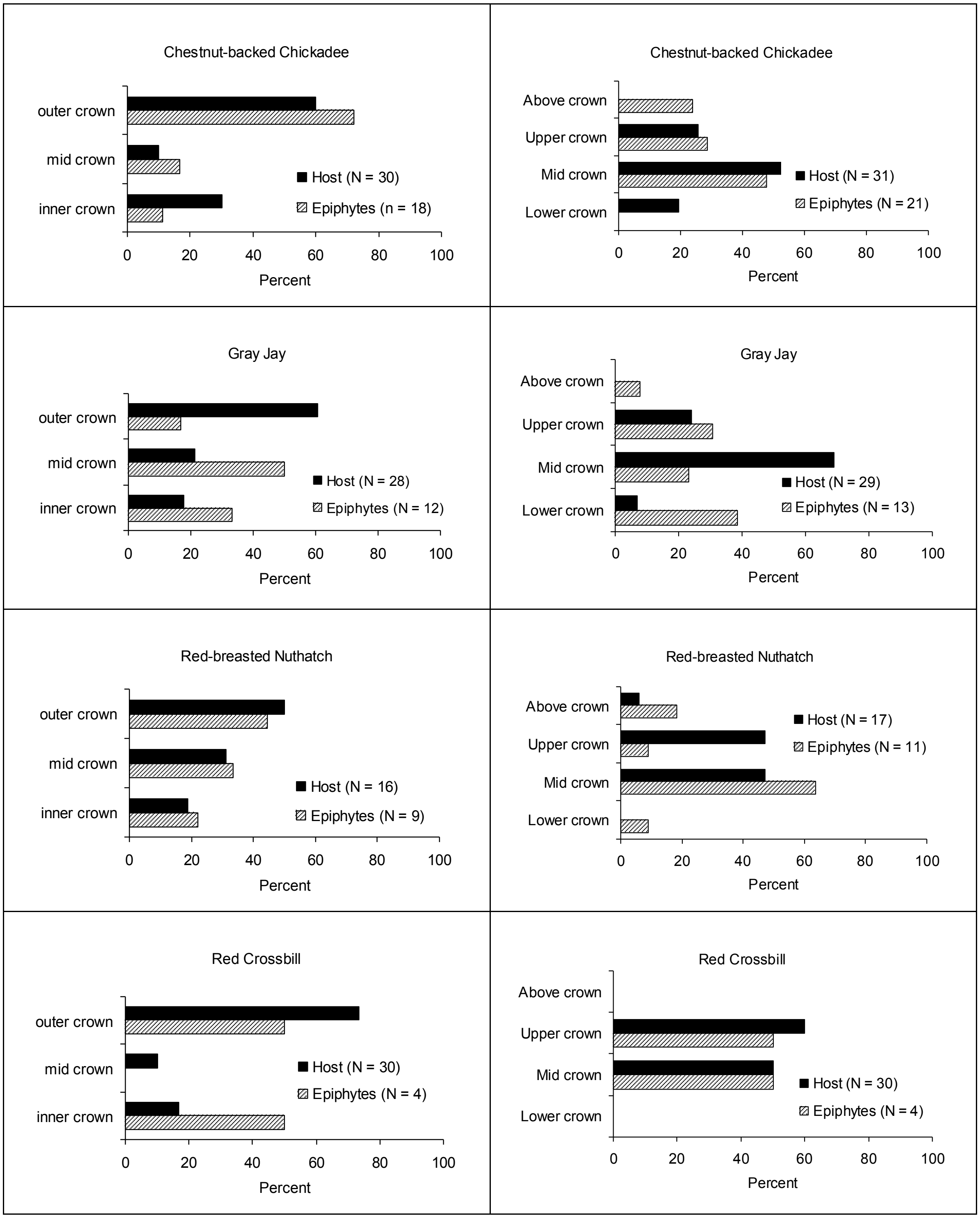
STANDARD NAME	ENGLISH NAME
ANATIDAE	**SWANS, GEESE &DUCKS**
Branta canadensis[1]	Canada Goose
Mergus merganser	Common Merganser
PHASIANIDAE	**QUAIL, PHEASANTS & RELATIVES**
Bonasa umbellus	Ruffed Grouse
ARDEIDAE	**HERONS & BITTERNS**
Ardea herodias[1]	Great Blue Heron
CATHARTIDAE	**NEW WORLD VULTURES**
Cathartes aura	Turkey Vulture
ACCIPITRIDAE	**HAWKS, OLD WORLD VULTURES & HARRIERS**
Haliaeetus leucocephalus[1]	Bald Eagle
Accipiter striatus	Sharp-shinned Hawk
Accipiter gentilis	Northern Goshawk
Buteo jamaicensis	Red-tailed Hawk
COLUMBIDAE	**PIGEONS**
Patagioenas fasciata	Band-tailed Pigeon
STRIGIDAE	**TYPICAL OWLS**
Glaucidium gnoma	Northern Pygmy-Owl
Strix varia	Barred Owl
CAPRIMULGIDAE	**NIGHTJARS**
Chordeiles minor	Common Nighthawk
APODIDAE	**SWIFTS**
Chaetura vauxi	Vaux’s Swift
TROCHILIDAE	**HUMMINGBIRDS**
Selasphorus rufus	Rufous Hummingbird
ALCEDINIDAE	**KINGFISHERS**
Ceryle alcyon	Belted Kingfisher
PICIDAE	**WOODPECKERS**
Sphyrapicus ruber	Red-breasted Sapsucker
Picoides villosus	Hairy Woodpecker
Colaptes auratus	Northern Flicker
Dryocopus pileatus	Pileated Woodpecker
TYRANNIDAE	**TYRANT FLYCATCHERS**
Contopus cooperi	Olive-sided Flycatcher
Contopus sordidulus	Western Wood-Pewee
Empidonax traillii	Willow Flycatcher
Empidonax hammondii	Hammond's Flycatcher
Empidonax difficilis	Pacific-slope Flycatcher
VIREONIDAE	**TYPICAL VIREOS**
Vireo cassinii	Cassin's Vireo
Vireo gilvus	Warbling Vireo
CORVIDAE	**JAYS, MAGPIES & CROWS**
Perisoreus canadensis	Gray Jay
Cyanocitta stelleri	Steller’s Jay
Corvus corax	Common Raven

STANDARD NAME	ENGLISH NAME
HIRUNDINIDAE	**SWALLOWS**
Progne subis	Purple Martin
Tachycineta bicolor	Tree Swallow
Tachycineta thalassina	Violet-green Swallow
Stelgidopteryx serripennis	Northern Rough-winged Swallow
Riparia riparia	Bank Swallow
Hirundo rustica	Barn Swallow
PARIDAE	**TRUE TITS**
Poecile rufescens	Chestnut-backed Chickadee.
SITTIDAE	**NUTHATCHES**
Sitta canadensis	Red-breasted Nuthatch
CERTHIIDAE	**HOLARCTIC TREECREEPERS**
Certhia americana	Brown Creeper
TROGLODYTIDAE	**WRENS**
Troglodytes troglodytes	Winter Wren
REGULIDAE	**KINGLETS**
Regulus satrapa	Golden-crowned Kinglet
Regulus calendula	Ruby-crowned Kinglet
TURDIDAE	**THRUSHES**
Catharus ustulatus	Swainson’s Thrush
Catharus guttatus	Hermit Thrush
Turdus migratorius	American Robin
Ixoreus naevius	Varied Thrush
STURNIDAE	**STARLINGS & ALLIES**
Sturnus vulgaris	European Starling
BOMBYCILLIDAE	**WAXWINGS**
Bombycilla cedrorum	Cedar Waxwing
PARULIDAE	**WOOD WARBLERS & RELATIVES**
Dendroica coronata	Yellow-rumped Warbler
Dendroica nigrescens	Black-throated Gray Warbler
Dendroica townsendi	Townsend’s Warbler
Dendroica occidentalis	Hermit Warbler
Oporornis tolmiei	MacGillivray’s Warbler
Geothlypis trichas	Common Yellowthroat
Wilsonia pusilla	Wilson’s Warbler
THRAUPIDAE	**TANAGERS & HONEYCREEPERS**
Piranga ludoviciana	Western Tanager
EMBERIZIDAE	**EMBERIZINES**
Pipilo maculatus	Spotted Towhee
Spizella passerina	Chipping Sparrow
Melospiza melodia	Song Sparrow
Zonotrichia leucophrys	White-crowned Sparrow
Junco hyemalis	Dark-eyed Junco
CARDINALIDAE	**CARDINALS, GROSBEAKS & ALLIES**
Pheucticus melanocephalus	Black-headed Grosbeak
ICTERIDAE	**BLACKBIRDS, ORIOLES & ALLIES**
Agelaius phoeniceus	Red-winged Blackbird
Xanthocephalus xanthocephalus	Yellow-headed Blackbird

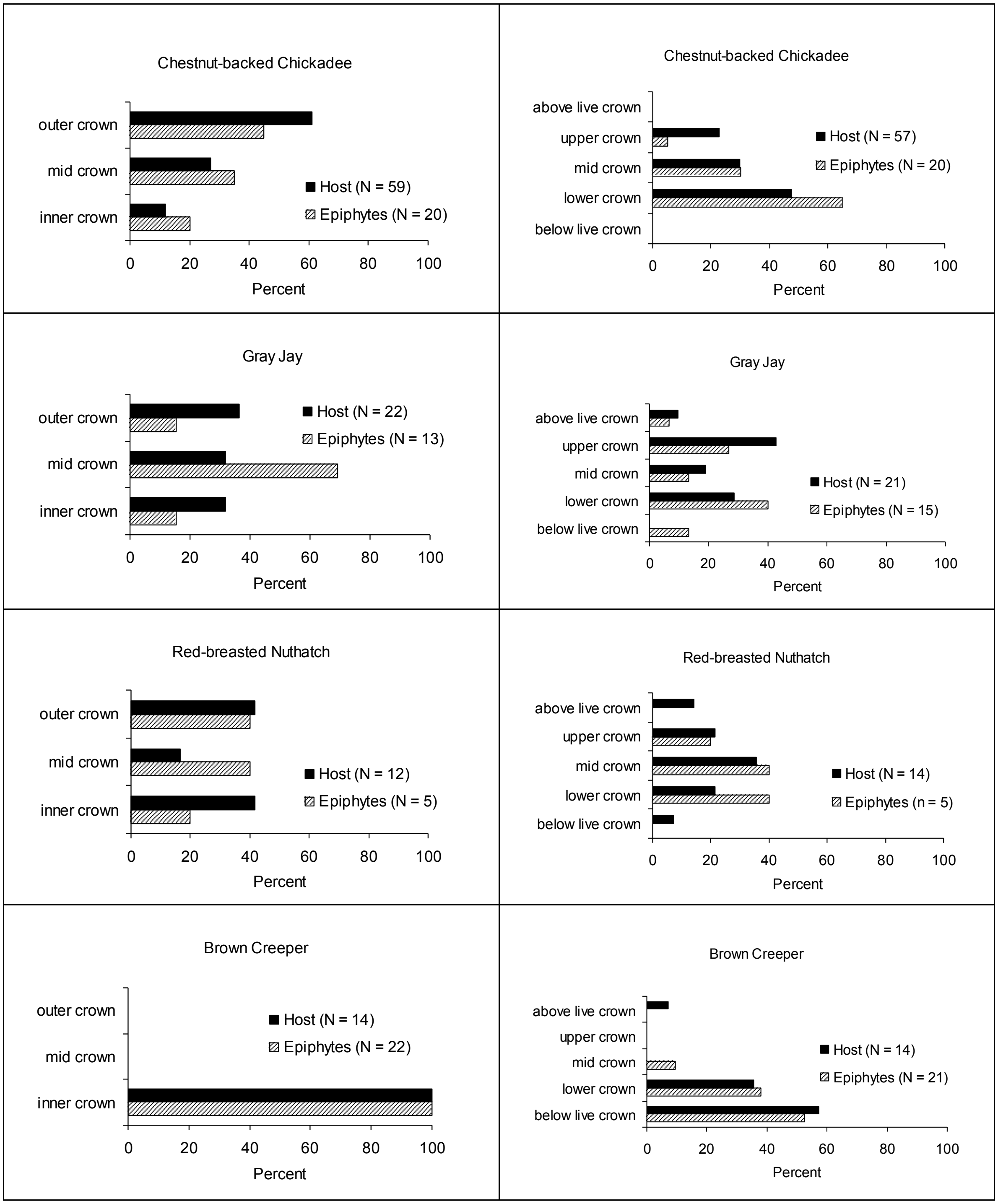
STANDARD NAME	**ENGLISH NAME**
Molothrus ater	Brown-headed Cowbird
FRINGILLIDAE	**FRINGILLINE FINCHES**
Carpodacus purpureus	Purple Finch
Carpodacus cassinii	Cassin’s Finch
Loxia curvirostra	Red Crossbill
Carduelis pinus	Pine Siskin
Carduelis tristis	American Goldfinch
Coccothraustes vespertinus	Evening Grosbeak

Sources: Taxonomy - American Ornithologists' Union Checklist of North American Birds - Seventh Edition (2005): http://www.aou.org/checklist/index.php3, [1] = species detected flying/presumably migrating over the RNA only

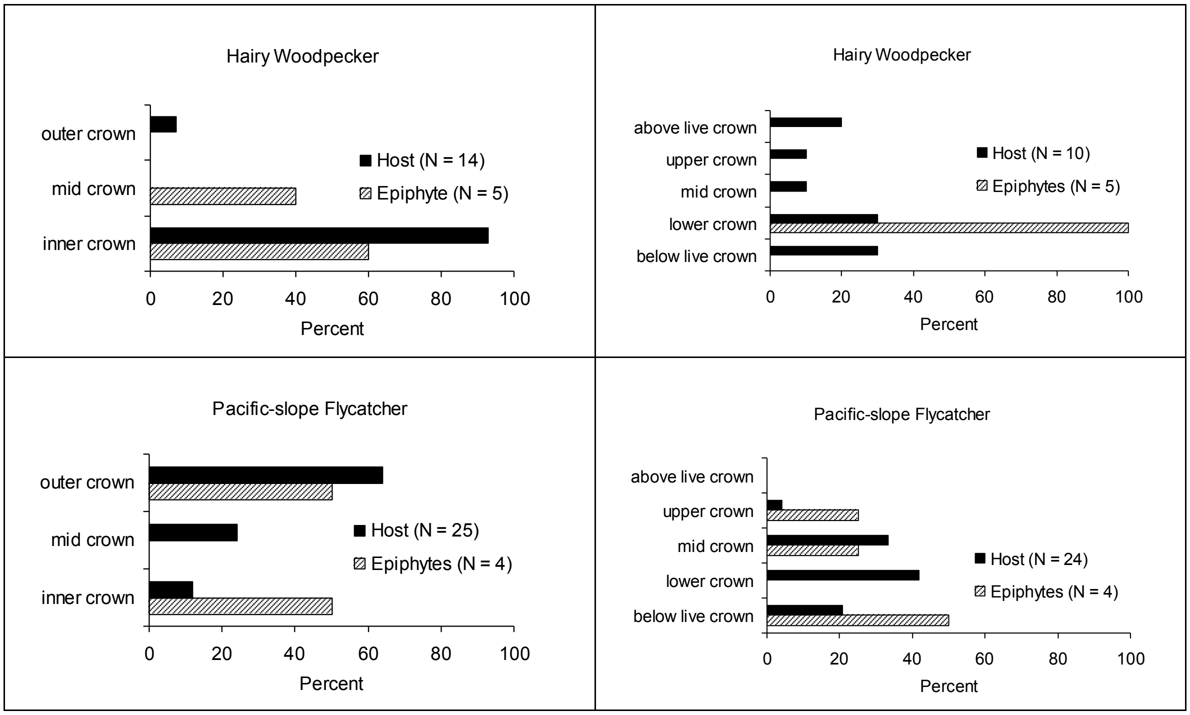
Appendix D: Comparative use of horizontal and vertical tree zones by four birds during foraging bouts on host and epiphyte substrates, Tree Plots.



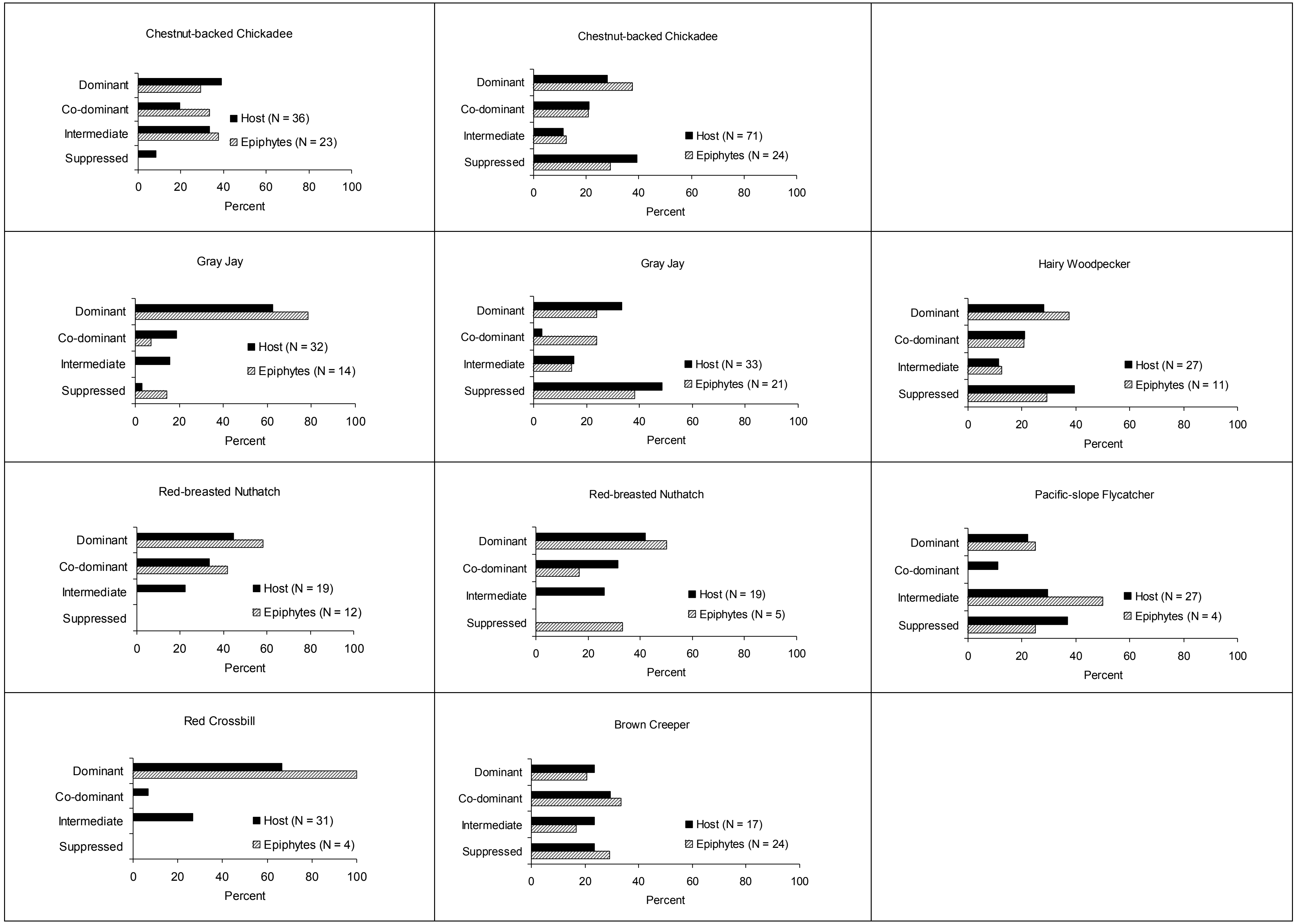
Appendix E: Comparative use of horizontal (left) and vertical (right) tree zones by six foraging birds during foraging bouts on host and epiphyte substrates, Walking Transects.



Appendix E (cont.): Comparative use of horizontal (left) and vertical (right) tree zones by six foraging birds during foraging bouts on host and epiphyte substrates, Walking Transects.



Appendix F: Epiphyte and host use of tree classes by six foraging birds; Tree Plots (left) and Walking Transects (center and right).



Chestnut-backed Chickadee

Chestnut-backed Chickadee

Gray Jay

Gray Jay

Hairy Woodpecker

Red-breasted Nuthatch

Red-breasted Nuthatch

Pacific-slope Flycatcher

Red Crossbill

Brown Creeper

Appendix G: Relative availability of host and epiphyte resources (g Cm^{-1}) and their proportional use (%) by five species by survey type.

		Resource Pool					
		Foliage	Branches and Stem Bark	Epiphytes			
Available Resources^1 (%)		941 (10.2)	8144 (88.7)	100 (1.1)			
English Name	**Survey Type^2 (n)**	**Proportional Use**			G_{adj}	**Critical χ^2**	***P***
Chestnut-backed Chickadee	TP (61)	39.3	21.3	39.3	106.71	3.84	< 0.05
	WT (99)	46.5	29.3	24.2	132.59	3.84	< 0.05
	Pooled (160)	43.8	26.3	30.0	238.83	3.84	< 0.05
Red-breasted Nuthatch	TP (30)	16.7	43.3	40.0	2.92	3.84	> 0.1
	WT (26)	23.1	53.8	23.1	9.14	3.84	> 0.1
	Pooled (56)	19.6	48.2	32.1	54.91	5.99	< 0.01
Gray Jay	TP (48)	35.4	35.4	29.2	79.85	5.99	< 0.01
	WT (56)	23.2	37.5	39.3	89.41	5.99	< 0.01
	Pooled (104)	28.8	36.5	34.6	170.20	5.99	< 0.005
Brown Creeper	TP (10)	0.0	70.0	30.0	4.16	5.99	> 0.1
	WT (41)	2.4	39.0	58.5	78.21	5.99	< 0.01
	Pooled (51)	2.0	45.1	52.9	77.29	5.99	< 0.01
Hairy Woodpecker	TP (5)	0.0	60.0	40.0	*	*	*
	WT (38)	0.0	71.1	28.9	20.48	5.99	< 0.025
	Pooled (43)	0.0	69.8	30.2	23.66	5.99	< 0.025
All five species	TP (154)	29.9	34.4	35.7	380.40	5.99	< 0.005
	WT (260)	25.4	41.2	33.5	551.10	5.99	< 0.005
	Pooled (414)	27.1	38.6	34.3	930.13	5.99	< 0.005

[1] Estimated stores of carbon associated with live biomass (Harmon *et al*. 2004; [2] TP = Tree Plots, WT = Walking Transects; * not enough data.

Appendix H: Relative availability of epiphyte groups (kgha^{-1}) and their proportional use (%) by five species by survey type.

		Epiphyte Group					
		Alectorioid lichens	**Cyanolichens & Other lichens**	**Bryophytes**			
Available Resources[1] (%)		934 (14.1)	2382 (35.9)	3316 (50.0)			
English Name	**Survey Type[2] (n)**	**Proportional Use**			**G_{adj}**	**Critical χ^2**	***P***
Chestnut-backed Chickadee	TP (24)	20.8	79.2	0.0	18.41	3.84	> 0.05
	WT (24)	12.5	41.7	45.8	0.33	3.84	> 0.1
	Pooled (48)	16.7	60.4	22.9	15.53	5.99	< 0.05
Red-breasted Nuthatch	TP (12)	8.3	91.7	0.0	15.87	3.84	> 0.05
	WT (6)	16.7	50.0	33.3	*	*	*
	Pooled (18)	11.1	77.8	11.1	12.06	3.80	> 0.05
Gray Jay	TP (14)	21.4	50.0	28.6	2.56	3.84	> 0.1
	WT (22)	22.7	31.8	45.5	0.18	3.84	> 0.1
	Pooled (36)	22.2	38.9	38.9	2.44	5.99	> 0.1
Brown Creeper	TP (3)	0.0	66.7	33.3	*	*	*
	WT (24)	16.7	33.3	50.0	0.15	3.84	> 0.1
	Pooled (27)	14.8	37.0	48.2	0.04	5.99	> 0.1
Hairy Woodpecker	TP (2)	0.0	100.0	0.0	*	*	*
	WT (11)	0.0	27.3	72.7	2.26	3.84	> 0.1
	Pooled (13)	0.0	38.5	61.5	3.67	3.84	> 0.1
All five species	TP (55)	16.4	74.5	9.1	44.98	5.99	< 0.025
	WT (87)	14.9	35.6	49.4	0.05	5.99	> 0.1
	Pooled (142)	15.5	50.7	33.8	16.19	5.99	< 0.05

[1] McCune 1993, McCune *et al.* 1997; [2] TP = Tree Plots, WT = Walking Transects; * not enough data.

Appendix I: Availability of tree species (%) and their proportional use (%) by five species during foraging bouts on epiphyte substrates.

Species[1]	Survey Type[2] (n)	Tree Species[3]					G_{adj}	Critical χ^2	*P*
		ABSP	PSME	TSHE	THPL	OTHERS			
CBCH	TP (24)	0	33.3	66.7	0	0	0.49	3.84	> 0.1
	WT (24)	16.7	16.7	45.8	0	20.8	2.16	5.99	> 0.1
	Pooled (48)	8.3	25	56.3	0	10.4	3.17	7.82	> 0.05
RBNU	TP (12)	8.3	8.3	75.0	0.0	8.3	0.92	3.84	> 0.1
	WT (6)	0.0	16.7	50.0	0.0	33.3	*	*	*
	Pooled (18)	5.6	11.1	66.7	0.0	16.7	2.43	3.84	> 0.1
GRAJ	TP (14)	7.1	42.9	42.9	0.0	7.1	1.55	3.84	> 0.1
	WT (22)	4.5	9.1	54.5	0.0	31.8	0.001	3.84	> 0.1
	Pooled (36)	5.6	22.2	50.0	0.0	22.2	0.97	5.99	> 0.1
BRCR	TP (3)	0	25	75	0	0	*	*	*
	WT (24)	12.5	4.2	70.8	0.0	12.5	5.78	5.99	> 0.05
	Pooled (27)	11.1	11.1	66.7	0.0	11.1	1.56	5.99	> 0.1
HAWO	TP (2)	0	50	50	0	0	*	*	*
	WT (11)	27.3	18.2	18.2	0.0	36.4	6.04	3.84	> 0.1
	Pooled (13)	23.1	23.1	23.1	0.0	30.8	6.06	3.84	> 0.1
All five species	TP (55)	3.6	30.9	61.8	0.0	3.6	15.93	7.82	*< 0.025*
	WT (87)	12.6	11.5	51.7	0.0	24.1	8.19	7.82	*< 0.05*
	Pooled (142)	9.2	19.7	54.9	0.0	16.2	5.85	7.82	*< 0.05*
Available Resources[4] # trees (%)	TP (24)	57 (14.73)	60 (15.5)	231 (59.69)	10 (2.58)	29 (7.49)			
	WT (24)	56 (13.79)	72 (17.73)	223 (54.93)	14 (3.45)	41 (10.1)			
	Pooled (48)	56.5 (14.25)	66 (16.65)	227 (57.25)	12 (3.03)	35 (8.83)			

[1] CBCH = Chestnut-backed Chickadee, RBNU = Red-breasted Nuthatch, GRAJ = Gray Jay, BRCR = Brown Creeper, HAWO = Hairy Woodpecker;[2] TP = Tree Plots, WT = Walking Transects ; [3] ABSP = *Abies* spp., PSME = *Pseudotsuga menziesii*, TSHE = *Tsuga heterophylla*, THPL = *Thuja plicata*; [4] Data were provided by the Permanent Study Plot program, a partnership between the H.J. Andrews Long-Term Ecological Research program and the U.S. Forest Service Pacific Northwest Research Station, Corvallis, OR.; * not enough data.

Appendix J: Multi-response permutation procedures (MRPP) pairwise comparisons by epiphyte foraging activity, data pooled (N = 191). Bonferroni-adjusted significant *P*-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups	**Pooled Data (N = 191)**	
	A value	***P* - value**
Major Epiphyte Groups	**0.177**	**< 0.001**
alectorioid lichen vs. bryophytes	**0.155**	**< 0.001**
alectorioid lichen vs. cyanolichen & other lichen	0.002	0.276
alectorioid lichen vs. lichen/bryophyte admixture	0.088	0.003
bryophyte vs. cyanolichen & other lichen	**0.169**	**< 0.001**
bryophyte vs. lichen/bryophyte admixture	0.007	0.132
cyanolichen & other lichen vs. lichen/bryophyte admixture	0.025	0.005
Finer-Scale Epiphyte Groups	**0.215**	**< 0.001**
alectorioid lichen vs. foliose and fruticose lichen	0.012	0.135
appressed bryophyte vs. alectorioid lichen	**0.264**	**< 0.001**
appressed bryophyte vs. foliose and fruticose lichen	**0.268**	**< 0.001**
appressed bryophyte vs. foliose lichen	**0.254**	**< 0.001**
appressed bryophyte vs. lichen/bryophyte admixture	0.046	0.010
appressed bryophyte vs. pendant bryophyte	0.045	**< 0.001**
foliose lichen vs. alectorioid lichen	0.003	0.268
foliose lichen vs. foliose and fruticose lichen	-0.002	0.466
foliose lichen vs. pendant bryophyte	**0.172**	**< 0.001**
fruticose lichen vs. alectorioid lichen	0.017	0.150
fruticose lichen vs. appressed bryophyte	**0.108**	**< 0.001**
fruticose lichen vs. foliose and fruticose lichen	0.032	0.104
fruticose lichen vs. foliose lichen	0.008	0.188
fruticose lichen vs. lichen/bryophyte admixture	**0.152**	0.009
fruticose lichen vs. pendant bryophyte	0.054	0.001
lichen/bryophyte admixture vs. alectorioid lichen	0.088	0.003
lichen/bryophyte admixture vs. foliose and fruticose lichen	**0.167**	**< 0.001**
lichen/bryophyte admixture vs. foliose lichen	0.053	0.003
lichen/bryophyte admixture vs. pendant bryophyte	-0.001	0.438
other lichen vs. alectorioid lichen	0.059	0.007
other lichen vs. appressed bryophyte	0.084	**< 0.001**
other lichen vs. foliose and fruticose lichen	**0.118**	**0.001**
other lichen vs. foliose lichen	0.061	**< 0.001**
other lichen vs. fruticose lichen	0.053	0.058
other lichen vs. lichen/bryophyte admixture	0.012	0.284
other lichen vs. pendant bryophyte	0.030	0.010
pendant bryophyte vs. alectorioid lichen	**0.168**	**< 0.001**
pendant bryophyte vs. foliose and fruticose lichen	**0.183**	**< 0.001**
Guilds (see Appendix K for pairwise comparison)	**0.178**	**< 0.001**
Species (see Appendix L for pairwise comparison)	**0.231**	**< 0.001**

Groups	Pooled Data (N = 191)	
	A value	*P* - value
Crown class	**0.225**	**< 0.001**
codominant vs. dominant	0.011	0.045
codominant vs. intermediate	0.015	0.029
codominant vs. suppressed	**0.278**	**< 0.001**
dominant vs. intermediate	**0.508**	**< 0.001**
dominant vs. suppressed	**0.229**	**< 0.001**
suppressed vs. intermediate	**0.159**	**< 0.001**
Horizontal Crown	0.063	< 0.001
Vertical Crown	**0.149**	**< 0.001**
below live crown vs. above live crown	**0.298**	**< 0.001**
lower live crown vs. above live crown	**0.123**	**< 0.001**
lower live crown vs. below live crown	0.030	0.002
lower live crown vs. upper live crown	0.076	< 0.001
mid live crown vs. above live crown	0.050	0.002
mid live crown vs. below live crown	**0.171**	**< 0.001**
mid live crown vs. lower live crown	0.081	< 0.001
mid live crown vs. upper live crown	0.011	0.106
upper live crown vs. above live crown	0.039	0.051
upper live crown vs. below live crown	**0.183**	**< 0.001**
Foraging Maneuver	0.038	0.001
Foraging Posture	**0.105**	**<0.001**
hang upside-down vs. hover	0.022	0.169
hang upside-down vs. reach under	-0.032	0.824
hang upside-down vs. short flight	0.009	0.346
hang upside-down vs. stand	**0.418**	**0.000**
hang upside-down vs. walk/run	**0.345**	**0.000**
hang vs. hang upside-down	0.015	0.054
hang vs. hop	0.029	0.012
hang vs. hover	0.029	0.012
hang vs. lean over or into	0.026	0.018
hang vs. perch	0.009	0.054
hang vs. reach under	-0.006	0.690
hang vs. short flight	-0.001	0.447
hang vs. stand	**0.116**	**0.000**
hang vs. walk/run	0.072	0.000
hop vs. hang upside-down	**0.116**	**0.002**
hop vs. hover	**0.145**	**0.003**
hop vs. lean over or into	0.094	0.012
hop vs. reach under	0.034	0.173
hop vs. short flight	0.007	0.361
hop vs. stand	**0.189**	**0.005**
hop vs. walk/run	0.117	0.044
hover vs. reach under	0.004	0.407

Groups	Pooled Data (N = 191)	
	A value	***P* - value**
hover vs. short flight	0.086	0.078
hover vs. stand	**0.464**	**0.000**
hover vs. walk/run	**0.420**	**0.002**
lean over or into vs. hang upside-down	0.048	0.052
lean over or into vs. hover	0.028	0.161
lean over or into vs. reach under	0.007	0.357
lean over or into vs. short flight	0.083	0.069
lean over or into vs. stand	**0.273**	**0.003**
lean over or into vs. walk/run	**0.264**	**0.006**
perch vs. hang upside-down	0.024	0.019
perch vs. hop	0.012	0.081
perch vs. hover	0.043	0.002
perch vs. lean over or into	0.026	0.018
perch vs. reach under	-0.001	0.415
perch vs. short flight	0.001	0.385
perch vs. stand	0.095	0.000
perch vs. walk/run	0.057	0.001
reach under vs. short flight	-0.055	0.687
reach under vs. stand	**0.457**	**0.002**
reach under vs. walk/run	**0.482**	**0.014**
short flight vs. walk/run	**0.608**	**0.023**
stand vs. short flight	0.578	0.002
stand vs. walk/run	0.282	0.024
Tree Species	**0.215**	**<0.001**
TSHE vs. Ground, Log or Other	**0.181**	**<0.001**
TSHE vs. ABSP	0.022	0.003
TSHE vs. ACCI and TABR	**0.154**	**<0.001**
TSHE vs. PSME	0.019	0.004
TSHE vs. PIMO, THPL or SNAG	0.011	0.044
Ground, Log or Other vs. ABSP	**0.199**	**<0.001**
Ground, Log or Other vs. ACCI and TABR	**0.119**	**<0.001**
Ground, Log or Other vs. PSME	**0.392**	**<0.001**
Ground, Log or Other vs. PIMO, THPL or SNAG	**0.314**	**<0.001**
ABSP vs. ACCI and TABR	0.082	<0.001
ABSP vs. PSME	**0.106**	**<0.001**
ABSP vs. PIMO, THPL or SNAG	0.081	0.012
ACCI and TABR vs. PSME	**0.333**	**<0.001**
ACCI and TABR vs. PIMO, THPL or SNAG	**0.222**	**<0.001**
PSME vs. PIMO, THPL or SNAG	0.017	0.100
Tree Condition (live versus dead)	0.081	< 0.001
Tree Position	**0.108**	**<0.001**
bole vs. branch	0.047	<0.001
bole vs. dead branch/let	0.059	<0.001

Groups	**Pooled Data (N = 191)**	
	A value	***P* - value**
branch vs. dead branch/let	0.014	0.031
branchlet vs. bole	**0.178**	**<0.001**
branchlet vs. branch	0.093	<0.001
branchlet vs. dead branch/let	0.049	0.001
branchlet vs. foliage	-0.001	0.428
foliage vs. bole	0.142	**<0.001**
foliage vs. branch	0.071	<0.001
foliage vs. dead branch/let	0.041	0.008

Appendix K: Multi-response permutation procedures pairwise comparisons of foraging guilds by epiphyte foraging activity, data pooled (N = 191). Bonferroni-adjusted significant *P*-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups	**A**	**P**
bark insectivore vs. nectarivore	0.001	0.429
timber-foliage insectivore vs. nectarivore	0.011	0.190
omnivore/scavenger vs. nectarivore	0.012	0.256
timber-foliage insectivore vs. omnivore/scavenger	0.017	0.020
bark insectivore vs. aerial insectivore	0.023	0.025
bark insectivore vs. omnivore/scavenger	0.024	0.005
bark insectivore vs. timber-foliage insectivore	0.026	0.002
low-understory herbivore/insectivore vs. nectarivore	0.033	0.045
timber-foliage insectivore vs. aerial insectivore	0.036	0.007
omnivore/scavenger vs. aerial insectivore	0.039	0.019
timber-foliage insectivore vs. timber-seed eater	0.054	0.001
omnivore/scavenger vs. timber-seed eater	0.056	0.008
bark insectivore vs. timber-seed eater	0.058	0.001
aerial insectivore vs. nectarivore	0.094	0.158
low-understory herbivore/insectivore vs. aerial insectivore	**0.157**	**<0.001**
bark insectivore vs. low-understory herbivore/insectivore	**0.181**	**<0.001**
low-understory herbivore/insectivore vs. omnivore/scavenger	**0.195**	**<0.001**
low-understory herbivore/insectivore vs. timber-seed eater	**0.244**	**<0.001**
timber-foliage insectivore vs. low-understory herbivore/insectivore	**0.273**	**<0.001**
aerial insectivore vs. timber-seed eater	**0.424**	**0.004**
nectarivore vs. timber-seed eater	**0.471**	**0.017**
All Guilds	**0.178**	**<0.001**

Appendix L: Multi-response permutation procedures pairwise comparisons of species by epiphyte foraging activity, data pooled (N = 191). Bonferroni-adjusted significant *P*-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups	**A**	**P**
Brown Creeper vs. Golden-crowned Kinglet	0.025	0.121
Brown Creeper vs. Hairy Woodpecker	0.044	0.006
Brown Creeper vs. Hermit Thrush	**0.113**	**<0.001**
Brown Creeper vs. Pacific-slope Flycatcher	0.066	0.002
Brown Creeper vs. Red Crossbill	**0.212**	**<0.001**
Brown Creeper vs. Rufous Hummingbird	**0.612**	**<0.001**
Brown Creeper vs. Steller's Jay	0.074	0.002
Chestnut-backed Chickadee vs. Brown Creeper	**0.101**	**<0.001**
Chestnut-backed Chickadee vs. Dark-eyed Junco	0.009	0.181
Chestnut-backed Chickadee vs. Golden-crowned Kinglet	0.006	0.312
Chestnut-backed Chickadee vs. Gray Jay	0.018	0.024
Chestnut-backed Chickadee vs. Hairy Woodpecker	0.037	0.004
Chestnut-backed Chickadee vs. Hermit Thrush	**0.118**	**<0.001**
Chestnut-backed Chickadee vs. Pacific-slope Flycatcher	0.037	0.007
Chestnut-backed Chickadee vs. Red Crossbill	0.055	0.001
Chestnut-backed Chickadee vs. Rufous Hummingbird	0.013	0.179
Chestnut-backed Chickadee vs. Steller's Jay	0.005	0.266
Chestnut-backed Chickadee vs. Winter Wren	**0.311**	**<0.001**
Dark-eyed Junco vs. Brown Creeper	0.026	0.081
Dark-eyed Junco vs. Golden-crowned Kinglet	**0.642**	**<0.001**
Dark-eyed Junco vs. Hairy Woodpecker	**0.454**	**<0.001**
Dark-eyed Junco vs. Hermit Thrush	0.092	0.099
Dark-eyed Junco vs. Pacific-slope Flycatcher	0.035	0.257
Dark-eyed Junco vs. Red Crossbill	**0.279**	**0.007**
Dark-eyed Junco vs. Rufous Hummingbird	0.011	0.445
Dark-eyed Junco vs. Steller's Jay	**0.535**	**<0.001**
Golden-crowned Kinglet vs. Hermit Thrush	**0.207**	**0.024**
Golden-crowned Kinglet vs. Red Crossbill	**0.425**	**0.019**
Gray Jay vs. Brown Creeper	0.088	<0.001
Gray Jay vs. Dark-eyed Junco	**0.667**	**<0.001**
Gray Jay vs. Golden-crowned Kinglet	0.001	0.453
Gray Jay vs. Hairy Woodpecker	0.017	0.092
Gray Jay vs. Hermit Thrush	0.087	0.001
Gray Jay vs. Pacific-slope Flycatcher	0.039	0.025
Gray Jay vs. Red Crossbill	0.062	0.008
Gray Jay vs. Rufous Hummingbird	0.012	0.279
Gray Jay vs. Steller's Jay	**0.540**	**<0.001**
Hairy Woodpecker vs. Golden-crowned Kinglet	0.037	0.200
Hairy Woodpecker vs. Hermit Thrush	**0.155**	**0.004**
Hairy Woodpecker vs. Pacific-slope Flycatcher	0.021	0.200

Groups	A	P
Hairy Woodpecker vs. Red Crossbill	**0.209**	**0.001**
Hairy Woodpecker vs. Rufous Hummingbird	0.023	0.284
Hairy Woodpecker vs. Steller's Jay	0.037	0.149
Hermit Thrush vs. Red Crossbill	**0.610**	**0.003**
Pacific-slope Flycatcher vs. Golden-crowned Kinglet	0.115	0.159
Pacific-slope Flycatcher vs. Hermit Thrush	**0.329**	**0.003**
Pacific-slope Flycatcher vs. Red Crossbill	**0.424**	**0.004**
Pacific-slope Flycatcher vs. Rufous Hummingbird	0.094	0.158
Pacific-slope Flycatcher vs. Steller's Jay	**0.142**	**0.032**
Red-breasted Nuthatch vs. Brown Creeper	**0.181**	**<0.001**
Red-breasted Nuthatch vs. Chestnut-backed Chickadee	0.018	0.037
Red-breasted Nuthatch vs. Dark-eyed Junco	0.076	0.027
Red-breasted Nuthatch vs. Golden-crowned Kinglet	0.062	0.069
Red-breasted Nuthatch vs. Gray Jay	0.043	0.010
Red-breasted Nuthatch vs. Hairy Woodpecker	**0.105**	**0.002**
Red-breasted Nuthatch vs. Hermit Thrush	**0.292**	**<0.001**
Red-breasted Nuthatch vs. Pacific-slope Flycatcher	**0.153**	**0.001**
Red-breasted Nuthatch vs. Red Crossbill	0.059	0.032
Red-breasted Nuthatch vs. Rufous Hummingbird	0.074	0.055
Red-breasted Nuthatch vs. Steller's Jay	0.018	0.209
Red-breasted Nuthatch vs. Winter Wren	**0.395**	**<0.001**
Rufous Hummingbird vs. Golden-crowned Kinglet	0.010	<0.001
Rufous Hummingbird vs. Hermit Thrush	**0.159**	**0.029**
Rufous Hummingbird vs. Red Crossbill	**0.471**	**0.017**
Rufous Hummingbird vs. Steller's Jay	0.115	0.176
Steller's Jay vs. Golden-crowned Kinglet	**0.481**	**<0.001**
Steller's Jay vs. Hermit Thrush	**0.275**	**0.010**
Steller's Jay vs. Red Crossbill	**0.176**	**0.023**
Winter Wren vs. Brown Creeper	**0.237**	**<0.001**
Winter Wren vs. Dark-eyed Junco	0.077	0.001
Winter Wren vs. Golden-crowned Kinglet	**0.097**	**0.001**
Winter Wren vs. Gray Jay	**0.230**	**<0.001**
Winter Wren vs. Hairy Woodpecker	**0.201**	**<0.001**
Winter Wren vs. Hermit Thrush	0.006	0.282
Winter Wren vs. Pacific-slope Flycatcher	**0.237**	**<0.001**
Winter Wren vs. Red Crossbill	**0.353**	**<0.001**
Winter Wren vs. Rufous Hummingbird	0.062	0.009
Winter Wren vs. Steller's Jay	**0.178**	**<0.001**
All Species	**0.178**	**<0.001**

Appendix M: Number of species, guilds, and individuals (% of all substrates) that used epiphyte, phorophyte and other substrates by survey type.

Substrate		Tree Plots			Walking Transects		
		No. species	No. guilds	No. inds	No. species	No. guilds	No. inds
Epiphyte	Alectorioid lichen	4	4	10	7	5	16
	Cyanolichen and other lichen						
	Foliose lichen	6	5	30	8	4	18
	Fruticose lichen	2	1	2	1	1	2
	Other lichen	2	2	3	7	4	11
	Admixture (fruticose & foliose)	5	4	13	4	3	5
	Subtotal	6	5	48	10	5	36
	Bryophyte						
	Pendant bryophyte	2	2	3	10	6	50
	Appressed bryophyte	3	3	5	8	4	35
	Subtotal	3	3	8	12	7	85
	Admixture (lichen & bryophyte)	---	---	---	3	3	4
	Epiphyte Total	9 (50.0%)	6	66 (28.0%)	14 (56.0%)	7	141 (28.3%)
Phorophyte	Foliage (live and dead foliage)	12	7	68	14	7	115
	Bark	11	7	47	18	8	121
	Dead wood (includes rootwads)	6	5	18	11	5	56
	Cone	1	1	23	1	1	7
	Other (flower)	1	1	1	1	1	7
	Mistletoe brooms	2	2	3	3	3	5
	Phorophyte Total	15 (83.3%)	7	160 (67.8%)	22 (88.0%)	9	311 (62.4%)
Other	Air	4	6	7	6	4	16
	Perched litter	2	2	2	1	1	1
	Ground	1	1	1	5	3	17
	Terrestrial herbs/mosses	---	---	---	4	2	10
	Other	---	---	---	2	2	2
	Other Total	7 (38.9%)	6	10 (4.2%)	10 (40.0%)	6	46 (9.2%)
All Substrates Total		18	8	236	25	9	498

Appendix N: Percent total foraging, postures, maneuvers, and mean foraging height (m) of 6 bird species searching epiphyte functional groups, relative to all substrates, Tree Plots only.

English Name (n, total observations)	Alectorioid Lichens	Cyanolichens and Other Lichens	Bryophytes	Epiphyte Foraging Posture[1]	Epiphyte Foraging Maneuver[2]	Epiphyte Foraging Height (range)	Foraging Height of Non-Epiphytes (range)
REGULAR USERS							
Brown Creeper (10)	0	20.0	10.0	HA	S	19.3 (12-32)	28.0 (22-41)
Chestnut backed Chickadee (63)	7.9	30.2	0	HA, HP, PE, SF, LE/HG	S, GL, PR	31.9 (9-45)	28.4 (1-55)
Gray Jay (48)	6.3	14.6	8.3	PE, HA, RU, HG	S, GL, PK/PR, PL/HA	26.9 (2.25-50)	33.6 (0-60)
Red-breasted Nuthatch (33)	3.0	33.3	0	HA, PE, HG, HP	S, PR, HA/PK	37.6 (24-60)	35.3 (24-60)
Winter Wren (14)	0	7.1	21.4	HP, PE/RP	S, GL/PK	0.9 (0.2-1.75)	0.6 (0-2)
OCCASIONAL USERS/GENERALISTS							
Red Crossbill (35)	2.9	8.6	0	PE	S, PK/PR	45.0 (40-50)	45.3 (30-60)

[1] postures: HA = hang, PE = perch, HG = hang upside-down, HP = hop, RU = reach under, LE = lean into, RP = reach up, SF = short flight (within substrate);
[2] maneuvers: S = search, PR = probe, HA = hammer, PK = peck, GL = glean, PL = pluck; postures and maneuvers listed in order of importance.

Appendix O: Percent total foraging, postures, maneuvers and foraging height (m) of 12 bird species searching epiphyte functional groups, relative to all foraging substrates, Walking Transects only.

English Name (n, total observations)	Alectorioid Lichens	Cyanolichens and Other Lichens	Bryophytes	Epiphyte Foraging Posture[1]	Epiphyte Foraging Maneuver[2]	Epiphyte Foraging Height (mean, range)	Foraging Height of Non-Epiphytes (mean, range)
REGULAR USERS							
Brown Creeper (41)	9.8	19.5	29.3	HA, HG/PE	S/PK, PR, GL, PL	10.7 (1-23)	11.6 (1-25)
Hairy Woodpecker (38)	0	5.3	23.7	HA, PE, HG	HA, PK, S	12.4 (1-40)	19.3 (2-60)
Gray Jay (60)	8.3	11.7	16.7	PE, HA, LE, HG/RU	S, PK, GL, PR	18.0 (2-50)	18.4 (0-58)
Winter Wren (85)	0	3.5	35.3	HP/PE, HA/SD, LE/RP, AM, HO	PK, S, GL, PR	1.5 (0-8)	0.9 (0-10)
Hermit Thrush (17)	0	5.9	23.5	PE, LE, AM	S, PK	1.3 (0-2)	1.5 (0-5.5)
OCCASIONAL USERS/GENERALISTS							
Red-breasted Nuthatch (27)	3.7	11.1	7.4	HA, PE	PK/S	27.5 (3-60)	32.8 (11-58)
Chestnut backed Chickadee (104)	2.9	1.9	6.7	HA, HG, PE, HP/LE/HO, SF	S, GL, PK, PR, PL	14.5 (1.5-55)	16 (1.5-55)
Golden crowned Kinglet (18)	0	11.1	0	PE	S	12.0 (6-18)	16.3 (6-35)
Dark-eyed Junco (22)	4.5	4.5	9.1	LE/PE/RU/SD	PK, GL/S	11.2 (0.75-23)	1.3 (0-5)
Pacific-slope Flycatcher (43)	0	2.3	7.0	HO	GL	15.8 (6-27)	14 (0-40)
Red Crossbill (8)	0	0	0	---	---	---	36.9 (27-45)
Rufous Hummingbird (14)	7.1	0	7.1	HO	S	11.8 (5.5-18)	5.6 (0.5-40)

[1] Postures: HA = hang, PE = perch, HG = hang upside-down, HP = hop, RU = reach under, LE = lean into, RP = reach up, SF = short flight (within substrate), SD = stand, AM = walk/run on ground, HO = hover; [2] Maneuvers: S = search, PR = probe, HA = hammer, PK = peck, GL = glean, PL = pluck; postures and maneuvers listed in order of importance.

Appendix P: Multi-response permutation procedures pairwise comparisons of finer scale epiphyte substrates used by all birds observed in the Tree Plots and Walking Transects. Significant *P*-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups[1]	Tree Plots		Walking Transects	
	A value	*P* - value	A value	*P* - value
AB vs. AL	**0.222**	**0.001**	**0.201**	**< 0.001**
AB vs. MIX	**---**	**---**	0.055	0.004
AB vs. OL	-0.023	0.587	0.069	< 0.001
AB vs. PB	-0.019	0.498	0.062	< 0.001
AL vs. MIX	---	---	0.066	0.043
AL vs. OL	**0.135**	**0.025**	0.032	0.081
AL vs. PB	**0.391**	**0.003**	**0.106**	**< 0.001**
FF vs. AB	0.099	0.014	**0.150**	**< 0.001**
FF vs. AL	0.050	0.034	-0.00001	0.379
FF vs. FR	-0.001	0.422	-0.004	0.421
FF vs. MIX	---	---	**0.216**	**0.005**
FF vs. OL	0.021	0.259	0.090	0.031
FF vs. PB	**0.150**	**0.017**	0.077	< 0.001
FO vs. AB	**0.088**	**< 0.001**	**0.147**	**< 0.001**
FO vs. AL	0.040	0.006	0.038	0.028
FO vs. FF	-0.010	0.864	0.060	0.019
FO vs. FR	0.001	0.422	0.019	0.195
FO vs. MIX	---	---	-0.0003	0.439
FO vs. OL	0.026	0.061	0.032	0.047
FO vs. PB	0.089	0.004	0.044	< 0.001
FR vs. AB	-0.005	0.489	0.084	< 0.001
FR vs. AL	0.090	0.022	0.014	0.283
FR vs. MIX	**---**	**---**	**0.161**	**0.035**
FR vs. OL	-0.056	---	0.066	0.086
FR vs. PB	**0.117**	**---**	0.039	0.004
OL vs. MIX	---	---	0.011	0.313
OL vs. PB	0.092	---	0.024	0.016
PB vs. MIX	---	---	0.003	0.546
All epiphytes	**0.111**	**< 0.001**	**0.151**	**< 0.001**

[1] AL = alectorioid lichen, FO = foliose lichen, FR = fruticose lichen, FF = fruticose and foliose lichen, PB = pendant bryophyte, AB = appressed bryophyte, OL = other lichen, MIX = bryophyte and lichen

Appendix Q: Multi-Response Permutation Procedures pairwise comparisons of foraging guilds by finer scale epiphyte substrate foraging activity in the Tree Plots and Walking Transects. Significant *P*-values indicating among group dissimilarity and within group similarity are highlighted in bold.

Groups[1]	**Tree Plots**		**Walking Transects**	
	A value	***P* - value**	**A value**	***P* - value**
AI vs. BI	---	---	0.043	0.005
AI vs. LUHI	**---**	**---**	**0.111**	**< 0.001**
AI vs. N	---	---	0.198	0.054
AI vs. OS	---	---	0.077	0.007
AI vs. TFI	---	---	0.046	0.013
BI vs. LUHI	**0.293**	**< 0.001**	**0.134**	**< 0.001**
BI vs. N	---	---	-0.001	0.468
BI vs. OS	0.025	0.066	0.033	0.004
BI vs. TFI	0.004	0.298	0.017	0.024
BI vs. TS	**0.093**	**0.006**	**---**	**---**
N vs. LUHI	---	---	0.029	0.036
OS vs. LUHI	**0.180**	**0.001**	**0.124**	**< 0.001**
OS vs. N	---	---	0.013	0.286
OS vs. TS	0.077	0.020	---	---
TFI vs. LUHI	**0.263**	**< 0.001**	**0.162**	**< 0.001**
TFI vs. N	---	---	0.007	0.316
TFI vs. OS	0.036	0.011	0.015	0.080
TFI vs. TS	0.089	0.002	---	---
TS vs. LUHI	**0.579**	**0.009**	**---**	**---**
All Guilds	**0.159**	**< 0.001**	**0.144**	**< 0.001**

[1] AI = aerial insectivores, BI = bark insectivores, LUHI = low understory herbivores/insectivores, N = nectarivores, OS = omnivore/scavenger, TFI = timber-foliage insectivores, TS = timber-seed eaters

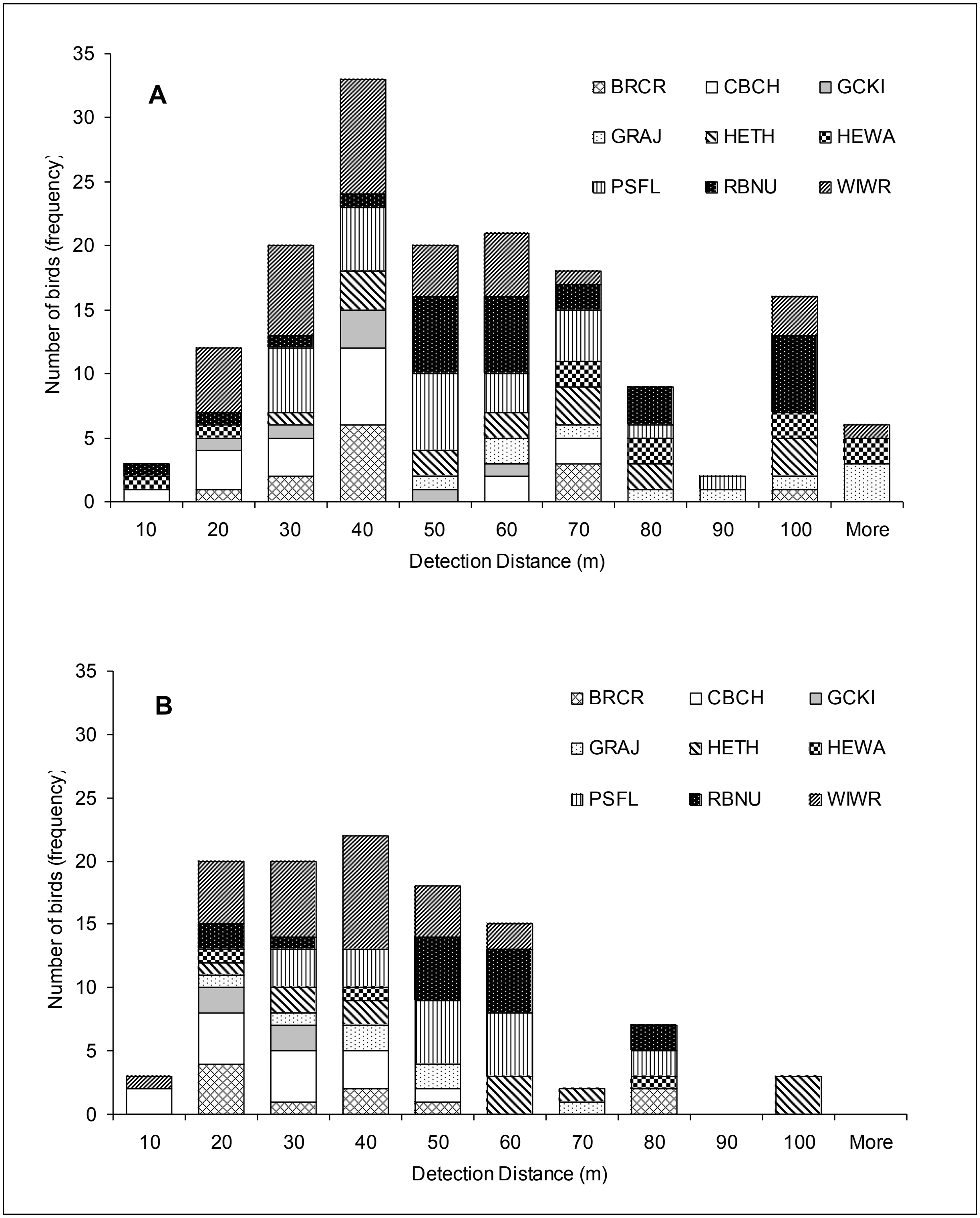
Appendix R: Mean number of birds detected in 30 m- and unlimited-radius VCP by observer location (flyovers, juveniles, and flushed birds included).

English Name	Unlimited-Radius		30 m-Radius	
	Canopy	**Ground**	**Canopy**	**Ground**
Red Crossbill	2.8 ± 1.73	2.4 ± 1.13	2.7 ± 1.73	2.35 ± 1.13
Winter Wren	1.75 ± 0.22	1.35 ± 0.18	0.7 ± 0.18	0.65 ± 0.21
Pacific-slope Flycatcher	1.35 ± 0.25	0.95 ± 0.2	0.3 ± 0.15	0.2 ± 0.12
Red-breasted Nuthatch	1.3 ± 0.18	0.75 ± 0.12	0.15 ± 0.08	0.15 ± 0.08
Vaux's Swift	1.25 ± 0.35	0.5 ± 0.21	1.25 ± 0.35	0.5 ± 0.21
Chestnut-backed Chickadee	1.25 ± 0.26	0.85 ± 0.25	0.7 ± 0.28	0.75 ± 0.25
Hermit Thrush	0.75 ± 0.22	0.6 ± 0.23	0.05 ± 0.05	0.15 ± 0.08
Brown Creeper	0.65 ± 0.15	0.5 ± 0.15	0.15 ± 0.08	0.25 ± 0.12
Hermit Warbler	0.55 ± 0.21	0.15 ± 0.08	0.15 ± 0.11	0.05 ± 0.05
Steller's Jay	0.55 ± 0.21	0.4 ± 0.13	0.05 ± 0.05	0 ± 0
Gray Jay	0.5 ± 0.14	0.35 ± 0.13	0 ± 0	0.1 ± 0.07
Golden-crowned Kinglet	0.35 ± 0.13	0.25 ± 0.16	0.1 ± 0.07	0.25 ± 0.16
Tree Swallow	0.25 ± 0.1	0.05 ± 0.05	0.25 ± 0.1	0.05 ± 0.05
Pine Siskin	0.2 ± 0.14	0.05 ± 0.05	0 ± 0	0.05 ± 0.05
Common Raven	0.2 ± 0.09	0 ± 0	0 ± 0	0 ± 0
American Robin	0.15 ± 0.08	0.1 ± 0.07	0 ± 0	0 ± 0
Dark-eyed Junco	0.15 ± 0.08	0.1 ± 0.07	0.05 ± 0.05	0.05 ± 0.05
Rufous Hummingbird	0.15 ± 0.08	0.15 ± 0.08	0.15 ± 0.08	0.15 ± 0.08
Western Tanager	0.15 ± 0.08	0 ± 0	0 ± 0	0 ± 0
Hammond's Flycatcher	0.1 ± 0.1	0.05 ± 0.05	0 ± 0	0 ± 0
Barred Owl	0.05 ± 0.05	0.05 ± 0.05	0 ± 0	0 ± 0
Black-headed Grosbeak	0.05 ± 0.05	0.05 ± 0.05	0.05 ± 0.05	0 ± 0
Evening Grosbeak	0.05 ± 0.05	0.15 ± 0.08	0.05 ± 0.05	0.05 ± 0.05
Hairy Woodpecker	0.05 ± 0.05	0.1 ± 0.07	0 ± 0	0 ± 0
Northern Flicker	0.05 ± 0.05	0.05 ± 0.05	0 ± 0	0 ± 0
Olive-sided Flycatcher	0.05 ± 0.05	0 ± 0	0 ± 0	0 ± 0
Purple Finch	0.05 ± 0.05	0 ± 0	0 ± 0	0 ± 0
Red-breasted Sapsucker	0.05 ± 0.05	0.05 ± 0.05	0 ± 0	0 ± 0
Ruby-crowned Kinglet	0.05 ± 0.05	0.05 ± 0.05	0.05 ± 0.05	0.05 ± 0.05
Swainson's Thrush	0.05 ± 0.05	0.05 ± 0.05	0.05 ± 0.05	0.05 ± 0.05
Western Wood-Pewee	0.05 ± 0.05	0 ± 0	0 ± 0	0 ± 0
Yellow-rumped Warbler	0.05 ± 0.05	0.05 ± 0.05	0 ± 0	0.05 ± 0.05
American Goldfinch	0 ± 0	0.05 ± 0.05	0 ± 0	0.05 ± 0.05
Common Nighthawk	0 ± 0	0.05 ± 0.05	0 ± 0	0.05 ± 0.05
Pileated Woodpecker	0 ± 0	0.05 ± 0.05	0 ± 0	0 ± 0
Song Sparrow	0 ± 0	0.05 ± 0.05	0 ± 0	0 ± 0
No. of individuals/plot	**15.05 ± 1.86**	**10.4 ± 1.34**	**6.95 ± 1.72**	**6.0 ± 1.07**
No. of species/plot	**8.45 ± 0.55**	**6.4 ± 0.56**	**3.25 ± 0.28**	**3.0 ± 0.32**

Appendix S: Frequency of occurrence of all bird species by observer location (flyovers, juveniles, and flushed birds included).

English Name	Unlimited Radius		30 m Radius	
	Canopy	**Ground**	**Canopy**	**Ground**
Winter Wren	90	85	55	40
Red-breasted Nuthatch	85	70	15	15
Pacific-slope Flycatcher	75	65	20	15
Chestnut-backed Chickadee.	65	50	30	40
Vaux’s Swift	60	25	60	25
Brown Creeper	55	40	15	20
Hermit Thrush	50	35	5	15
Purple Finch	5	0	0	0
Swainson’s Thrush	5	5	5	5
Evening Grosbeak	5	15	5	5
Northern Flicker	5	5	0	0
Olive-sided Flycatcher	5	0	0	0
Western Wood-Pewee	5	0	0	0
Yellow-rumped Warbler	5	5	0	5
Hammond's Flycatcher	5	5	0	0
Black-headed Grosbeak	5	5	5	0
Hairy Woodpecker	5	10	0	0
Ruby-crowned Kinglet	5	5	5	5
Red-breasted Sapsucker	5	5	0	0
Barred Owl	5	5	0	0
Gray Jay	45	30	0	10
Steller’s Jay	40	35	5	0
Red Crossbill	35	40	35	40
Hermit Warbler	30	15	10	5
Golden-crowned Kinglet	30	15	10	15
Tree Swallow	25	5	25	5
Common Raven	20	0	0	0
Dark-eyed Junco	15	10	5	5
Western Tanager	15	0	0	0
Rufous Hummingbird	15	15	15	15
American Robin	15	10	0	0
Pine Siskin	10	5	0	5
American Goldfinch	0	5	0	5
Common Nighthawk	0	5	0	5
Pileated Woodpecker	0	5	0	0
Song Sparrow	0	5	0	0

Appendix T: Histogram of A) canopy-level and B) ground-level observer detection distances (m) for nine core species (BRCR = Brown Creeper, CBCH = Chestnut-backed Chickadee, GCKI = Golden-crowned Kinglet, GRAJ = Gray Jay, HETH = Hermit Thrush, HEWA = Hermit Warbler, PSFL = Pacific-slope Flycatcher, RBNU = Red-breasted Nuthatch and WIWR = Winter Wren).



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