AN ABSTRACT OF THE DISSERTATION OF

Joan C. Hagar for the degree of Doctor of Philosophy in Forest Science, presented on October 31, 2003.

Title: Functional Relationships among Songbirds, Arthropods, and Understory Vegetation in Douglas-fir Forests, Western Oregon.

Abstract approved: Signature redacted for privacy.

Edward E. Starkey

Arthropods are important food resources for birds. Forest management activities can influence shrub-dwelling arthropods by affecting the structure and composition of understory shrub communities. Changes in abundance and species composition of arthropod communities in turn may influence the distribution and abundance of insectivorous birds. I examined relationships among bird abundance, availability of arthropod prey, and composition of understory vegetation in managed and unmanaged Douglas-fir forests in western Oregon. I sampled bird abundance, arthropod intensity in terms of abundance and biomass, and habitat structure in 13 forest stands representing a range of structural conditions. I used fecal analysis to describe the diets of five bird species that forage in the understory of conifer forests, and compared the abundance of food resources for Wilson's warblers among shrub species and silvicultural treatments. I also quantified the foraging patterns of Wilson's warblers, MacGillivray's warblers, and orange-crowned warblers to determine which shrub species were used for foraging. Variation in deciduous shrub cover provided the best explanation of variation in the abundances of Wilson's warbler, MacGillivray's warbler, and Swainson's thrush among study sites. Stands occupied by Wilson's and MacGillivray's warblers had significantly greater cover of deciduous shrubs than unoccupied stands, and both of these species foraged extensively on these shrubs. Their association with deciduous shrubs may be related to prey abundance because tall, deciduous shrubs supported high abundances of arthropod taxa selected as prey by Wilson's warblers, especially Lepidoptera larvae. Abundance of aerial arthropod prey also was positively correlated with deciduous shrub cover. These shrub species responded positively to partial removal of the overstory by thinning and group selection harvests. Furthermore, small gaps in the canopy of commercially thinned stands and larger gaps created by group selection harvests supported higher abundances of aerial arthropod prey than surrounding matrix forest. I conclude that understory vegetation in general, and deciduous shrubs in particular, make an important contribution to food resources for birds in conifer-dominated habitats. Management activities that promote the development and maintenance of understory vegetation can positively influence songbird diversity by maintaining habitat for shrub-associated species.

Functional Relationships among Songbirds, Arthropods, and Understory Vegetation in Douglas-fir Forests, Western Oregon

By
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Chapter 1

INTRODUCTION

Vegetation structure and composition are among the most important features believed to influence habitat selection by birds (Cody 1985) and the relationships between the distribution and abundance of birds and habitat features have long been a focus of avian ecological research (Holmes 1981, Block and Brennan 1993). While correlations between bird community and vegetation characteristics have been widely established, underlying causal factors rarely have been identified (Holmes 1981). Vegetation structure and composition usually are proximate indicators of the availability of the resources, such as food and nesting sites, which ultimately affect survival and reproduction (Hilden 1965). Relationships between vegetation structure and bird density can be obscure and unpredictable because birds do not usually respond directly to the variables chosen by human observers to quantify habitat (Morse 1985). More direct measurements of resources, such as arthropod biomass available to insectivorous birds, may better predict habitat use than variables that describe vegetation (Brush and Stiles 1986). Even when bird abundance may be well correlated with vegetation structure, management strategies based solely on assumed associations with vegetation may fail to meet all habitat requirements unless functional relationships underlying the observed correlations are understood (Holmes 1981). For example, availability of nesting sites as indicated by habitat structure may not necessarily also reflect suitable foraging habitat (Weikel and Hayes 1999). Therefore, evaluation of habitat on the basis of vegetation structure may be unreliable unless associations between wildlife and vegetation are based on a detailed knowledge of species-specific resource requirements (Van Horne 1983).

Our knowledge of the response of birds to management practices in western forests is based largely on correlations between bird abundance and vegetation structure, suggesting a strong need for more information on functional relationships.

Several studies have addressed the effects of forest management on the potential for nesting success (e.g., Chambers 1996, Hanski et al. 1996, Schmiegelow 1997), but few studies have directly examined how management practices influence food availability for forest birds (Hagar 1992, Weikel and Hayes 1999, Hagar 1960). Food availability is a basic, critical habitat component that often limits the reproductive success and survival of breeding birds (Martin 1987), and is therefore a key factor in habitat selection and use (Block and Brennen 1993). Although most bird species may not be directly associated with particular plant species, they may be linked to certain plant taxa through their insect prey (Recher et al. 1991, Robinson and Holmes 1984) because many forest insects select specific host plant species (Edwards and Wratten 1980). Holmes and Shultz (1988) provided evidence that the structure of forest bird communities is associated with variation in types and abundances of arthropod prey among tree species in eastern hardwood forests. While some studies have examined bird diets in western coniferous systems (Beaver and Baldwin 1975, Otvos and Stark 1985), few have related food resources for birds to vegetation composition. Knowledge of bird diets may allow identification of plant species that are important in supporting food resources, establishing a functional link between vegetation and habitat.

An understanding of functional relationships among organisms also may facilitate the implementation of ecosystem management and help managers achieve goals related to the maintenance of biodiversity. Managers faced with the challenge of managing biodiversity often lack information and a good framework for assessment and monitoring. The mandate to manage for biodiversity may well seem logistically and fiscally overwhelming if each species must be considered independently. Furthermore, no species is independent of its community, but rather is related to other species through a web of interactions. As Noss (1990) points out: "… processes such as interspecific interactions … are crucial to maintaining biodiversity." Besides being logistically and fiscally unfeasible, enhancing diversity one species at a time is unlikely to be successful unless relationships among organisms are understood. Trophic interactions or food webs are one of the important ecosystem processes that link many organisms. Because energy stored by plants is passed through the ecosystem by a series of consumers, changes in vegetation may influence organisms at all trophic levels. In spite of the importance of basic trophic processes in maintaining ecosystem functions, little is known about how forest practices are likely to affect organisms at the lowest trophic levels, and how these effects will move through food chains. A food web approach to understanding functional relationships between birds and habitat could facilitate management for biodiversity because it links the habitat requirements of multiple species.

In recent years, an emphasis on managing for timber production on public forested lands of the Northwest has shifted to the more holistic approach of ecosystem management (Kohm and Franklin 1997). Ecosystem function and performance has been linked to biodiversity (Schulze and Mooney 1993, Tilman and Downing 1994, Naeem et al. 1994), making the maintenance of biodiversity central to ecosystem management (Temple 1997). Information on biodiversity is therefore a high priority need, especially for federal land managers faced with implementing the Northwest Forest Plan (NWFP; Muir et al. 2002). Goals of the NWFP include promoting biodiversity in both designated reserves and in stands managed for timber production (USDA and USDI 1994). Young (<100 years) forests currently occupy much of the land under the jurisdiction of the NWFP. There are two main challenges involved with the management of these young stands to achieve the biodiversity goals of the NWFP. First, managers are concerned with the immediate need to promote and restore biodiversity. Young stands that are the legacy of past clear-cut harvesting often lack the structural heterogeneity of natural stands (Hansen et al. 1991), and are therefore biologically depauperate. One important structural feature that is typically not well developed in dense young stands is understory vegetation. Secondly, managers need tools for accelerating the development of late-successional habitat in reserves that are currently occupied by young forest. Partial harvests such as thinning and group selection are among the practices being developed to simultaneously manage forests for biodiversity and timber production (McComb et al. 1993, Chambers 1996, Carey et al. 1999b). These practices have the potential to increase structural diversity by increasing the availability of light and other resources for vegetation below the forest canopy.

However, partial harvests traditionally have been used for timber production, and their use as tools for managing wildlife habitat needs to be refined. Predicting the response of understory vegetation, and hence forest bird communities, to partial removal of overstory cover is complicated by the interaction of many variables, including harvest intensity, time since harvest, and stand history.

I chose to investigate the relationship of forest understory to food resources for songbirds in order to contribute information on the effects of forest management on biodiversity. My research links three important components of biodiversity in Pacific Northwest forest ecosystems: understory vegetation, arthropods, and songbirds. Understory vegetation represents a large portion of the plant diversity in Pacific Northwest forest (Halpern and Spies 1995). Arthropods contribute hugely to biodiversity on regional and global scales. This contribution comes not only from the overwhelming taxonomic richness of arthropods, but also from the diverse and critically important roles arthropods perform in ecosystem functioning (Kim 1993). However, little is known about arthropod assemblages on understory vegetation in western coniferous forests. Several species of birds are associated with shrubs and understory vegetation (Morrison and Meslow 1983, Marshall et al. 2003). Bird species that primarily nest and forage in the forest understory are among those that respond positively to commercial thinning in western Oregon coniferous forests (Hagar 1992, Hagar and Howlin submitted, Hayes et al. 2003). I hypothesized that forest management may influence food resources for these species via the following pathways. Forest practices that reduce overstory cover can influence cover, density, and frequency of understory shrubs (Bailey et al. 1998, Klinka et al. 1996), which in turn is likely to influence the diversity and biomass of shrub-dwelling arthropods (Humphrey et al. 1999, Jokimaki et al. 1998). Changes in abundance and species composition of arthropod communities in turn may influence the distribution and abundance of avian insectivores (Brush and Stiles 1986).

In this work, I compare the abundance and explore habitat relationships of several species of shrub-associated birds among stands with varied structural characteristics reflecting different silvicultural histories (Chapter 2). In Chapters 3 and 4, I describe the foraging patterns and diets of shrub-associated birds in order to establish which food resources are important and which plant species support them. I focus primarily on food resources for Wilson's warblers and Swainson's thrushes. Both of these species nest and forage in dense thickets of shrubs in forest understories. In Chapter 4, I also describe the patterns of distribution of arthropod prey and other food resources on common understory plant species, and the influences of forest management on these resources. Chapter 5 addresses factors influencing the abundance of aerial prey for Wilson's warblers and other bird species that feed on airborne arthropods.

Chapter 2

MAINTAINING HABITAT FOR SHRUB-ASSOCIATED BIRDS IN MANAGED CONIFER FORESTS

INTRODUCTION

Past management practices focusing on timber production have created forests that differ in structure and composition from naturally regenerated forests (Hansen et al. 1991, Perry 1998). Loss of late-seral habitat is one obvious consequence of decades of clear-cutting and contemporary short-rotation management of production forests in the Pacific Northwest. Concern over the accompanying threats to biodiversity and ecosystem function spurred a surge of research and debate on old-growth organisms and ecosystems (Franklin et al. 1981, Old-Growth Definition Task Group 1986, Ruggiero et al. 1991), with much attention given to developing silvicultural strategies for managing young conifer forests to achieve old forest habitat and maintaining habitat for mature forest species in managed forests (Nyberg et al. 1987, McComb et al. 1993, Carey et al. 1999a, Carey et al. 1999b). The restoration of old forest structure currently is a focus of management policies on federal (USDA and USDI 1994) and state lands in Oregon (McAllister et al. 1999). Much less attention has been given to the effects of past forest management practices on early seral habitats and the structure of young forests, although these also have important implications for biodiversity and ecosystem function (Franklin et al. 1986, Perry 1998). The stage of forest succession dominated by shrubs, with conifer regeneration providing less than 30% cover, typically supports higher animal diversity than any other stage (Harris 1984, Hall et al. 1985). A focus on early establishment of conifers on forestlands managed for timber production has truncated this diverse shrub-dominated stage of forest succession (Hansen et al. 1991). Rapid establishment of conifers following clear-cutting, involving vegetation management and narrow spacing of conifer seedlings to reduce competition from other species (Walstad and Kuch 1987), has produced young, closed-canopy second-growth across millions of hectares in the Pacific Northwest. This forest condition is productive from a timber management perspective, but the homogenous structure supports low diversity of wildlife (Hayes et al. 1997). The dense canopy allows minimal penetration of sunlight, so understory vegetation is depauperate. In contrast, wide spacing and delayed dominance of conifers in naturally regenerating stands (Tappeiner et al. 1997a) would maintain a vigorous understory throughout much of stand development. This difference in structure between naturally regenerated stands and those that are the legacy of past clear-cuts could explain why densities of shrub-associated bird species such as Wilson's warbler and Swainson's thrush did not differ among age classes in natural stands (Carey et al. 1991), but occurred at much lower abundances in young plantations than in old-growth (Muir et al. 2002).

Shrubby understories in young forests and/or early seral shrub fields are the primary breeding habitat for several species of songbirds, including Wilson's warbler, MacGillivray's warbler, orange-crowned warbler, and Swainson's thrush (Dillingham 2003, Dowlan 2003a, Hagar 2003a, Hagar 2003b). While Wilson's warblers and Swainson's thrushes use understory in old-growth, they are more abundant in younger forests that have well-developed understories (Hansen et al. 1995). MacGillivray's and orange-crowned warblers are common in early successional forests, but less frequently use closed-canopy mid-seral and old-growth forests. Populations of these four species have decreased significantly in all or portions of their western North America breeding range over the past three decades (Sauer et al. 2003). Although late-seral forests are likely to offer improved habitat over dense young forests for some shrub associates, conversion of large portions of the landscape to old-growth is unlikely to provide optimal habitat for these species. A challenge to managers charged with maintaining biodiversity is to restore old-growth forests from young conifer plantations while simultaneously providing habitat for species that use understory vegetation and shrubby openings.

Partial harvests may be an important means of simultaneously addressing these multiple and apparently conflicting management goals. Commercial thinning is a forest management practice that traditionally manipulates the density of overstory trees in order to optimize timber production, but that may be modified to achieve a broad array of economic, ecological, and sociological objectives (Hayes et al. 1997, Curtis et al. 1998, Carey 2000). By reducing canopy cover and increasing light availability to the understory, thinning can promote the development of forest floor vegetation (Tappeiner et al. 1991, Tappeiner and Zasada 1993, Huffman et al. 1994, O'Dea et al. 1995). Evidence is accumulating for the potential of commercial thinning in second-growth conifer stands to increase songbird diversity (Hagar et al. 1996, Haveri and Carey 2000, Hagar and Howlin, submitted). Commercial thinning may therefore be a valuable tool for increasing structural diversity in the short-term while promoting development of old-forest structure over the long-term (McComb et al. 1993, Hayes et al. 1997, Bailey and Tappeiner 1998). Alternatives to clear-cut regeneration systems, or uneven-aged management, may offer options for maintaining habitat for understory species in older stands (McComb et al. 1993). Group selection involves the removal of small clusters of mature trees to create a mosaic of even-aged patches within a stand (Nyland 1996), and may mimic natural disturbances such as root-rot pockets (Chambers et al. 1999). Early seral conditions in recently harvested patches approach those in a clear-cut as patch size increases (Curtis et al. 1998), potentially providing habitat for some shrub-associated species. Chambers (1996) found that 80-year old Douglas-fir (*Pseudotsuga menziesii*) stands that had been partially harvested in ½ acre group selection patches supported a higher abundance of orange-crowned warblers than uncut control stands. However, few studies other than Chambers et al. (1999) have examined wildlife response to uneven-aged management in western coniferous forests, perhaps because these systems have not been widely applied (Tappeiner et al. 1997b).

While songbird diversity may increase in response to partial harvests, little is known about the functional reasons underlying such responses. Further, empirical evidence for a hypothesized increase in bird species richness with increasing structural diversity following thinning (Hagar et al. 1996) is lacking. For example, some shrub-associated species have not shown a consistent positive response to thinning (Hagar et al. 1996, Hayes et al. 2003). The response of shrub-associated species is undoubtedly linked to the response of understory vegetation to partial harvesting, but little is known about the relationship of these species to specific characteristics such as shrub height and species composition. Given the knowledge and expertise available for silvics of Pacific Northwest forests (Tappeiner et al. 2002), site-specific silvicultural prescriptions probably could be designed to create habitat for shrub-associated species if more precise information on habitat requirements were available. Concern over declining populations of shrub-associated species makes this information particularly relevant to the maintenance of biodiversity in managed forests.

This study builds upon a similar investigation I reported in Muir et al. (2002), comparing bird assemblages among young thinned, young unthinned, and mature forests. My objective in this study was to investigate whether partial harvests support higher abundances of shrub-associated birds than unharvested stands, and to determine which habitat features most influence variation in abundance. Specifically, I compared the abundance of four shrub-associated bird species (Swainson's thrush, Wilson's warbler, orange-crowned warbler, and MacGillivray's warbler) among stands that had been partially harvested with commercial thinning or group selection to abundance in unharvested young and mature stands.

METHODS

Study Area

In order to link my results to a larger ecological framework, and build upon existing data, I used a subset of study sites from an integrated study that assessed differences in the diversity of various organisms among young unthinned, young thinned, and old-growth Douglas-fir stands in western Oregon (Muir et al. 2002). I used two triads of stands, each consisting of a geographically grouped set of one young unthinned, one young thinned, and one unmanaged, mature stand (sites 1 and 2 in Fig. 2.1). Young unthinned stands represented the “control” condition; young thinned stands represented the current “treatment”; and mature stands represented the desired future condition. This selection of sites allowed me to address the short-term effects of thinning relative to the unthinned control, and to assess the long-term effects on shrub-associated species of promoting late-seral conditions on a landscape scale. I added two pairs of stands not used in the study described by Muir et al. (2002) in order to investigate the potential use of an alternative regeneration method, group selection, to maintain habitat for shrub-associated species in managed forests. These sites consisted of two unmanaged, mature stands each paired with stands of the same age that had been partially harvested with a group selection method (sites 5 and 6 in Fig. 2.1). I chose these sites because they are some of few areas in the region have been harvested with a group selection method, and because they were part of an experiment on which vegetation and bird data had been previously collected (Chambers 1996).

Study sites were located in forests of the Oregon Coast Range, in the Western Hemlock Vegetation (*Tsuga heterophylla*) forest zone (Fig. 2.1; Franklin and Dyrness 1988). Mild, wet winters and dry summers characterize regional climate. Sites were on public lands managed by three agencies (Table 2.1). Stand size averaged approximately 25 ha (range: 15 – 45 ha). The young stands (thinned and unthinned) regenerated naturally following clear-cut harvesting and were 55 – 65 years old. A single age cohort dominated the overstory, with very few large trees and well-decayed snags (<1/ ha) persisting from previous stands. Unthinned stands were in the stem-exclusion stage of forest development (Oliver and Larson 1990), and were characterized by a dense, uniform overstory of Douglas-fir, and a sparse understory. Clumps of tall shrubs, mainly vine maple (*Acer circinatum*) and oceanspray (*Holodiscus discolor*), that occurred in unthinned stands tended to be scattered, and were primarily composed of a few tall stems with sparse foliage. Thinned stands had been thinned to uniform spacing 19 – 27 years prior to this study. Residual tree densities were typical for standard thinning operations meant to optimize timber yield. In other words, the goal of thinning at the time it was performed did not include the fostering of structural and biological diversity. In contrast, stands harvested with a group selection method (hereafter referred to as GS stands), were part of an experiment to assess wildlife response to alternatives to clear-cutting aimed at maintaining biodiversity in managed forests (Chambers et al. 1999). In these 120-year-old stands, one-third of the volume was removed by clear-cutting 0.2-ha circular patches. Within each stand, various intensities of vegetation management techniques, ranging from none to herbicide application, were applied to patches (Ketchum 1994).

Figure 2.1. Map of study sites showing county lines and major drainages. Study site groups identified by number are 1) D-line, 2) Mary's Peak, 3) Sand Ck. young stands, 4) Sand Ck. mature stand, 5) Lewisburg Saddle, and 6) Peavy Arboretum.

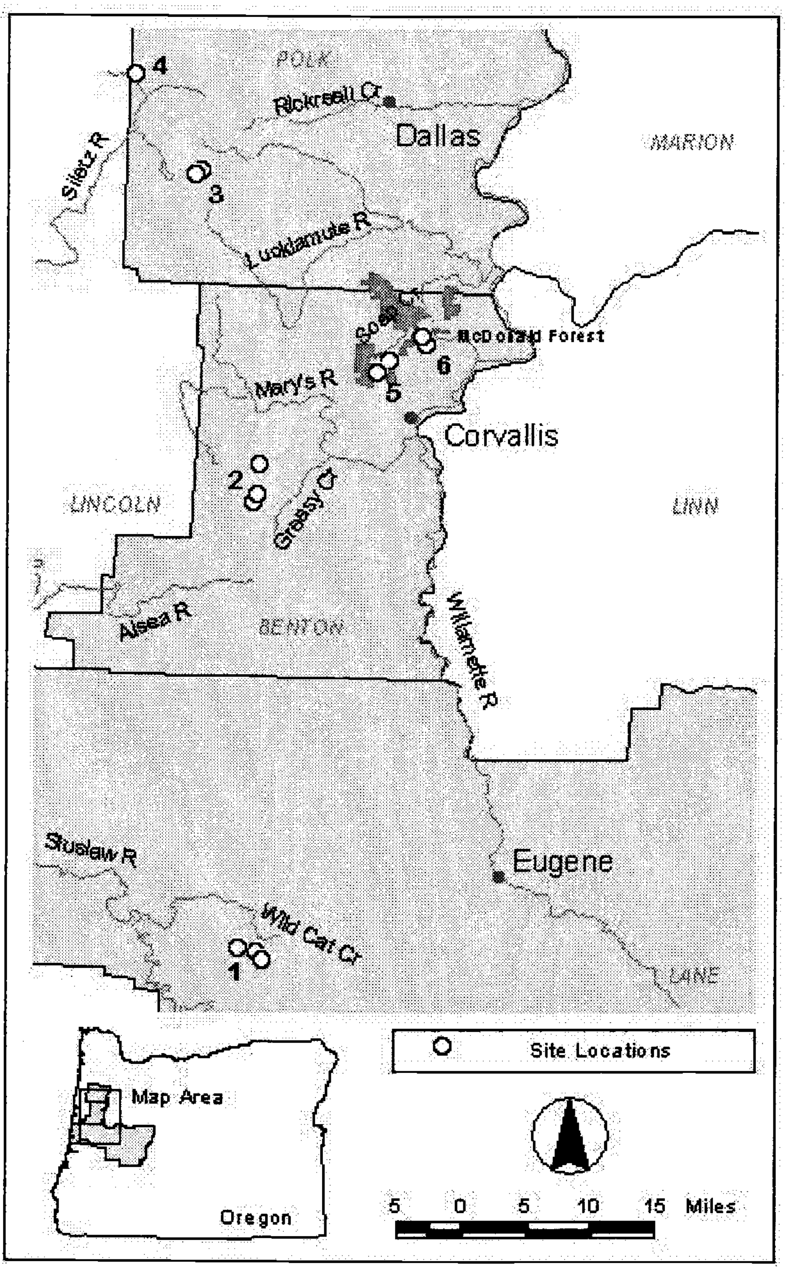


Table 2.1. Description of study stands.

Stand Name	Managing Agency[1]	Silvicultural History	Mean DBH (cm) Overstory Trees	Overstory[2] Tree Density	Elevation (m)
Mary's Peak Thinned	USFS	Regeneration harvest 1945; commercial thin 1980	52	120	430
Mary's Peak Unthinned	USFS	Regeneration harvest 1945	40	530	470
Mary's Peak Mature	USFS	Unmanaged	130	249	450
D-line Thinned	BLM	Regeneration harvest 1935; commercial thin 1972	54	183	370
D-line Unthinned	BLM	Regeneration harvest 1935	40	388	350
D-line Mature	BLM	Unmanaged	95	214	325
Lewisburg GS	OSU	Group Selection harvest 1989	73	167[3]	335
Lewisburg Mature	OSU	Unmanaged	59	192	396
Peavy GS	OSU	Group Selection harvest 1990	62	189[3]	200
Peavy Mature	OSU	Unmanaged	75	149	280

1) USFS = United States Forest Service; BLM = Bureau of Land Management; OSU = Oregon State University, McDonald-Dunn Research Forest.
2) Trees >30-cm dbh /ha
3) Density in matrix; does not include canopy gaps

Mature stands represented a range of stand ages >80 years, but none had evidence of active management. The Mary's Peak and D-line mature stands had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). Mature stands on McDonald-Dunn forest were 100 – 140 years old and were the first conifer stands to occupy those sites since cessation of fire used by Native Americans prior to European settlement (Towle 1982).

Bird Surveys

Stations for counting birds were established in each stand such that each station was $\geq$250 m from any other station and $\geq$100 m from a stand edge. I established three to six bird count stations/stand. Point counts of breeding birds (Reynolds et al. 1980) were conducted during five visits to each station between 19 May and 2 July 1999. Bird counts were conducted between ½ hour before sunrise to 4 hours after sunrise on days when wind and/or rain did not inhibit bird activity or the observers' ability to detect birds. Observers recorded the species of each bird detected, and estimated the horizontal distance (m) to each bird.

Habitat Data Collection

I used line transects and circular plots to describe bird habitat in terms of vegetation cover and tree density (Brower et al. 1990). Within each stand, parallel line transects separated by 30 m were arranged to sample habitat within 100 m of all point count stations. Total length of transect in each stand ranged from 250 – 925 m, depending on the arrangement of count stations. I recorded the length (cm) of intercept with transect (meter tape) for shrubs by species, herbs as a group, and bare ground. Plant material intercepting the vertical plane of each transects up to 3 m above ground was recorded. I estimated density of tree stems in nested circular plots centered every 50 m (center to center) on transects. Conifer and hardwood stems <10-cm diameter at breast height (dbh) were tallied by 2-cm size classes in 5 m radius plots (0.008 ha). Stems 10- to100-cm dbh were tallied by 10-cm size classes, and stems 100- to 140-cm dbh by 20-cm size classes, in 10-m radius plots (0.03 ha) on transects. Diameters of trees >140-cm dbh within the 10-m radius plots were recorded individually.

Data Analysis

Bird Abundance

I calculated an index of abundance as the number of observations/stand, averaged across stations and visits for each stand. The probability of detecting an individual bird decreases with the distance from the observer, so in calculating abundance indices, I included only individuals that were observed within a distance from observer that incorporated 90% of all observations. This distance was 75 m for Wilson's warblers, 65 m for MacGillivray's warblers and orange-crowned warblers and 80 m for Swainson's thrushes.

For Wilson's warblers, MacGillivray's warblers, and Swainson's thrushes, I modeled abundance as a function of stand condition using analysis of variance (ANOVA), and calculated the 90% confidence intervals around the least-square means for each condition (mature, group-selection, thinned, and unthinned). Abundance was log-transformed when necessary to meet model assumptions of normal distribution and constant variance among stand conditions. I evaluated the effect of stand condition on abundance of each species by comparing confidence intervals among conditions. If confidence intervals in one condition did not overlap the mean or median in another condition, the response variable was considered to differ significantly between the conditions (Steidl et al. 1997). I did not conduct an analysis of stand condition effect for orange-crowned warblers because they were observed in only 4 of the 10 stands.

Habitat Variables

I calculated a Linear Coverage Index (LCI) for each shrub species as the sum of the length of transect intercepted / total length of transect (Brower et al. 1990). I calculated the LCI for herbaceous cover, bare ground, and nine shrub species that occurred on ≥40% of the transects and in ≥70% of the stands. In addition, I made four variables by summing cover across species within plant types that I believed to be relevant to the birds: conifer, non-coniferous evergreen, low deciduous, and tall deciduous (see Table 2.2 for species included in each type). For each cover variable, I calculated the LCI on each transect within a stand, and averaged over transects for a stand-level summary.

I summed tree density data across size classes to condense them into four size classes for conifers and three for deciduous hardwoods: small conifers and hardwoods were <10-cm, medium conifers and hardwoods were 10- to 50-cm, large conifers were 50- to 100-cm, large hardwoods were >50-cm, and very large conifers were >100-cm dbh. These seven tree density variables were averaged over plots within each stand. Variables that did not meet assumptions of constant variance and normal distribution were log-transformed. I used ANOVA to compare each habitat variable among the four conditions (mature, GS, thinned, and unthinned). I evaluated overlap of 90% confidence intervals among conditions. If confidence intervals in one condition did not overlap the mean in another condition, the response variable was considered to differ significantly between the conditions (Steidl et al. 1997).

Habitat Relationship Models

I used an information-theoretic approach to selecting the "best" model from a set of pre-defined candidate models (Burnham and Anderson 2002). For each bird species, I selected variables I believed to be relevant to its ecology and life history, based on personal observation and literature, to include in regression models. Models were limited to a maximum of two variables due to small sample size (n=10). I examined plots of predictor versus response variables, and log-transformed variables that appeared to have non-constant variance. Using stand-level bird abundance and habitat variable means, I modeled bird abundance as a function of each single- and two-variable model. I also included a null model in the set of candidates to ensure that habitat variables better predicted bird abundance than models based solely on average abundance. The models with the lowest Akaike Information Criteria (AIC) score was considered the "best" in the set if it met assumptions of constant variance and normal distribution of residuals. For each of the remaining models in the set, I calculated Δ as the difference between the AIC score of the best model and that of the model under consideration. Models within 2 Δ units of best model were considered equally plausible as long as they met model assumptions (Burnham and Anderson 2002). I calculated the Akaike weight (w_i) to evaluate the strength of evidence supporting the best models. Models with w_i values close to 1 are more plausible than those with values close to 0.

Table 2.2. Species included in plant life-form groups used to describe and model bird habitat in the understory (<3 m) of Douglas-fir forests, Oregon Coast Range, 1999.

Conifer Trees

- Grand fir (*Abies grandis*)
- Douglas-fir (*Pseudotsuga menziesii*)
- Pacific yew (*Taxus brevifolia*)
- Western redcedar (*Thuja plicata*)
- Westen hemlock (*Tsuga heterophylla*)

Evergreen Shrubs

- Oregon grape (*Berberis nervosa*)
- Blackberry (*Rubus* spp.)
- Golden chinquapin (*Chrysolepsis chrysophylla*)
- Scotch broom (*Cytisus scoparius*)
- Salal (*Gaultheria shallon*)
- Holly (*Ilex aquifolium*)
- English Ivy (*Hedera helix*)
- Sword fern (*Polystichum munitum*)

Low Deciduous Shrubs

- Bracken fern (*Pteridium aquilinum*)
- Poison oak (*Rhus diversiloba*)
- Currant spp. (*Ribes* spp.)
- Thimbleberry (*Rubus parviflora*)
- Snowberry (*Symphoricarpos* spp.)
- Red huckleberry (*Vaccinium parvifolium*)

Deciduous Trees and Tall Shrubs

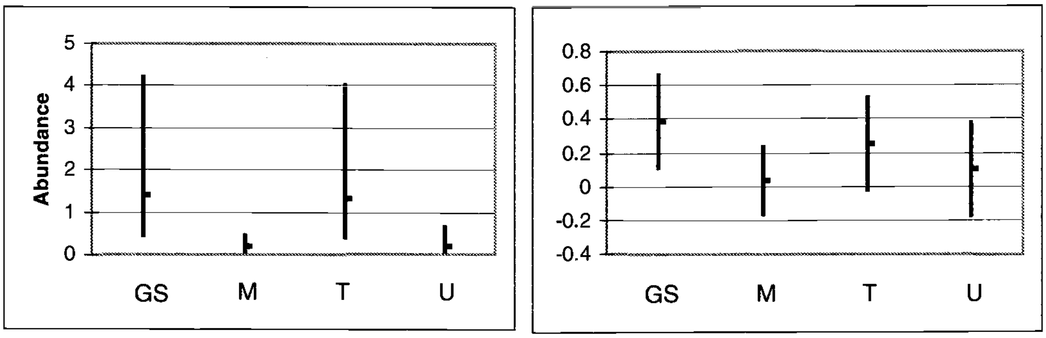
- Vine maple (*Acer circinatum*)
- Bigleaf maple (*Acer macrophyllum*)
- Red alder (*Alnus rubra*)
- California hazel (*Corylus cornuta*)
- Dogwood (*Cornus nuttalli*)
- Oceanspray (*Holodiscus discolor*)
- Indian plum (*Oemleria cerasiformis*)
- Bitter Cherry (*Prunus* emarginata)
- Oregon white oak (*Quercus garryanna*)
- Cascara (*Rhamnus purshiana*)
- Salmonberry (*Rubus spectabilis*)

RESULTS

Stand Condition Effects on Bird Abundance

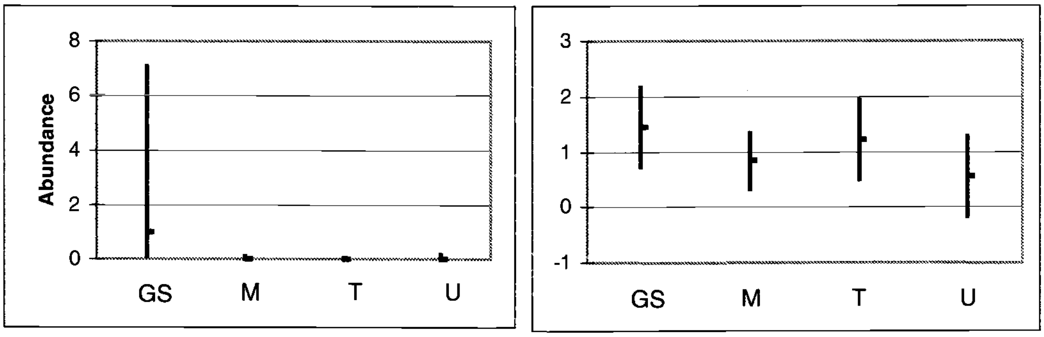
Wilson's warblers were observed in all stands, but median abundance was >6 times greater in GS and thinned conditions than in mature and unthinned (Fig. 2.2A). The very small overlap in only the tail ends of confidence intervals between GS and thinned vs. mature and unthinned provided evidence that Wilson's warbler abundance was significantly greater in partially harvested stands than in either mature or young unharvested stands.

Figure 2.2. Median (Wilson's warbler and orange-crowned warbler) or mean (MacGillivray's warbler and Swainson's thrush) abundance index (birds/stand/visit) with 90% confidence intervals in 4 silvicultural conditions (GS: group selection, M: mature, T: young thinned, and U: young unthinned) in the Oregon Coast Range, 1999.



A. Wilson's warbler

B. MacGillivray's warbler



C. Orange-crowned warbler

D. Swainson's thrush

MacGillivray's warblers were observed in six stands, and were absent from two mature, one thinned and one unthinned stand. Abundance in the remaining two mature stands was very low (only one bird observed in each stand for the entire season). Average abundance of MacGillivray's warblers in GS stands was more than 11 times greater than in mature stands. Overlapping confidence intervals for thinned, mature and unthinned stands (Fig. 2.2B) indicated a lack of significant difference in abundance among these three conditions.

The majority of orange-crowned warbler observations (n = 47; 98%) were from the two GS stands (Fig. 2.2C). Observations of this species in thinned and unthinned stands were rare enough to indicate an absence of breeding pairs.

Based on frequency of observations of Swainson's thrushes, this species likely was breeding in all stands. Average abundance of Swainson's thrushes was greater in partially harvested than unharvested stands, but this difference was not statistically significant because confidence intervals overlapped means (Fig. 2.2D).

Stand Condition Effects on Habitat Variables

Mature stands averaged significantly higher densities of conifers >100-cm dbh and deciduous hardwoods >10-cm dbh, and significantly lower densities of 10- to 100-cm dbh conifers (Fig. 2.3B, C, D, F, G) compared to thinned stands. The only tree density variable that differed significantly between mature and GS stands was density of 10- to 50-cm dbh deciduous trees, which was greater in GS stands (Fig. 2.3F). Mature stands had the lowest median cover of bracken fern of all the stand conditions, and significantly less cover of low deciduous shrubs than thinned and GS stands (Figs. 2.4A, G). Median cover of swordfern was significantly greater in mature stands than in any of the other conditions (Fig. 2.4B).

Unthinned stands had significantly higher mean densities of 10- to 50-cm dbh conifers than any of the other conditions (Fig. 2.3B). Understory in unthinned stands was characterized by a relatively high percentage of bare ground (Fig. 2.4L) and sparse cover of bracken fern and other short deciduous shrubs (Figs. 2.4A, G). Although not significantly different from thinned stands, cover of conifer foliage within 3 m of the forest floor and hazel cover were less in unthinned than in other stand conditions, especially compared to mature and GS stands (Figs. 2.4F, J).

Thinned stands had significantly lower median densities of 10- to 50-cm dbh conifers than unthinned stands (Fig. 2.3B), but greater median density of 50- to 100-cm dbh conifers, although the 90% CI of this variable in thinned stands slightly overlapped the median value for unthinned stands (Figs. 2.3C). The understory of thinned stands was most distinguished from other conditions by significantly greater median cover of bracken fern (Fig. 2.4A) and evergreen shrub cover (Fig. 2.4D), the latter primarily contributed by salal (Fig. 2.4E). Thinned and GS had significantly greater median cover of short deciduous shrubs than mature and unthinned conditions (Fig. 2.4G).

GS stands had the lowest median density of 10- to 50-cm dbh conifers and the highest median density of 10- to 50-cm dbh deciduous hardwoods of all the conditions (Fig. 2.3B, F). The understory in GS stands was characterized by relatively high percentages of herbaceous, blackberry, hazel, and low (<3 m) conifer cover (Figs. 2.4C, J, F). Median bracken fern cover was significantly greater in GS than in mature stands (Fig. 2.4A).

The density of small (<10-cm dbh) conifer and deciduous hardwood stems did not differ significantly among conditions (Fig. 2.3A, E). However, both medians and variability of small deciduous stem density were greatest in thinned and GS stands. Median cover of tall deciduous shrubs was greatest in thinned and mature stands, although this difference was non-significant, with broadly overlapping confidence intervals (Fig. 2.4H).

Figure 2.3. Median density (stems/ha) with 90% confidence intervals for four size classes of conifers and three size classes of deciduous hardwood stems in four silvicultural conditions (GS: group selection, M: mature, T: young thinned, and U: young unthinned) in the Oregon Coast Range, 1999.

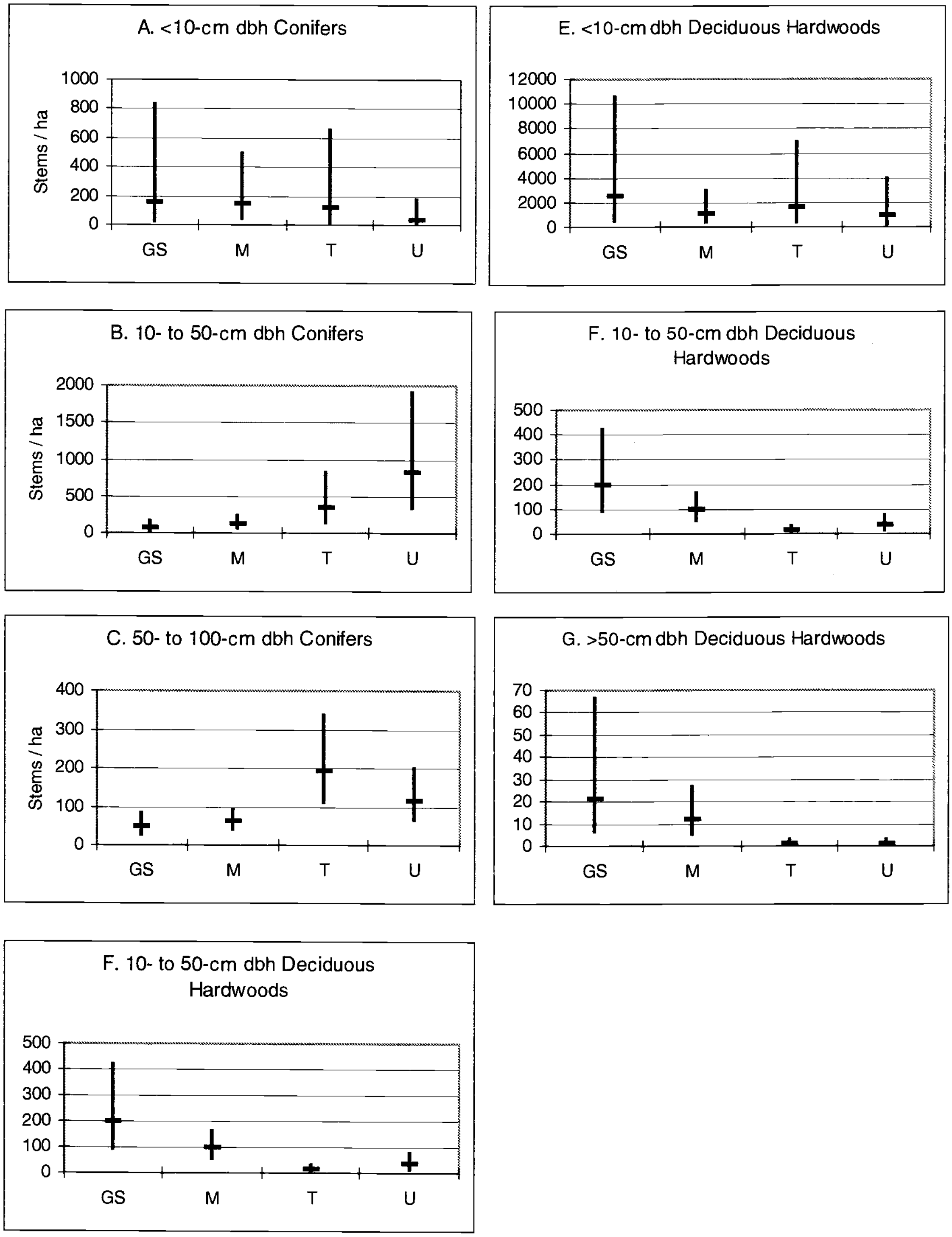


Figure 2.4. Median cover with 90% confidence intervals for understory vegetation (within 3 m of forest floor) in four silvicultural conditions (GS: group selection, M: mature, T: young thinned, and U: young unthinned) in the Oregon Coast Range, 1999.

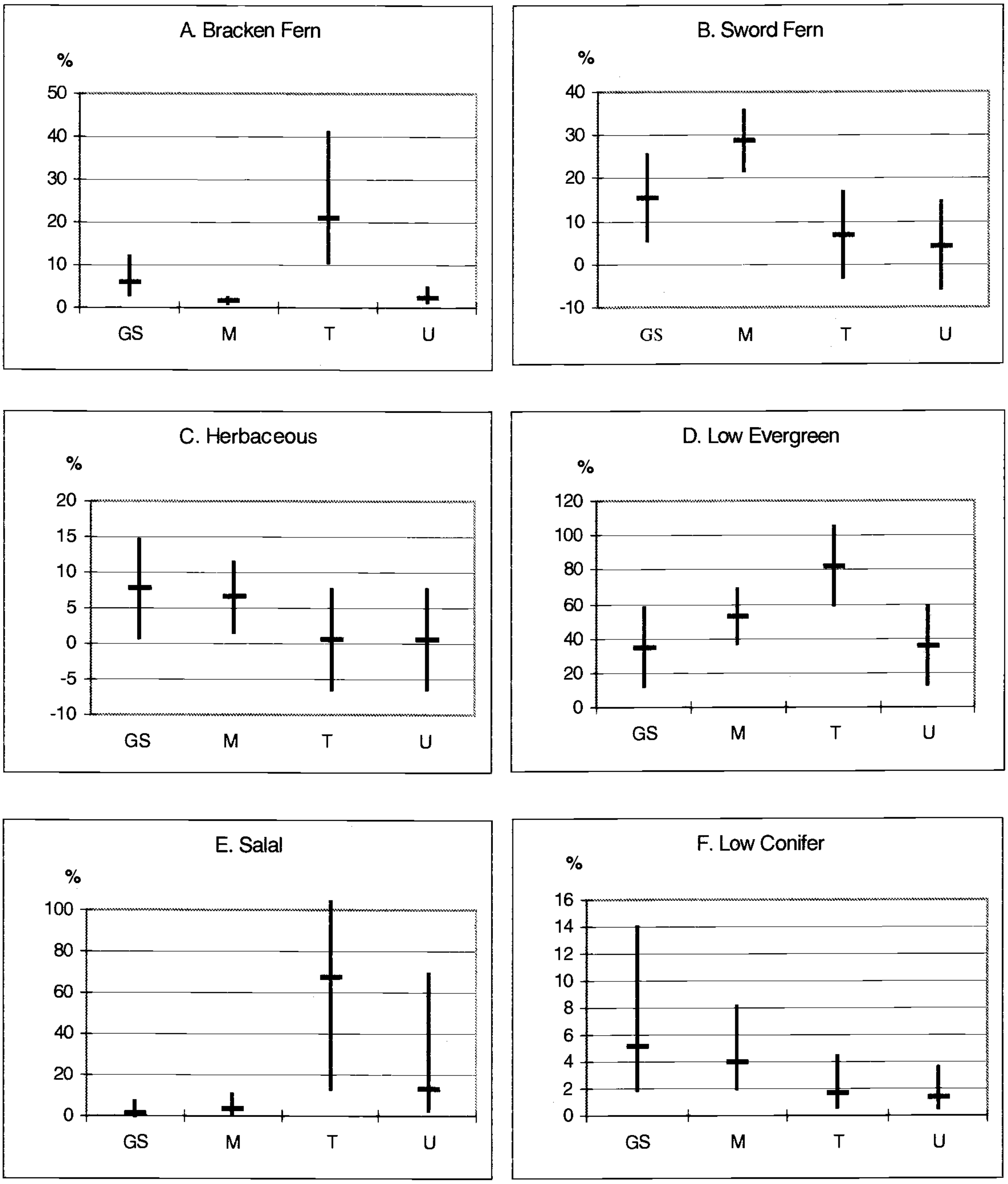
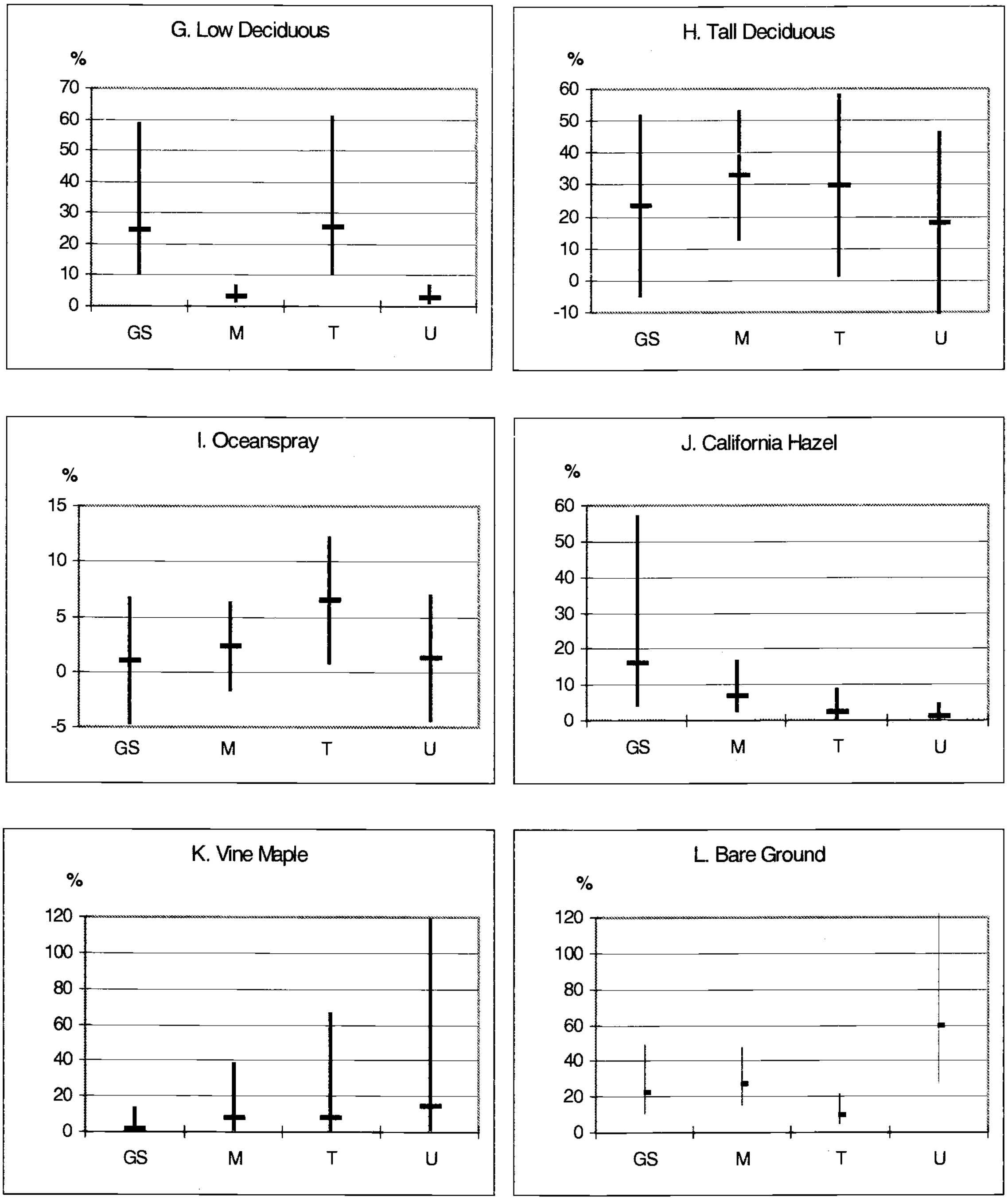


Figure 2.4. Continued.



Bird Habitat Relationships

The best model selected to explain variation in Wilson's warbler abundance included the density of small (<10-cm dbh) deciduous tree stems and cover of bracken fern, both of which were positively correlated with abundance (Table 2.3). All other candidate models were >2 Δ units away from the selected model, although all models that were better than the null model included variables describing deciduous vegetation. The second best model (Δ = 2.8) indicated a positive relationship between Wilson's warbler abundance and cover of tall deciduous shrubs. The evidence ratio (based on Akaike weights) for the selected model versus the null model was 61, suggesting strong evidence that this model had greater explanatory power than simply the average abundance across all sites. Except for bracken fern, cover of most individual shrub species such as vine maple, hazel, and oceanspray, performed poorly as predictors of Wilson's warbler abundance (Δ >9).

MacGillivray's warbler abundance varied positively with increasing cover of short, deciduous shrubs and density of small conifer stems (Table 2.3). However, the evidence that this model best represents the true source of variation in MacGillivray's warbler abundance was weak: only about one-third of the variation in abundance was explained, and four other models were within 2 Δ units of the selected model. Cover of short, deciduous shrubs was included in the top two models and was by itself equally as plausible as the selected model, but explained only 25% of the variation in MacGillivray's warbler abundance among stands. Bracken fern cover and density of small conifer stems were selected alone and together in three other models with Δ <2, explaining 14 to 21% of the variation in MacGillivray's warbler abundance. Although all models met assumptions of constant variance and normal distribution of residuals, the absence of MacGillivray's warbler's from 4 of the 10 stands may have increased variability and reduced the strength of models.

Variation in the abundance of Swainson's thrushes was positively associated with cover of short, deciduous shrubs and conifer foliage within 3 m of the ground (Table 2.3). All other candidate models were >2 Δ units away from the selected model. The evidence ratio (based on Akaike weights) for the selected model versus the null model was 189, suggesting very strong evidence that this model had greater explanatory power than simply the average abundance across all sites. Other models that were better than the null model included cover of bracken fern, and densities of small and medium deciduous hardwoods and small conifers.

Table 2.3. "Best" models according to Akaike Information Criteria for explaining variation in abundance of three bird species as a function of habitat variables. Potential values of Akaike Weight range from 0 to 1, with greater values indicating stronger evidence in support of the best model. Bird abundance was log-transformed for Wilson's warbler and MacGillivray's warbler.

Species	**Model Variables**	**Parameter Estimate (90% CI)**	**Akaike Weight**	**Adjusted R^2**
Wilson's warbler	Log density (#/ha) of deciduous tree stems <10-cm dbh	2.06 (1.27, 3.33)		
	Log cover (%) of bracken fern	1.80 (1.21, 2.70)	0.54	0.62
MacGillivray's warbler	Log cover (%) of short, deciduous shrubs	2.01 (0.93, 4.33)		
	Log density (#/ha) of conifer tree stems <10-cm dbh	1.70 (0.78, 3.71)	0.17	0.31
Swainson's thrush	Log cover (%) of short, deciduous shrubs	1.36 (1.16, 1.60)		
	Log cover (%) of conifer foliage within 3 m of ground	1.48 (1.17, 1.84)	0.55	0.70

DISCUSSION

Habitat Relationships

Patterns of shrub cover among the different stand conditions provided the best explanation of variation in the abundances of Wilson's warblers, MacGillivray's warblers, and Swainson's thrushes. Although my sites represented a range of densities of conifer stems >10-cm dbh that tended to vary by stand condition (Fig. 2.3), these variables were not useful in explaining variation in bird abundance. Rather, variables describing density and cover of deciduous vegetation near the forest floor were consistently selected as the best correlates of bird abundance in models of habitat relationships. Except for bracken fern, cover of individual shrub species was not as important as broader categories of deciduous and evergreen vegetation, and shrub height. From a bird's perspective, structure (i.e., cover) and food resources are probably more similar among species of tall, deciduous shrubs than between deciduous shrubs, short evergreen shrubs, and conifer saplings (see Chapter 4).

Wilson's warblers are associated with tall, deciduous shrubs throughout their breeding range and especially on the Pacific Coast (Ammon and Gilbert 1999, Hagar 2003b). Density of small (<10-cm dbh) stems of deciduous trees and shrubs was one of the best predictors of variability in the abundance of Wilson's warblers on my study sites; cover of tall shrubs was highly correlated with density of small, deciduous stems ($r = 0.71$), and was included in a model that closely contended ($\Delta = 2.8$) with the selected model (Table 2.3). Deciduous trees and shrubs support abundant arthropod prey (Willson and Comet 1996a, Chapter 4), are an important foraging substrate, and are positively associated with habitat occupancy by Wilson's warblers (Morrison 1981, Chapter 3). Swainson's thrushes also are strongly associated with deciduous shrubs and trees, especially red alder, in Pacific coastal forests (Morrison and Meslow 1983, Chambers 1996, Mack and Yong 2000, Hagar 2003a).

All three bird species for which I modeled habitat were positively associated with short deciduous vegetation. On my sites, bracken fern and red huckleberry were both important components of short deciduous cover. Bracken fern supports abundant arthropod prey, and huckleberry fruits were consumed by Swainson's thrushes (Chapter 4). MacGillivray's warblers require dense undergrowth to conceal their nests, which are built on or near (<3m) the ground (Pitocchelli 1995). MacGillivray's warblers are associated with low shrubs in early seral patches (Morrison 1981, Morrison and Meslow 1983), and unlike Wilson's warblers and Swainson's thrushes, rarely use mature, closed-canopy forests (Chambers 1996, Dowlan 2003a). Both Swainson's thrushes and MacGillivray's warblers were positively associated with conifer cover within 3 m of the forest floor combined with cover of short deciduous species. Conifer saplings provide dense cover and nest sites for Swainson's thrushes (Mack and Yong 2000). MacGillivray's warblers were observed foraging on Douglas-fir foliage within 3 m of the ground (Chapter 3).

Habitat in Thinned versus Unthinned Stands

Previous studies of bird response to thinning and group selection have reported mixed results for Wilson's warblers and Swainson's thrushes. Experimental studies that measured response within the first few years after thinning tended to find either no change or a decrease in the abundance of these species in thinned stands (Hagar and Howlin, submitted, Hayes et al. 2003). Within six years of thinning, Swainson's thrush abundance decreased and Wilson's warbler abundance did not change in the Oregon Coast Range (Hayes et al. 2003), while the abundance of both species remained unchanged after thinning in the Oregon Cascades (Hagar and Howlin, submitted) and after group selection harvest in the Coast Range (Chambers 1996). In contrast, abundances of these species were greater in stands thinned 5 to 15 years prior to data collection than in their unthinned pairs (Muir et al. 2002). This pattern of delayed positive response to partial harvesting by Wilson's warblers and Swainson's thrushes appears to parallel the development of tall shrubs in thinned stands. The mechanical process of thinning may damage tall shrubs, resulting in a short-term decrease of shrub cover (Curtis et al. 1998) and a corresponding decrease in habitat suitability for species associated with tall shrubs. In addition, tall shrubs require time to respond to thinning. Differences in abundance of understory plants between thinned and unthinned stands in the Coast Range may take more than a decade to emerge (Alaback and Herman 1988). A positive response of Wilson's warblers and Swainson's thrushes to partial overstory removal may be delayed until a dense layer of tall shrubs develops.

Although the stands I studied had been thinned operationally, with the goal of optimizing timber production, they had been thinned intensively enough and sufficient time had passed for development of understory habitat. Tall shrub cover in thinned stands was at least as great as in unthinned (Fig. 2.4H). Bailey (1996), working in the same region but with a much larger sample size, found significantly greater density of tall shrubs in thinned than unthinned stands. My very small sample size (n=2 pairs) may have been the reason that I found only weak evidence for higher abundance of Swainson's thrushes in thinned compared to unthinned stands. However, this trend is consistent with the significantly higher abundance of this species in thinned compared to unthinned stands reported in Muir et al. (2002). Manuwal and Palazzotto (2003) reported both higher density and reproductive success for Swainson's thrushes in thinned stands, where shrub cover was significantly greater, versus unthinned stands in western Washington. Density and cover of small conifers, which were positively associated with the abundance of MacGillivray's warblers and Swainson's thrushes, also may increase in response to thinning. Establishment of conifer seedlings and saplings is favored by thinning (Del Rio and Berg 1979), leading to greater density, frequency, and rates of height growth in thinned than unthinned stands in western Oregon (Bailey 1996).

Thinning has the potential to significantly increase habitat availability for shrub-associated birds over unthinned plantations. However, the benefits of thinning are conditional on the impact of harvest and the time required for recovery of understory shrubs. The cover of low, deciduous shrubs, with which abundances of MacGillivray's warbler and Swainson's thrush were positively associated, was significantly greater in thinned than unthinned stands. Whereas a positive response of Swainson's thrushes to partial overstory removal may be delayed until a dense layer of tall shrubs develops, MacGillivray's warblers are able to take advantage of overstory removal almost immediately following harvest. Chambers (1996) observed a six-fold increase in detections of MacGillivray's warblers within the first two years after group selection harvest in mid-age conifer stands. Hagar and Howlin (submitted) also observed establishment of MacGillivray's warblers in young (50-yr old) Douglas-fir stands within three years of a harvest that removed 20% of stand area in 0.2 ha openings. This rapid effect is consistent with my modeling results, indicating that MacGillivray's warblers are likely responding to understory vegetation that responds quickly to canopy reduction, including bracken fern and herbs (Crane 1989, Bohac et al. 1997). Models including bracken fern and herbaceous cover were as plausible as the preferred model that included cover of low deciduous shrubs for explaining variation in the abundance of MacGillivray's warblers among stands. The habitat in my thinned stands may have been moving beyond the optimum post-harvest stage of understory development for MacGillivray's warblers. MacGillivray's warblers occurred mainly along skid trails in thinned stands where bracken was most prevalent, and avoided the stand interiors where tall shrubs were better developed (pers. obs.). However, at this stage these stands may have been just beginning to provide optimal habitat for Swainson's thrushes.

Habitat in GS and Thinned versus Mature Stands

Group selection is an uneven-aged alternative to clear-cut regeneration systems. This technique has potential as a tool for maintaining structural components of late-seral habitat while simultaneously extracting timber (McComb et al. 1993, Chambers et al. 1999), although it has not been widely used in practical applications in the Pacific Northwest since early in the last century (Tappeiner et al. 1997b). Chambers et al. (1999) found that bird assemblages in stands that had one-third of the timber volume extracted in 0.6-ha patches differed little from those in uncut control stands. Furthermore, bird species richness may increase in GS stands because the creation of small ‘clear-cuts’ provides habitat for some early-seral associates within the mature forest matrix. This was the case with MacGillivray's and orange-crowned warblers, which were rare in or absent from uncut forests in my study. Although I regularly observed orange-crowned warblers only in the low elevation McDonald-Dunn Forest sites on the eastern fringe of the Coast Range, I do not believe that elevation was more important than stand condition in influencing their abundance. Orange-crowned warblers breed in appropriate habitat throughout the Coast Range, up to elevations well above the range encompassed by my study sites (Dillingham 2003). Furthermore, Chambers (1996) observed an increase in orange-crowned warbler abundance immediately following harvest of the GS stands, indicating that suitable habitat may have been created.

My results indicate that thinning and group selection harvests can eventually promote greater shrub cover and higher abundances of Wilson's warblers than are found in mature stands. Muir et al. (2002) also reported higher abundances of Wilson's warblers in young thinned compared to old-growth stands. Compared to uncut mature stands, both thinned and GS stands supported higher abundances of Wilson's warblers. This result was unexpected for Wilson's warblers because they are known to use understory shrubs in mature and old-growth forests (Brown 1985, Chambers 1996), and densities of this species were similar across of range of ages in natural forests in the Coast Range (Carey et al. 1991). Chambers (1996) studied habitat relationships of songbirds in the same mature and GS stands that I resampled 6 to 10 years later. Contrary to my findings, she found no difference in the abundance of Wilson's warblers between the uncut mature stands and the recently harvested GS stands of the same age. However, both Carey et al. (1991) and Chambers (1996) found no difference in cover of low shrubs among the stands they were comparing, so it is likely that habitat for Wilson's warblers also was similar among stands. In the several years between when Chambers (1996) conducted her study and when I resampled bird abundance in some of the same stands, average shrub cover in GS stands had surpassed that in uncut mature stands (Table 4.12). Similarly, greater cover of low shrubs in thinned than mature stands (Bailey 1996) likely provided better habitat for Wilson's warblers.

In contrast to Wilson's warblers, MacGillivray's warblers showed a consistent pattern of greater abundance in GS than uncut mature stands in both Chamber's (1996) and my study. Given the different habitat affinities of Wilson's and MacGillivray's warblers, it is interesting that I found a high abundance of both species together in GS stands. It seems likely that gap centers provided habitat for MacGillivray's warblers, while the taller shrubs around the edges of gaps and in the matrix between gaps provided habitat for Wilson's warblers. The use of vegetation management (application of herbicides and manual cutting to reduce shrub competition with conifer regeneration) in some patches and not in others within each GS stand also may have influenced habitat for these species. Wilson's warblers would be more likely to use patches in which no vegetation management had been applied, whereas MacGillivray's warblers may have found suitable habitat where openings were actively maintained in low stature vegetation.

Management Implications

Understory characteristics that are relevant to birds may not necessarily be directly correlated with stocking levels of conifers, the typical focus of forest management. Factors such as stand development and management history interact with stem density to influence understory vegetation. Managers seeking to provide habitat for a diversity of bird species must pay explicit attention to the understory as well as to density of overstory trees.

Ideally, management of forests to provide habitat for species associated with tall shrubs, such as Wilson's warbler and Swainson's thrush, would begin early in stand development. Controlling density at an early age, before canopy closure, can help to maintain diverse stand structure throughout the life of a stand, and can preserve future management options (Tappeiner et al. 2002). However, given the current dominance of dense young conifer stands on western Oregon and Washington landscapes, commercial thinning can be an effective tool for long-term improvement of habitat for some species. Thinning has the potential to significantly increase habitat availability for shrub-associated birds over unthinned plantations, as shown here for Wilson's warbler and Swainson's thrush. However, the benefits of thinning are conditional on the impact of harvest and the time required for recovery of understory shrubs. In order to minimize the immediate negative impacts of thinning on habitat for Wilson's warblers and Swainson's thrushes, managers should consider maintaining as much existing tall shrub cover as possible by avoiding damage to shrub patches during harvest operations.

Variable density thinning (Carey et al. 1999b) may be the best way to accomplish this goal. Variable density thinning also would address the tradeoff between providing tall shrub habitat for Wilson's warblers and Swainson's thrushes and low shrub habitat for MacGillivray's; areas of intensive thinning would be most suitable for MacGillivray's warblers. Heavy or repeated thinnings may be required to maintain a sufficiently open canopy to allow for the development of shrubs.

Thinning of young stands probably will play an important role in helping managers achieve the goal of restoring late seral habitat on public lands (Muir et al. 2002). Widespread thinning of dense young stands is likely to result in an immediate, short-term increase in habitat availability for MacGillivray's warblers, and a delayed improvement in habitat for Wilson's warblers and Swainson's thrushes. The improvement in habitat for Swainson's thrushes is likely to be sustained once stands achieve maturity because abundance of Swainson's thrushes is similar between young thinned and old-growth stands (Muir et al. 2002). However, because abundance of Wilson's warblers in mature forests is lower than in young thinned stands (Muir et al. 2002), this species is likely to decrease in abundance over the long-term, as area of late-seral forest increases under NWFP. Group selection harvests in federal matrix and Oregon Department of Forestry lands could help maintain habitat for Wilson's and MacGillivray's warblers under this scenario of increasing mature forest cover. Furthermore, GS can provide early seral habitat required by orange-crowned warblers. GS harvests are likely to be most effective at providing habitat for these species if vegetation management programs aimed at rapidly establishing conifer dominance in gaps are limited, in order to allow persistence of shrubs for a longer period of time. Clearly, landscape level planning will be required to ensure available habitat for all species.

Chapter 3

HABITAT SELECTION BY SHRUB-ASSOCIATED BIRDS AT TWO SPATIAL SCALES IN OREGON COAST RANGE DOUGLAS-FIR FORESTS

INTRODUCTION

Habitat selection is hierarchical, occurring from the scale of geographic range to the selection of feeding and nesting sites at a micro-site scale (Manly et al. 1993). Organisms can exhibit different patterns of habitat use at different spatial scales (Bergin 1992), so basing conclusions about habitat relationships at just one level of the hierarchy can be misleading (Johnson 1980, Wiens et al. 1986). For example, birds select territories that provide food, cover and nesting sites from among patches in a landscape. Within the territory, foraging patterns reveal fine-scale habitat selection.

Studies of foraging can offer important clues to functional relationships underlying fine-scale habitat selection (Morrison et al. 1990). Optimal foraging theory predicts that organisms will select prey for which the potential gain in energy exceeds the cost of pursuit and capture (Krebs 1978). Because it is energetically unprofitable for predators to spend time where prey density is low (Royama 1970), birds are expected to concentrate foraging efforts on substrates where prey availability is highest (Zach and Falls 1976).

The availability of prey for an insectivorous bird depends not only on abundance of prey items, but also on constraints associated with the acquisition of arthropod prey (Wolda 1990). An interaction between vegetation structure and the morphological and behavioral constraints of each bird species influences ability to perceive and capture prey, thereby affecting prey availability (Robinson and Holmes 1982, Holmes and Schultz 1988). For example, the morphology and behavioral repertoire of a given bird species may allow it to forage more efficiently on one species of vegetation than another (Holmes and Schultz 1988). Furthermore, methods used by ecologists to sample arthropods may represent a different perspective on prey availability than that experienced by foraging birds (Hutto 1990). Such methods may not discriminate among characteristics that influence the ability of a bird to perceive, handle, or digest prey items. Cryptic arthropods or those that are inaccessible (e.g., rolled inside a leaf or active only at night) may be difficult to perceive (Schowalter 2000). Arthropods that are chemically or mechanically defended may be avoided as prey items by many insectivores (Eisner 1970, Davies 1977, Sherry and McDade 1982, Heinrich and Collins 1983). Determination of the diet of a bird species can refine the definition of available prey types from those that are sampled in the environment (Robinson and Holmes 1982, Smith and Shugart 1987). However, identification of prey items in the diet is frequently limited to broad taxonomic categories, typically order, and usually no more precise than family. A given order of arthropods may include species representing a wide variety of availability based on crypticity, accessibility, and defenses. Lepidoptera, a group including favored prey for many bird species, is a good example of the variation in prey characteristics that affect availability within a single taxonomic order.

Assuming that the proportion of time spent foraging on a plant species would be positively correlated with prey availability, I quantified foraging patterns in order to investigate the relative contribution of various species of understory vegetation to the arthropod prey base for four shrub-associated bird species. This approach was used to compliment the approach described in Chapter 4, in which I compared the abundance of prey arthropods among shrub species in order to determine which, if any, shrub species were most important in supporting food resources for birds. I focused on Swainson's thrushes, Wilson's warblers, MacGillivray's warblers, and orange-crowned warblers because these species forage extensively in the understory (Marshall et al. 2003). Three of these bird species (the warblers) used only some of the sites I sampled for breeding. I wanted to describe habitat characteristics associated with their selection of stands within the landscape, in addition to describing fine-scale selection of foraging sites within the stands in which they established breeding territories. Therefore, I compared the cover of shrubs used for foraging among stands to determine if characteristics of stands in which breeding territories were established (occupied) were different from those not used for breeding (not occupied).

METHODS

Study Sites

Study sites were located in the Oregon Coast Range (Fig. 2.1), in the Western Hemlock Vegetation (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988). Mild, wet winters and dry summers characterize regional climate. Sites were on public lands managed by three agencies (Table 2.1). Stand size averaged approximately 25 ha (range: 15 – 45 ha). The young stands (three pairs of thinned and unthinned) regenerated naturally following clear-cut harvesting and were 55 – 65 years old. One age cohort dominated the overstory, with very few large trees and well-decayed snags (<1/ ha) persisting from previous stands. Unthinned stands were in the stem-exclusion stage of forest development (Oliver and Larson 1990), and were characterized by a dense, uniform overstory of Douglas-fir (*Pseudotuga menziesii*), and a sparse understory. Clumps of tall shrubs, mainly vine maple (*Acer circinatum*) and oceanspray (*Holodiscus discolor*), that occurred in unthinned stands tended to be scattered, and were primarily composed of a few tall stems with sparse foliage. Thinned stands had been thinned to uniform spacing 19 – 27 years prior to this study. Residual tree densities were typical for standard thinning operations meant to optimize timber yield. In other words, the goal of thinning at the time it was performed did not include the fostering of structural and biological diversity. In contrast, the two stands harvested with a group selection method (hereafter referred to as GS stands), were part of an experiment to assess wildlife response to alternatives to clear-cutting aimed at maintaining biodiversity in managed forests (Chambers et al. 1999). In these stands, 1/3 of the volume was removed by clear-cutting 0.2-ha circular patches. Within each stand, various intensities of vegetation management techniques, ranging from none to herbicide application, were applied to patches (Ketchum 1994).

Mature stands (N = 5) represented a range of stand ages >80 years, but none had evidence of active management. The Mary's Peak and D-line mature stands had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). Mature stands on McDonald-Dunn forest were 100 – 140 years old and were the first conifer stands to occupy those sites since cessation of fire used by Native Americans prior to European settlement (Towle 1982).

Bird Surveys

Stations for counting birds were established in each stand such that each station was ≥250 m from any other station and ≥100 m from a stand edge. I established 3 – 6 bird count stations/stand. Point counts of breeding birds (Reynolds et al. 1980) were conducted during five visits to each station between 19 May and 2 July, 1999. Bird counts were conducted between ½ hour before sunrise to four hours after sunrise on days when wind and/or rain did not inhibit bird activity or the observers' ability to detect birds. Observers recorded the species of each bird detected, and estimated the horizontal distance (m) to each bird.

Collection of Foraging Data

Swainson's thrushes, Wilson's warblers, MacGillivray's warblers, and orange-crowned warblers (the focal species) were captured in mist-nets in each stand where they occurred and marked with unique combinations of plastic color bands in order to enable identification of individuals in the field. Marking individuals allowed observers to be confident that each "new" observation was not a bird previously recorded that had moved, and thus ensured the independence of observations required for analysis of foraging data (Noon and Block 1990). Between mid-May and early August, 2000, foraging observations were made in two of the thinned and the two GS described above, and in one of the mature stands paired with a thinned stand, and one of the mature stands paired with a GS stand, but not all bird species were observed foraging in all stands. I did not try to collect foraging data in the remaining stands, either because densities of focal species were too low or I did not color-band birds in those stands. Foraging data was collected on 7 to 10 dates in four of the stands (one thinned, two GS, and one mature), but on only one date each in the other two stands. Observations were made throughout daylight hours, from 0600 to 1930 h. To collect foraging data, observers systematically traversed each study area until a bird of one of the focal species was encountered. If the bird was foraging at the time of encounter, the observer recorded data for the first prey attack maneuver after a 5 second waiting period (Hejl et al. 1990). If the bird was not foraging at the time of encounter, the observer attempted to follow it until it began to forage and recorded data for the first prey attack maneuver observed. Observers recorded bird species, band combinations, foraging height, and data on foraging substrate, including plant species.

Habitat Data Collection

I used line transects to estimate understory cover (Brower et al. 1990). Within each stand, parallel line transects separated by 30 m were arranged to sample habitat within 100 m of all point count stations. Total length of transect in each stand ranged from 250 – 925 m, depending on the arrangement of count stations. I recorded the length (cm) of intercept with transect (meter tape) for shrubs by species, herbs as a group, and bare ground. Plant material intercepting the vertical plane of each transect up to 3 m above ground was recorded.

Data Analysis

I adapted a metric used to compare use and availability of food items, Manly's Alpha, to compare use and availability of shrub species as foraging substrates (Krebs 1989:394-397, Garshelis 2000). Manly's Alpha is the proportional use divided by the proportional availability of each shrub species used for foraging, standardized so that the values for all shrub species sum to 1. (Equation 3.1). Manly's Alpha has values ranging from 0 to 1, and is interpreted in terms of the relative expected use of a foraging substrate had all types been equally available. Thus, I used deviations of Manly's Alpha from 1/m (Equation 3.1) as a selection index, indicating relative selection for or against a foraging substrate. A species of vegetation was *selected* if it was used for foraging more than expected based on its availability in the environment (Johnson 1980). Positive selection indices indicated that a substrate was used for foraging more than expected based on availability (i.e., was selected), negative indices indicated that use was less than expected based on availability, and a value of 0 indicated that use was in proportion to availability. For each warbler species, selection indices for each shrub species were averaged across all stands in which warbler and plant species co-occurred.

Equation 3.1. Calculation of Manly's Alpha for comparing use and availability of foraging substrates.

$$\text{Manly's Alpha} = \frac{r_i}{\sum_{i-m} r}$$

Where

r = % used / % available

m = number of substrates available

Note: 1/m is expected value if substrate used in proportion to availability.

To calculate the percentage of each shrub species used for foraging by each bird species, I summed the instantaneous observations of foraging on each shrub species in each stand and divided by the total number of foraging observations in the stand. I calculated the percentage of each shrub species in the environment by dividing the length of each transect intercepted by each shrub species by the total length of the transect to derive a linear coverage index (Brower et al. 1990), then averaging this index over all transects within each stand. I included in the analyses all shrub species that had ≥1% cover; shrub species with <1% cover were included if they were used for foraging ≥1 time for a given bird species.

I had a sufficient number of foraging observations to analyze the foraging patterns of three bird species: Wilson's, MacGillivray's, and orange-crowned warblers. Only instantaneous observations were included in the analysis; instantaneous observations were independent and represented the substrate a bird was using at the first observed foraging event. Only foraging events that occurred within 3 m of the forest floor were included in preference index analyses because the height of understory vegetation sampled by line transects was limited to 3 m in height.

To compare cover of shrubs used for foraging between occupied and unoccupied stands, I calculated average percent cover by stand occupancy category for each bird species for the plant species that were used more than three times for foraging. I also grouped plants into deciduous, conifer, and non-coniferous evergreen categories because cover of individual plant species varied widely among stands, and this allowed me to include foraging observations for plant species with few foraging observations. The criteria I used for determining stand occupancy by a given bird species were that ≥1 individual per visit was observed for three of the five visits, and that the species was observed at >1 station per stand. I believed these criteria would distinguish stands that encompassed most or all of the breeding territory of at least one pair from those that were incidentally used by transitory individuals. I log-transformed cover variables that did not meet assumptions of normal distribution and constant variance. I considered cover to be significantly different between occupied and unoccupied stands if the 90% confidence interval of one category did not overlap the mean or median of the other (Steidl et al. 1997).

RESULTS

Wilson's warbler

Wilson's warblers were observed foraging on 18 plant species, and foraged throughout all layers of forest vegetation, although 75% of observations were within 3 m of the forest floor (Table 3.1). When Wilson's warbler's foraged above 3 m, they tended to use approximately equal proportions of conifers and deciduous trees overall, but slightly more deciduous vegetation from 3 – 10 m and more conifers above 10 m (Table 3.2).

Table 3.1. Number (and percentage) of foraging observations of 4 species of shrub-associated birds by categories of height above forest floor, Oregon Coast Range, 2000.

Species	**<0.3 m**	**0.3 – 1 m**	**1 – 3 m**	**3 – 10 m**	**>10 m**	**Total**
Swainson's thrush	12 (34%)	6 (17%)	9 (26%)	4 (11%)	4 (11%)	35
MacGillivray's warbler	16 (22%)	35 (48%)	16 (22%)	3 (4%)	3 (4%)	73
Orange-crowned warbler	4 (7%)	13 (22%)	22 (38%)	13 (22%)	6 (10%)	58
Wilson's warbler	33 (13%)	74 (29%)	82 (33%)	40 (16%)	21 (8%)	250

Tall, deciduous shrubs and trees, including vine maple, California hazel (*Corylus cornuta* var. *californica*), bigleaf maple (*Acer macrophyllum*), and oceanspray, were among the most frequently used foraging substrates within 3 m of the forest floor, collectively constituting approximately 70% of the observations in this layer of vegetation. However, vine maple and California hazel, along with bracken fern (*Pteridium aquilinum*), which was also frequently used for foraging, had negative preference indices, indicating that use by Wilson's warblers was less than expected based on availability (Table 3.3). Understory species that were both frequently used and preferentially selected as foraging substrates included Douglas-fir, oceanspray, and bigleaf maple (Table 3.3). Although not preferentially selected as a foraging substrate, cover of bracken fern was 5% greater on average in stands occupied by Wilson's warblers than in unoccupied stands (Table 3.4). I did not detect a difference in cover between occupied and unoccupied stands for other individual shrub species, but cover of all deciduous shrubs combined averaged 30% more in occupied stands (Table 3.5). There also was evidence that cover of all non-coniferous evergreen shrubs combined was greater by 18% in occupied than unoccupied stands, although Wilson's warblers were seldom observed foraging on evergreen species (Table 3.5).

Table 3.2. Number and percentage of foraging events that occurred >3 m above forest floor by bird species and vegetation type, Oregon Coast Range, 1999.

		Number of Observations by Bird Species			
Foraging Height Class	**Plant Species**	**Swainson's Thrush (n=8)**	**MacGillivray's Warbler (n=5)**	**Orange-Crowned Warbler (n=16)**	**Wilson's Warbler (n=61)**
3-10 m	Pacific Yew	1	0	0	0
	Douglas-Fir	1	1	7	15
	Grand Fir	0	0	0	3
	Conifer Total (%)	**2 (50)**	**1 (50)**	**7**	**18 (45)**
	Prunus Sp.	0	1	0	1
	Cascara			1	0
	Pacific Dogwood	0	0	1	3
	Vine Maple	0	0	1	1
	Bigleaf Maple	2	0	3	13
	Red Alder (*Alnus rubra*)	0	0	0	3
	Oregon White Oak (*Quercus garryanna*)	0	0	0	1
	Hardwood Total (%)	**2 (50)**	**1 (50)**	**6**	**22 (55)**
3-10 m Height Class Total		**4**	**2**	**13**	**40**
>10 m	Pacific Yew	0	0	0	0
	Douglas-Fir	4	2	3	14
	Grand Fir	0	0	0	0
	Conifer Total (%)	**4 (100)**	**2 (67)**	**3**	**14 (67)**
	Prunus Sp.	0	0	0	0
	Cascara			0	0
	Pacific Dogwood	0	0	0	0
	Vine Maple	0	0	0	0
	Bigleaf Maple	0	1	0	3
	Red Alder	0	0	0	4
	Oregon White Oak	0	0	0	0
	Hardwood Total (%)	**0 (0)**	**1 (33)**	**0**	**7 (33)**
>10 m Height Class Total		**4**	**3**	**3**	**21**

MacGillivray's warbler

MacGillivray's warblers used 13 plant species as foraging substrates, and concentrated activities within 3 m of the forest floor (92% of the observations); 70% of foraging observations were $\leq$1 m (Table 3.1). Five plant species composed approximately 80% of the foraging substrates within 3 m of the ground (Douglas-fir, scotch broom (*Cystisus scoparius*), vine maple, California hazel, and bracken fern; Table 3.3). Of these species, only Douglas-fir was selected as a foraging substrate *and* averaged greater cover in stands occupied by MacGillivray's warbler compared to unoccupied stands (Table 3.4). Vine maple and Scotch broom also were selected for foraging, but I did not detect a difference in cover of these species between occupied and unoccupied stands. Bracken fern was used less than expected based on availability (Table 3.3), although occupied stands averaged 9% more cover of bracken than unoccupied stands (Table 3.4). Stands occupied by MacGillivray's warbler averaged 25% greater cover of all deciduous shrubs combined than unoccupied stands (Table 3.5). Although approximately 20% of foraging observations of MacGillivray's warblers were on understory conifers, I did not detect a difference in cover of all conifer species combined between occupied and unoccupied stands (Table 3.5).

Orange-crowned warbler

Orange-crowned warblers foraged throughout all layers of forest vegetation, with the majority (83%) of observations occurring 0.3 – 10 m above ground (Table 3.1). Above 3 m, Douglas-fir and deciduous species, primarily bigleaf maple, were used in equal proportions as foraging substrates (Table 3.2). Twelve plant species were used as foraging substrates within 3 m of the forest floor. Approximately 70% of observations at heights $\leq$3 m occurred on three plant species (Douglas-fir, bigleaf maple, and California hazel). Of these species, Douglas-fir and bigleaf maple were preferentially selected for foraging, along with honeysuckle (*Lonicera hipidula*), Pacific dogwood (*Cornus nuttallii*), cascara (*Rhamnus purshiana*), and bitter cherry (*Prunus emarginata*; Table 3.3). Cover of Douglas-fir and bigleaf maple was greater in stands occupied by orange-crowned warblers than in unoccupied stands (Table 3.4). Although California hazel had the highest frequency of foraging observations of any plant species for orange-crowned warblers, it had a negative preference index, indicating that use for foraging was less than expected based on availability. However, average cover of hazel was more than three times greater in occupied than unoccupied stands (Table 3.4). Cover of all deciduous species combined did not differ between occupied and unoccupied stands, but herbaceous cover was approximately 5% greater in occupied stands (Table 3.5). Stands occupied by orange-crowned warblers had less cover of evergreen shrubs than unoccupied stands.

Table 3.3. Number of foraging observations (with percent of total in parentheses) on understory substrates (≤3 m in height), and selection index based on deviation from expected Manly's Alpha for three warbler species, Oregon Coast Range, 2000. Positive selection indices indicate that a substrate was used for foraging more than expected based on availability (bold type), negative indices indicate use was less than expected based on availability, and 0 indicates use was in proportion to availability. A selection index was not calculated for plant species that were not used for foraging and averaged <1% cover ("nc").

	Wilson's Warbler		**MacGillivray's Warbler**		**Orange-crowned Warbler**	
Plant Species	**# Obs. (%)**	**Sel. Index**	**# Obs. (%)**	**Sel. Index**	**# Obs. (%)**	**Sel. Index**
Conifers						
Douglas-fir	11 (6.0)	**0.22**	9 (15.0)	**0.21**	5 (13.5)	**0.04**
Grand fir	4 (2.2)	**0.15**	2 (3.3)	**0.47**	0 (0.0)	-0.05
Pacific yew	3 (1.6)	**0.21**	0 (0.0)	nc	0 (0.0)	nc
West. Hemlock (*Tsuga heterophylla*)	0 (0.0)	-0.05	1 (1.7)	-0.06	0 (0.0)	-0.05
Deciduous						
Bigleaf maple	18 (9.8)	**0.03**	2 (3.3)	**0.02**	5 (13.5)	**0.03**
Bitter cherry	3 (1.6)	**0.12**	1 (1.7)	-0.04	1 (2.7)	**0.07**
Cascara	1 (0.6)	**0.09**	0 (0.0)	-0.05	2 (5.4)	**0.11**
Or. White oak	1 (0.5)	-0.03	0 (0.0)	-0.05	0 (0.0)	-0.05
Pacific dogwood	2 (1.1)	0	0 (0.0)	-0.06	3 (8.1)	**0.17**
Red alder	0 (0.0)	nc	0 (0.0)	-0.05	0 (0.0)	-0.05
California hazel	27 (14.7)	-0.04	9 (15.0)	-0.02	13 (35.1)	-0.02

Table 3.3, Cont'd.

	Wilson's Warbler		**MacGillivray's Warbler**		**Orange-crowned Warbler**	
Plant Species	**# Obs. (%)**	**Sel. Index**	**# Obs. (%)**	**Sel. Index**	**# Obs. (%)**	**Sel. Index**
Oceanspray	11 (6.0)	**0.12**	1 (1.7)	**0.03**	1 (2.7)	-0.04
Vine maple	74 (40.4)	-0.02	16 (26.7)	**0.01**	0 (0.0)	-0.05
Thimbleberry (*Rubus parviflorus*)	4 (2.2)	-0.03	2 (3.3)	-0.03	0 (0.0)	-0.05
Red huckleberry (*Vaccinium parvifolium*)	4 (2.2)	-0.07	0 (0.0)	nc	0 (0.0)	nc
Snowberry (*Symphoricarpos* spp.)	0 (0.0)	-0.06	1 (1.7)	-0.06	0 (0.0)	-0.05
Honeysuckle	0 (0.0)	nc	0 (0.0)	nc	2 (5.4)	**0.49**
Bracken fern	13 (7.1)	-0.06	11 (18.3)	-0.06	2 (5.4)	-0.03
Baldhip rose (*Rosa gymnocarpa*)	0 (0.0)	-0.07	0 (0.0)	-0.09	0 (0.0)	-0.05
Poison oak (*Rhus diversiloba*)	0 (0.0)	-0.05	0 (0.0)	-0.05	0 (0.0)	-0.05
Evergreen						
Chinquapin (*Chrysolepsis chrysophylla*)	3 (1.6)	**0.05**	0 (0.0)	nc	0 (0.0)	nc
Scotch broom	0 (0.0)	nc	4 (6.7)	**0.17**	0 (0.0)	nc
Blackberries (*Rubus* spp.)	2 (1.1)	-0.05	0 (0.0)	-0.06	1 (2.7)	-0.05
Oregon-grape (*Berberis nervosa*)	0 (0.0)	-0.07	1 (1.7)	-0.03	0 (0.0)	-0.05
Salal (*Gaultheria shallon*)	1 (0.5)	-0.1	0 (0.0)	-0.11	0 (0.0)	-0.05
Sword fern (*Polystichum munitum*)	1 (0.6)	-0.06	0 (0.0)	-0.06	0 (0.0)	-0.05
Grass	0 (0.0)	-0.06	0 (0.0)	-0.06	1 (2.7)	-0.04
Herb	0 (0.0)	-0.06	0 (0.0)	-0.06	1 (2.7)	-0.02
Bare ground	0 (0.0)	-0.07	0 (0.0)	-0.08	0 (0.0)	-0.05
Total # Observations	183		60		37	

Table 3.4. Comparison of mean (90% CI) understory cover (≤3 m in height) between stands occupied and not occupied by each of three warbler species for plant species on which foraging was observed more than three times, Oregon Coast Range, 2000. A "+" in the % cover columns indicates that plant species was present, but averaged less than 1% cover in the vegetation layer ≤3 m above the ground.

	% Cover (90% CI)	
	Occupied	**Not Occupied**
a. Wilson's Warbler	**(n=5)**	**(n=5)**
Vine maple	6 (1.6, 22.1)	7 (2.0, 26.9)
California hazel	7 (2.6, 18.9)	3 (1.2, 8.5)
Bigleaf maple	2 (0.9, 3.5)	3 (1.3, 5.1)
Bracken fern	7 (3.1, 15.6)	2 (0.9, 4.6)
Douglas-fir	1.7 (1.1, 2.6)	1.2 (0.8, 1.9)
Oceanspray	3 (1.5, 6.1)	2 (1.1, 4.6)
Red huckleberry	1.7 (1.0, 2.8)	1.3 (0.8, 2.1)
Thimbleberry	+	+
Grand fir	+	+
b. MacGillivray's Warbler	**(n=3)**	**(n=7)**
Vine maple	5 (0.9, 24.7)	8 (2.6, 22.8)
Douglas-fir	2 (1.4, 3.6)	1 (0.9, 1.6)
Bracken fern	11 (4.2, 28.8)	2 (1.3, 4.5)
California hazel	6 (1.6, 24.4)	4 (1.7, 9.9)
Scotch broom	+	0
c. Orange-crowned Warbler	**(n=3)**	**(n=7)**
California hazel	11 (3.4, 36.3)	3 (1.5, 7.1)
Bigleaf maple	4 (2.1, 8.9)	2 (1.0, 2.5)
Douglas-fir	3 (1.9, 3.7)	1 (0.9, 1.4)
Bracken fern	4 (1.0, 13.2)	4 (1.6, 8.8)

Table 3.5. Number of foraging observations expressed as total and percent, and comparison of mean (with 90% confidence interval) understory cover ($\leq$3 m in height) between stands occupied and not occupied by each of three warbler species for plant categories on which foraging was observed, Oregon Coast Range, 2000.

a. Wilson's Warbler			% Cover (90% CI)	
Plant Category[1]	# Foraging Observations	% Foraging Observations	Occupied (n=5)	Not Occupied (n=5)
Deciduous	159	85	54 (40.7, 68.1)	24 (10.2, 37.5)
Conifer	18	10	3 (1.6, 6.5)	2.5 (1.2, 5.2)
Evergreen	7	4	61 (42.8, 79.0)	43 (24.5, 60.7)
Unidentified	5	1	---	---
TOTAL	189	100		

b. MacGillivray's Warbler			% Cover	
Plant Category[1]	# Foraging Observations	% Foraging Observations	Occupied (n=3)	Not Occupied (n=7)
Deciduous	43	64	57 (35.1, 78.0)	32 (17.6, 45.7)
Conifer	15	22	3 (1.2, 7.6)	3 (1.5, 5.1)
Evergreen	6	09	47 (21.6, 72.7)	54 (37.0, 70.4)
Unidentified	3	4	---	---
TOTAL	67	100		

c. Orange-crowned Warbler			% Cover	
Plant Category[1]	# Foraging Observations	% Foraging Observations	Occupied (n=3)	Not Occupied (n=7)
Deciduous	32	82	40 (23.1, 56.4)	38 (12.3, 63.2)
Conifer	5	13	4 (1.4, 9.0)	3 (1.4, 4.7)
Evergreen	1	3	36 (13.4, 58.7)	58 (43.6, 73.3)
Herb	1	3	7.5 (2.8, 19.9)	2.4 (1.3, 4.6)
TOTAL	39	100		

[1] See Table 3.3 for species included in each plant category

DISCUSSION

Shrub species selected as foraging substrates by warblers in the understory of Douglas-fir forests were not necessarily the same as those that distinguished habitat occupancy at a larger spatial scale. This observation is consistent with the model of hierarchical habitat selection described by Johnson (1980) in which selection of habitat by animals at a given spatial scale is conditional upon selection made at a higher order, although the criteria may vary between scales. Because foraging sites are not the only basis for habitat selection, birds choose territories that ideally meet all requirements for survival and breeding, including nest sites, resting cover, singing perches, etc. (Hilden 1965). Within these territories, various species of vegetation offer different foraging opportunities as a function of prey abundance and vegetation architecture, and will be exploited according to morphological and behavioral abilities of bird species (Holmes and Schultz 1988). For Wilson's and MacGillivray's warblers in my study area, a significant component of deciduous vegetation in the understory seemed to be an important factor in stand-level selection of habitat. In contrast, at a smaller spatial scale, conifers such as Douglas-fir, grand fir (*Abies grandis*) and Pacific yew (*Taxus brevifolia*) had some of the highest selection indices of any understory species for Wilson's and MacGillivray's warblers (Table 3.3). However, the majority (>66%) of foraging observations of these species were on deciduous vegetation, and correspondingly, cover of all deciduous species combined was greater in stands occupied by these two species than in unoccupied stands. Similarly, although California hazel was not selected as a foraging substrate by orange-crowned warblers, more foraging events were observed on California hazel than on any other species of vegetation and hazel cover was greater in occupied than unoccupied stands.

Two conclusions may be drawn from these results. First, an apparent lack of selection of some species of tall, deciduous as foraging sites may have been a result of a higher order selection for stands with high percent cover of these types of species. If stands were selected by Wilson's and MacGillivray's warblers for high deciduous shrub cover and by orange-crowned warblers for high cover of hazel, foraging on these shrub species would occur approximately in proportion to their availability (Johnson 1980). This conclusion is supported by Morrison (1981), who also described extensive use of deciduous vegetation by foraging Wilson's, MacGillivray's, and orange-crowned warblers in the Oregon Coast Range. Furthermore, Morrison (1981) found that density of Wilson's warblers was related to the presence of deciduous trees. The association I found between orange-crowned warblers and California hazel cover has not been previously reported, although breeding habitat has been characterized as including deciduous growth (Dillingham 2003).

A second conclusion may be that, except for oceanspray, species of tall, deciduous shrubs offered similar foraging opportunities, and thus were used interchangeably by Wilson's and MacGillivray's warblers. A generally high relative abundance of arthropod prey on vine maple, hazel, and oceanspray (see Chapter 4) may explain the concentrated foraging activities of Wilson's and MacGillivray's warblers on these species. Oceanspray, which was selected by both Wilson's and MacGillivray's warblers as a foraging substrate, is notable for its high diversity and abundance of lepidopteran larvae (Hammond and Miller 1998, Muir et al. 2002), a favored food of many insectivorous birds (Graber and Graber 1983, Holmes 1990).

Bird use of foraging substrates is affected by foliage structure as well as prey density (Holmes and Robinson 1981) because morphology and foraging strategy impose limits on the substrates that can be optimally exploited (Eckhardt 1979). Low foraging efficiency on bracken fern may explain why Wilson's and MacGillivray's warblers did not select it. These warblers forage actively by gleaning arthropods from foliage while perched or on the wing, in short hover-gleaning maneuvers (Stewart et al.1977, Eckhardt 1979, Hutto 1981a). The structure of bracken fern may be somewhat incompatible with this foraging strategy because it does not offer suitable perch sites, and lack of open space around fronds due to proximity to the ground and dense growth habit likely limits the use of hover-gleaning. Birds will switch foraging substrate preferences if prey biomass is sufficiently high (Whelan 1989). Thus, in spite of low foraging efficiency, warblers probably used bracken fern because of its exceptionally high arthropod biomass (see Chapter 4). It also is possible that for Wilson's and MacGillivray's warblers, bracken fern did not appear to be selected as a foraging substrate at the scale of foraging patches because these warblers selected stands with relatively high cover of bracken fern at the landscape scale (Table 3.4) and foraged on it in proportion to availability (Johnson 1980). Alternatively, the high bracken fern cover in stands occupied by Wilson's and MacGillivray's warblers may have been correlated with other favorable habitat attributes. Bracken fern indicates a light-rich environment (Emmingham 1972) that may promote development of other understory shrubs (Tappeiner and Zasada 1993, O'Dea et al. 1995, Klinka et al. 1996).

Deciduous vegetation was an important variable influencing habitat selection on at least one spatial scale for Wilson's, MacGillivray's, and orange-crowned warblers. These results have implications for the management of biodiversity and ecosystem function. In order to maintain populations of these warblers, managers will need to maintain cover of deciduous shrubs in the forest understory. Both Wilson's warblers and MacGillivray's warblers were rare in stands that averaged <35% cover of deciduous shrubs within 3 m of the forest floor, so I recommend that stands managed for these species maintain at least this level of cover. Managers concerned with protecting forest resources (i.e., timber) from insect damage may be motivated to provide habitat for these insectivores, because they forage selectively on conifers in the appropriate habitat. Arthropods consumed by Wilson's and MacGillivray's warblers include the two most important defoliators of conifers in the Pacific Northwest, western spruce budworm (*Choristoneura occidentalis*) and Douglas-fir tussock moth (*Orgyia pseudotsugata*; Langelier and Garton 1986, Torgersen et al. 1990). Bird predation can significantly depress the abundance of arthropod prey, most effectively at endemic levels of prey populations (Holmes et al. 1979, Holmes 1990, Torgersen et al. 1990). Although birds cannot respond sufficiently to depress defoliator populations once they are in an irruption stage, avian predation may be important in maintaining pest populations at endemic levels (Holmes 1990). Furthermore, bird predation on arthropods can have indirect effects on plant growth and productivity. In the absence of avian predation, an increase in damage to foliage by leaf-chewing insects (Murakami and Nakano 2000) can significantly reduce plant growth (Marquis and Whelan 1994). In conclusion, the maintenance of deciduous shrubs in managed forests is necessary to provide habitat for species of insectivorous birds that contribute to biodiversity and play important roles in forest food webs.

Chapter 4

THE EFFECTS OF UNDERSTORY VEGETATION AND FOREST MANAGEMENT ON FOOD RESOURCES FOR SONGBIRDS IN WESTERN OREGON

INTRODUCTION

The correlations of songbird abundance and diversity with structural or compositional attributes of habitats has been studied by avian ecologists for decades (MacArthur and Mac Arthur 1961, Karr and Roth 1971, Willson 1974, Wiens and Rotenberry 1981, Verner et al., 1986 Block and Brennan 1993), although mechanisms underlying such relationships are seldom studied and not well understood. Such correlational relationships have guided methods of habitat assessment and management (e.g., USF&W Habitat Evaluation Procedures), which tend to rely mainly on quantification of vegetation characteristics thought to be related to species' life requisites, rather than on measurements of the ultimate resources provided by the vegetation (i.e., food and cover). However, few empirical data are available to validate assumptions regarding the basis for relationships between vegetation and resource requirements of birds. This lack of information represents an obstacle for managers concerned with providing quality habitat for songbirds.

One factor that is likely to drive habitat relationships for any wildlife species is food. Food availability is a basic, critical habitat component that often limits the reproductive success and survival of breeding birds (Martin 1987). Distribution and abundance of food has been correlated with population size of birds and is a major factor in habitat selection (Wiens 1989, Gill 1994: 512 – 516). Food resources for forest birds may be directly or indirectly associated with vegetation. Seeds, fruits, and flowers provide a direct source of food for many bird species, while arthropod prey that live on plants indirectly link avian insectivores to vegetation. Although food availability is typically difficult to measure, an understanding of the trophic pathways from vegetation to songbirds would provide an empirical foundation for the management of vegetation to achieve objectives aimed at providing habitat for birds.

The first step in understanding trophic links between birds and vegetation is to determine the composition of birds' diets. Once the composition of the diet is known for a bird species, it should be possible to identify the plant species and or habitat conditions that are important in supporting those food resources. Because each bird species has a unique diet, food availability must be measured separately for each species (Holmes and Schultz 1988). Unfortunately, even basic information on the composition of diets is lacking for most avian species. Some authors have sidestepped this lack of information by assuming that abundance of actual prey is correlated with estimates of overall arthropod abundance (Hutto 1980, Hutto 1981b, Blake and Hoppes 1986). This method has been used successfully to predict bird density at the community level (Brush and Stiles 1986), but because many species are at least somewhat selective, this approach may not accurately represent food availability for individual species.

Although there is little detailed knowledge of bird diets (especially for birds that breed in Pacific Northwest forests), we know, in general, that arthropods that dwell on vegetation constitute an important portion of the diet of many forest bird species (Erlich et al. 1988, Marcot and Vander Heyden 2001). Because most forest insects use specific host plant species (Edwards and Wratten 1980), each plant species supports a characteristic assemblage of herbivorous insects. Both diversity and abundance of herbivores vary among plant species (Schowalter 2000). Herbivorous insects in turn can have associated arthropod predators and parasites, which also may be prey for birds. Therefore, although most bird species may not be directly associated with particular plant species, they may be linked to certain plant taxa through their insect prey (Holmes and Robinson 1981). Furthermore, some plant species provide direct food resources for birds in the form of seeds and fruits.

Understory plant species contribute a major proportion of the floristic diversity in Pacific Northwest conifer forests (Halpern and Spies 1995) and may therefore be presumed to be important in supporting faunistic diversity. However, little is known about arthropod assemblages on understory plants, particularly which plant species may be most important in supporting the arthropods that are prey for birds. In this chapter, I present basic information on dietary composition and distribution of food resources for several species of songbirds that commonly breed in forests of the Pacific Northwest. I chose to focus this investigation on birds associated with understory vegetation because of the important contribution to diversity made by the understory, and its accessibility for sampling birds and arthropods. Ultimately, I wanted to know how structure, composition, and management of understory vegetation influence food availability for songbirds that primarily forage in the forest understory.

METHODS

Study Sites

All study sites were located in the Western Hemlock Vegetation (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988) of the Oregon Coast Range. Mild, wet winters and dry summers characterize regional climate. Sites comprised lands managed by three public agencies (Bureau of Land Management, U.S. Forest Service, Oregon State University).

In order to link my results to a larger ecological framework, and build upon existing data, I sampled songbird diets and arthropod populations in a subset of study sites used in an integrated study that assessed differences in the diversity of various organisms among young unthinned, young thinned, and old-growth Douglas-fir stands in western Oregon (Muir et al. 2002). I used three triads of stands in the Oregon Coast Range, each consisting of a geographically grouped set of one young unthinned, one young thinned, and one unmanaged, mature stand (Sand Creek, Mary's Peak, and D-line Road (Fig. 2.1); Muir et al. 2002). The young stands (thinned and unthinned) regenerated naturally following clear-cut harvesting and were 55 – 75 years old. One age cohort dominated the overstory, with very few large trees and well decayed snags (<1/ ha) persisting from previous stands. Unthinned stands were in stem-exclusion stage of forest development (Oliver and Larson 1990), and were characterized by a dense, uniform overstory of Douglas-fir, and a sparse understory. Thinned stands had been thinned to uniform spacing 19 – 28 years prior to this study. Mature stands of the triads had vegetation and structure typical of old-growth, as described by Spies and Franklin (1991). The stands I sampled were chosen to represent a range of variability in understory structure and to maximize captures of birds associated with forest understory. I added two pairs of stands not used in the study described by Muir et al. (2002) to increase the number of fecal samples collected from focal bird species. These sites were located in McDonald-Dunn State Forest, and consisted of two unmanaged, mature (120 years old) stands, each paired with a stand of the same age that had been partially harvested with a group selection method. A study by Chambers (1996) indicated a high abundance of shrub-associated bird species in these stands. Characteristics of overstory tree density and understory vegetation cover for the McDonald-Dunn State Forest sites are described in Chapter 2. All stands were located in the Western Hemlock (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988) between 200 and 500 m elevation.

Field and Lab Methods

Mist-nets were used to capture birds for the purpose of collecting fecal samples. Eight to 10 nets were operated on two to three dates in each stand between mid-May and mid-July 1996, 1997, 1999 and 2000. Nets were 12 m in length, and were set to intercept birds moving between 0.3 to 2.5 m above ground. Within the boundaries of each stand, nets were placed opportunistically where vegetation provided sufficient screening to camouflage the mesh, and where bird activity was believed to be high. Nets were opened within ½ hour of sunrise, and remained in operation for ≥4 hours, or until rain or wind forced closing. Birds were held in a cloth bag for up to 45 minutes or until they defecated. Fecal samples were collected in glass vials and stored in 70% ethanol pending identification of contents.

I examined 87 fecal samples collected from Wilson's warblers in 1996 and 1997 and 96 samples from Swainson's thrushes in 1996, 1997, 1999, and 2000 under a binocular dissecting microscope. I identified fragments to the lowest taxonomic level possible, using well-illustrated entomology texts and guides (Borror and White 1970, Shattuck 1985, Moldenke et al. 1987, Borror et al. 1989) and expert opinion (Andrew Moldenke, Oregon State University; Greg Brenner, Pacific Analytics Inc., Albany, OR). Recognizable pieces from each sample were mounted on glass slides. I estimated the number of individuals within each taxon in a fecal sample by summing head capsules, pairs of mandibles, or sets of legs that were similar in size and color. Mandibles could usually be identified as originating from either the right or left side of a head capsule, so two mandibles from the same side could be inferred as representing two individuals. I measured length of whole femurs, tibias, mandibles, and head capsules using an ocular micrometer fitted on the microscope.

To estimate the length of arthropod prey from fragments, I developed regression equations quantifying relationship of whole body length to leg fragments for 11 taxonomic groups of adult arthropods and to mandible length for larvae (Table 4.1). I measured femur, tibia, and whole body lengths of adult arthropods (n=175), and mandible and body lengths of larvae (n=21) collected from understory vegetation (see below). I estimated original sizes of items eaten by birds by applying regressions to whole tibias, femurs, and mandibles in fecal samples. For spiders, I averaged predicted body lengths derived from femora and tibiae because I was unable to distinguish femurs from tibias in fecal samples.

I examined 139 fecal samples collected from Swainson's thrushes, and 27 samples collected from seven additional species in 1997, 1999, and 2000 for presence of seeds. Seeds from each sample were counted and identified. Reference seeds were collected from fruits simultaneously with collection of fecal samples in order to aid in identification of the plant of origin to genus or species. The proportion of fecal samples containing seeds was calculated for each plant species. I calculated the proportion of Swainson's thrush fecal samples with seeds for six 10-day periods between 21 May and 22 July.

Table 4.1. Regression equations used to reconstruct original sizes of prey items from fragments in fecal samples of songbirds, Oregon Coast Range.

Arthropod	N	Length Range[1] (mm)	Regression Equations	R^2
Insects[2]	175	1.2 – 12.5	ln(body) = 1.412 + 0.841* ln(femur length) ln(body) = 1.379 + 0.738* ln(tibia length)	0.58 0.48
Coleoptera	79	2.1 – 12.5	ln(body) = 1.612 + 0.808* ln(femur length) ln(body) = 1.645 + 0.794* ln(tibia length)	0.65 0.74
Cantharidae	20	2.5 – 9.3	ln(body) = 1.721 + 1.039* ln(femur length) ln(body) = 1.701 + 1.033* ln(tibia length)	0.81 0.78
Curculionidae	10	3.1 – 9.6	ln(body) = 1.315 + 0.929* ln(femur length) ln(body) = 1.437 + 0.853* ln(tibia length)	0.92 0.91
Mordellidae	10	2.7 – 4.6	ln(body) = 1.657 + 1.166* ln(femur length) ln(body) = 1.660 + 0.776* ln(tibia length)	0.91 0.91
Diptera	57	1.2 – 12.0	ln(body) = 1.134 + 0.843* ln(femur length) ln(body) = 1.114 + 0.886* ln(tibia length)	0.75 0.77
Hymenoptera (winged adults)	12	1.2 – 11.0	ln(body) = 1.428 + 0.936*ln(femur length) ln(body) = 1.467 + 1.007*ln(tibia length)	0.79 0.81
Formicidae	6	2.8 – 9.0	ln(body) = 1.387 + 0.773*ln(femur length) ln(body) = 1.486 + 0.786*ln(tibia length) ln(body) = 0.894 + 0.780*ln(leg length)	0.99 0.98 0.99
Homoptera / Hemiptera[3]	10	1.8 – 11.2	ln(body) = 1.609 + 1.193* ln(femur length) ln(body) = 1.444 + 0.864* ln(tibia length)	0.48 0.25
Aphididae	6	2.2 – 3.1	ln(body) = 0.932 + 0.372* ln(femur length)	0.35
Larvae[4]	21	6.5 – 26.0	ln(body) = 3.633 + 0.890* ln(mandible length)	0.64
Spiders	19	0.8 – 6.0	ln(body) = 0.956 + 0.078* ln(femur length) ln(body) = 1.125 + 0.590* ln(tibia length)	0.63 0.65

[1] Minimum and maximum body lengths (frons to tip of abdomen) of specimens measured for regression equations.

[2] Adults of all orders except spiders. Equation used for unidentified prey items.

[3] Excluding aphids.

[4] Includes Lepidoptera and Hymenoptera (sawfly) larvae

Collection of Arthropod Samples

Arthropods were collected from understory vegetation in the same stands where fecal samples were collected and within 10 days of each mist-netting session in each stand in order to coincide spatially and temporally with collection of fecal samples from birds. A shrub-beating method (Borror et al. 1989, Cooper and Whitmore 1990) was used to sample sedentary arthropods that are potential prey for foliage-gleaning songbirds on vegetation <2 m above forest floor. In 1996 and 1997, arthropods (and fecal samples) were collected from most sites during two periods each year: first between 26 May and 26 June, and again between 30 June and 30 July. In 1999 sampling took place during one period in each stand, between 27 May and 17 June.

Woody shrubs and/or ferns at 50- to 75-m intervals along randomly established transects in each stand were selected for sampling. Species of vegetation sampled varied within and between stands because the two most dominant (by cover) woody shrub and/or fern species at each sampling point were selected for beating. In each sampling period, 8 – 31 beating samples from each stand were collected. A different transect was established in each stand for each sample period within a year. One sample of a shrub was approximately equal to 100 leaves (vine maple, ocean spray, and salmonberry), 50 leaves (salal and hazel), 5 fronds of bracken fern and 8 of sword fern, or 1-m^2 branch (western hemlock). Arthropods were dislodged from branches and foliage onto a 1-m^2 canvas sheet and aspirated into vials. The foliage sampled was collected, dried, and weighed, and the arthropod specimens were preserved in 70% ethanol. Some shrub samples spoiled prior to weighing, resulting in missing data. Weights of unspoiled samples of the same species were averaged to derive an estimate of weights for missing measurements.

Data Analysis

I calculated the frequency of occurrence of arthropod groups in the diets of Hammond’s and Pacific-slope flycatchers, Swainson's thrushes, Wilson's warblers and MacGillivray's warblers. Frequency of occurrence in the diet was calculated as the number of fecal samples containing a given arthropod group divided by the total number of fecal samples. The lowest taxonomic levels that could be identified from fragments in fecal samples defined arthropod groups used for analyses. To derive a measure of prey available for Wilson's warblers, I calculated frequency of occurrence of arthropod groups from all beating samples (all shrub species pooled) collected in 1996 and 1997, the same years for which I had Wilson's warbler diet data. I compared the frequency of occurrence of arthropod groups in the diet of Wilson's warblers with frequency of occurrence on shrubs, and ranked groups by the ratio of frequency of occurrence in diet to that on shrubs. I used this forage ratio (Krebs 1989) as an index of prey selection by Wilson's warblers, with ratios >1 indicating greater than expected use based on availability *in the understory* (see Discussion for explanation of limitations of this approach). I focused analyses of prey sizes and comparisons of prey availability among plant species and shrub conditions on arthropod groups that occurred in >60% of Wilson's warbler diets and had forage ratios >1. I did not compare frequency of occurrence of arthropod groups in diets and on shrubs for other bird species because I did not believe beating samples adequately represented potential food for Swainson's thrushes (they frequently foraged on the ground; see Chapter 3), and because sample sizes were too small for the other three species.

I used the Kolmogorov-Smirnov statistic to test whether the distribution of arthropod sizes was the same for arthropods consumed by Wilson's warblers as for arthropods collected from vegetation (Steel and Torrie 1980). I used this method to compare size distributions for arthropod groups: larvae (including Lepidoptera and Symphyta (sawflies)), Diptera, Coleoptera, and Homoptera, and all adult arthropods pooled. I used an alpha level of 0.05 to determine a significant difference.

I calculated two indices of arthropod intensity: abundance and biomass. Intensity is a measure of the arthropod load per unit of plant material. Arthropod weights were calculated from regression models (Appendix A). To calculate average abundance and biomass intensity for each stand condition, I summed the total number of individuals and the total weight of all individuals in each category over all plant samples within a stand in each sample period in each year and divided by the corresponding total dry weight of plant material. These indices were averaged across stands within each condition, period, and year to derive stand condition means and 90% confidence limits. To calculate average abundance and biomass intensity on each plant species, I summed the total number of individual arthropods and the total weight of all individuals in each category over all samples of each plant species within a stand in each sample period in each year and divided by the corresponding total dry weight of plant material. These indices were averaged across all stands within each period and year in which each plant species was sampled.

I compared the intensity of four arthropod categories (adult Coleptera and Diptera >3 mm, larval Lepidoptera >6 mm in length, and all arthropod prey combined) among plant species and stand conditions using analysis of variance (ANOVA). I included sawfly larvae with the Lepidoptera larvae group because they are similar in form and also had a forage ratio >1. The combined category of arthropod prey included Coleptera and Diptera >3 mm, Lepidoptera and Symphyta larvae >6 mm, and all other arthropods >2 mm in length (except Diplopods), based on taxa and sizes of prey consumed by Wilson's warblers and other bird species.

I tested for the effects of plant species and stand condition separately because not all plant species occurred in all stand conditions. For all responses, except Lepidoptera intensity, I used ANOVA to test the null hypothesis of no difference in arthropod intensity among seven plant species that were sampled in ≥ 3 stands in ≥ 2 years. All data met assumptions of normal distribution and constant variance for ANOVA after log-transformations. I used the non-parametric Kruskal-Wallis test for comparing intensity of Lepidoptera larvae among plant species and stand conditions because the distribution of response values that resulted from a high proportion of samples with no larvae could not be corrected with a transformation. Because this was an exploratory analysis and I did not want to overlook possible biologically significant relationships, I used alpha = 0.10 to evaluate significance of effects. For tests of plant species effects with $P < 0.10$, I evaluated overlap of 90% confidence intervals to compare responses between each pair of plant species (Steidl et al. 1997). I tested for an overall effect of stand condition on the response variables with all plant species pooled within each stand condition. I also tested for an effect of stand condition separately for plant species that were sampled ≥ 3 times in ≥ 2 conditions (vine maple, salal, oceanspray, and sword fern). Group selection stands were not included because the sample size was too small (N=2). For tests of stand condition effects with $P < 0.10$, I evaluated overlap of 90% confidence intervals to compare responses between each pair of plant species.

The abundance and biomass intensity indices described above estimated arthropod prey loads per unit of plant material. Because prey load varied with plant species, and cover of each plant species varied among stands, I also calculated cover-weighted indices that would reflect abundance and biomass of arthropod prey at the stand level. To derive these indices, I summed abundance and biomass of all arthropods >2 mm in length, except taxa that were never found in bird diets, for each plant species sampled in each stand in each year and divided by the total dry weight of each plant species. I multiplied these indices by a standardized estimate of cover for each plant species sampled to derive the final cover-weighted indices for each stand. I used shrub cover data from line transect estimates (see Chapter 2) and unpublished data for the Sand Creek sites (not sampled in 1999 and therefore not included in Chapter 2). I averaged cover-weighted abundance and biomass indices over years, log-transformed both indices to meet model assumptions, and compared among thinned, unthinned, and mature stand conditions using ANOVA and 90% confidence intervals. I did not include the GS stands and their paired mature stands in this comparison because those data were limited to one year.

RESULTS

Arthropod Prey of Wilson's warblers

More than 10 orders of arthropods were found in 87 Wilson's warbler fecal samples from 1996 and 1997 (Table 4.2). I was able to identify few arthropod fragments from fecal samples to below the taxonomic level of order. Families identified were Homoptera: Achilidae, Aphididae and Cercopidae; Neuroptera: Chrysopidae; Coleoptera: Cantharidae and Mordellidae; Diptera: Empididae, Mycetophillidae and Sciaridae.

Lepidoptera larvae, Homoptera, Diptera, and Coleoptera had high frequencies of occurrence in fecal samples (>60%), and had forage ratios >1 (Table 4.2). Adult Lepidoptera and arthropod eggs had the highest forage ratios, but occurred relatively infrequently in the diet and were extremely rare on shrubs. In contrast, spiders occurred frequently in the diet, but were very common on vegetation.

Table 4.2. Percent occurrence of arthropods in diets of Wilson's warblers (n=87) and on shrubs (n=681 samples from beating), 1996-1997, Oregon Coast Range. The ratio of the frequency of occurrence in diet to that on shrubs (forage ratio) is interpreted as an index of prey selection, with ratios >1 indicating greater than expected use based on availability.

Arthropod Taxa	% Occurrence in Diet	% Occurrence on Shrubs	Forage Ratio
Lepidoptera, adults	0.18	<0.01	45.98
Unknown arthropod eggs	0.14	0.01	11.49
Lepidoptera, larvae *	0.63	0.12	5.06
Homoptera (all taxa) *	0.86	0.51	1.69
Diptera *	0.99	0.59	1.67
Hymenoptera, wasps	0.46	0.28	1.67
Hymenoptera, Symphyta larvae	0.20	0.12	1.64
Coleoptera (all taxa) *	0.84	0.58	1.45
Homoptera, Cercopidae	0.23	0.16	1.44
Araneida (all spiders)	0.85	0.90	0.94
Neuroptera	0.05	0.07	0.67
Acari (mites)	0.02	0.20	0.11
Collembola	0.05	0.56	0.08
Psocoptera	0.02	0.31	0.07
Hemiptera	0.01	0.19	0.06

* Groups selected for comparison of abundance and biomass intensity among shrub species and stand conditions

Sizes of adult arthropods consumed by Wilson's warblers averaged approximately 4 mm (Table 4.3), and ranged from 2 to 10 mm (Fig. 4.1A). The size distribution of adult arthropods consumed was significantly different than the distribution for available adult arthropods (Kolmogorov-Smirnov two-sample test, $P < 0.0001$), indicating that Wilson's warblers consumed prey that were larger than the most abundant items available. This pattern was consistently significant across the most frequently consumed arthropod groups (Fig. 4.1A - E). However, I did not find evidence of the largest size classes (>12 mm) of adult arthropods, including flies, beetles, and spiders, in the diet.

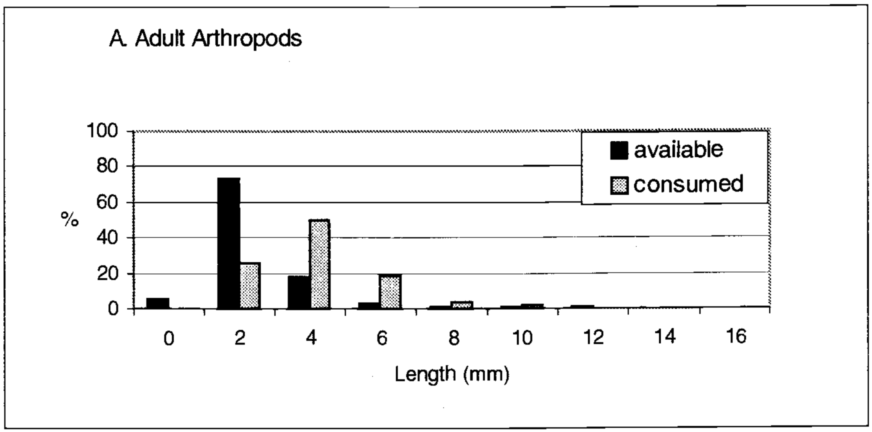
Larvae, primarily sawflies (Hymenoptera: Symphyta) and Lepidoptera, were the largest prey items consumed by Wilson's warblers. Larvae ranged from approximately 6 – 26 mm in length. As with adult arthropods, the size distribution of larvae consumed was significantly different than that of available larvae (Fig. 4.1E) because warblers were eating mostly the larger (>6 mm) larvae that occurred less frequently than those in the smaller size classes.

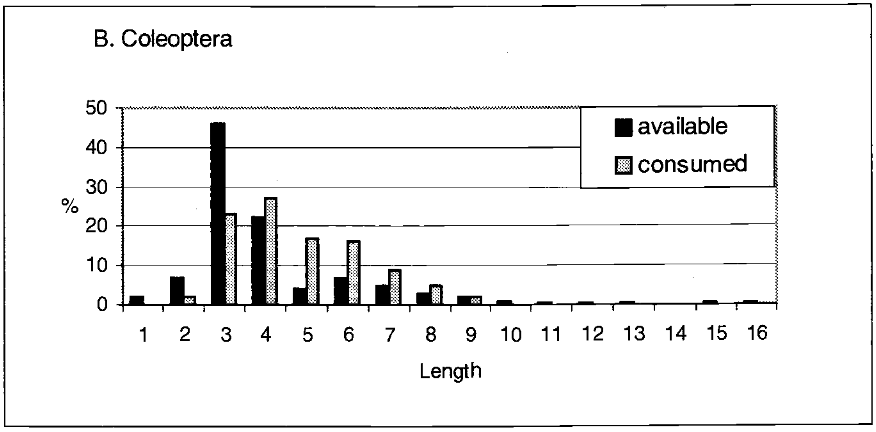
Table 4.3. Average lengths (mm), with confidence intervals, and ranges of arthropods in Wilson's warbler diet (1996, 1997) estimated from regressions of arthropod body length on leg length or mandible width. Confidence intervals not calculated for taxa with <10 size estimates.

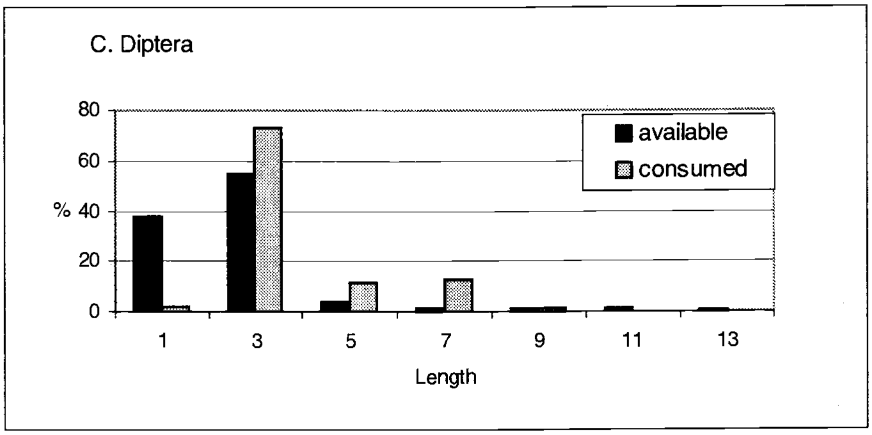
Arthropod Taxa	N[1]	Mean	95% CI	Range
Adult Arthropods	559	4.1	3.92, 4.18	0.9 – 9.8
Coleoptera	134	4.7	4.44, 4.98	2.2 – 9.1
Cantharidae	4	5.0	---	3.2 – 6.5
Mordellidae	3	3.7	---	3.0 – 5.0
Diptera	230	3.6	3.46, 3.85	1.4 – 9.8
Hymenoptera (adults)	53	4.2	3.81, 4.62	2.2 – 8.9
Homoptera (incl. Aphids)	33	5.7	5.06, 6.39	1.2 – 9.5
Aphids	9	4.3	3.73, 4.91	3.3 – 5.5
Larvae				
Lepidoptera	77	13.7	12.73, 14.62	5.9 – 25.8
Sawfly	19	14.9	12.97, 16.88	9.9 – 25.0
Collembola	5	1.5	---	0.9 – 1.8
Spiders	73	3.4	3.34, 3.52	2.6 – 4.5
Unknown Egg	7	0.6	---	0.6

[1] Number of individual arthropods in fecal samples from both years combined used to estimate size of items in diet.

Figure 4.1. Distribution among size classes of A) adult arthropods, B) Coleoptera, C) Diptera, D) sawfly and lepidoptera larvae, and E) Homoptera available as prey and those consumed by Wilson's warblers in the Oregon Coast Range, 1996 and 1997.







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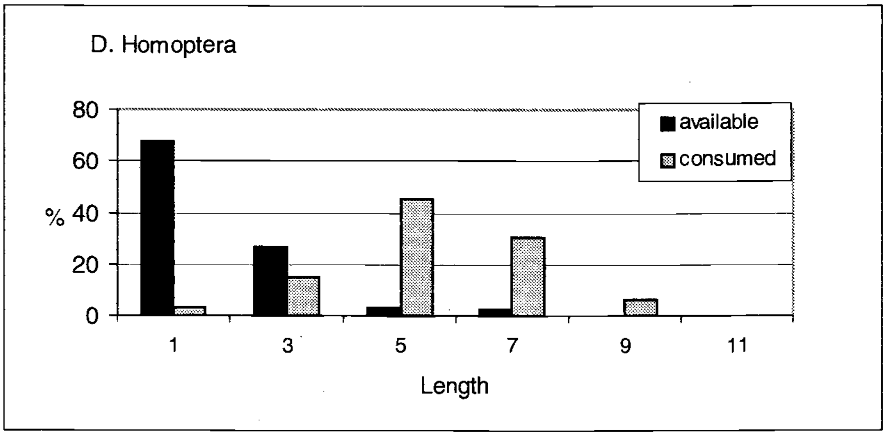
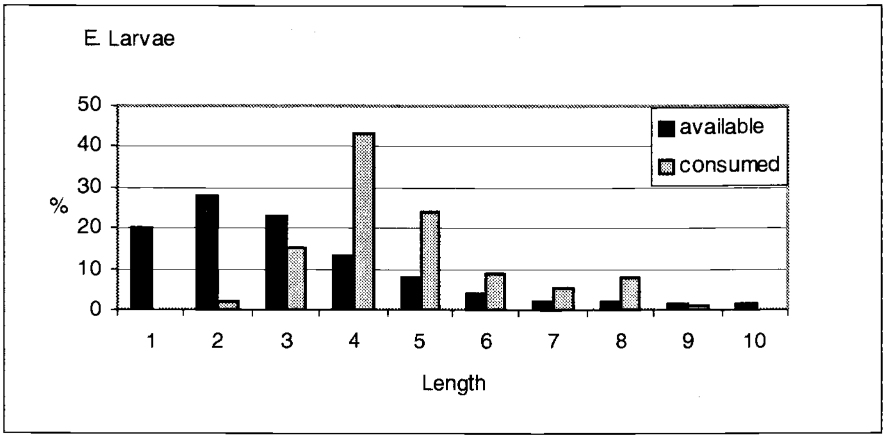




Arthropod Prey of Swainson's Thrushes

Twelve orders of arthropods were identified from fragments in 96 fecal samples collected from Swainson's thrushes during four years (1996, 1997, 1999, 2000; Table 4.4). Beetles and ants were the predominant prey items, occurring in >70% of the fecal samples. Of the 12 families of beetles identified from fragments, weevils (Curculionidae) occurred the most frequently. Swainson's thrushes also frequently consumed spiders and flies (each found in approximately 50% of fecal samples).

Sizes of arthropod prey consumed by Swainson's thrushes ranged from 1 – 30 mm, with an overall average of 6.95 mm (Fig. 4.2). Ninety-three percent of the prey items were ≥3 mm in length. The largest taxa consumed were Hymenoptera (sawfly) and Lepidoptera larvae (Table 4.4).

Table 4.4. Percent frequency of occurrence (proportion of total number of samples) and sizes of arthropod prey in 96 Swainson's thrush fecal samples from four years. Orders include all families identified; families identified in ≥3 samples also are listed independently.

		Prey Size (mm)			
Arthropod Taxon	**% Frequency**	**Average (SE)**	**Min**	**Max**	**N[1]**
Coleoptera[2]	91	7.92 (0.22)	2.06	16.72	146
Curculionidae	26	7.16 (0.49)	4.56	11.31	15
Scolytidae	3	-	-	-	-
Hymenoptera[3]	77	5.75 (0.26)	2.68	24.90	131
Formicidae	75	5.43 (0.19)	2.68	12.00	124
Tenthredinidae (larvae)	11	19.92 (2.52)	16.73	24.90	3
Arachnida	54	3.64 (0.25)	2.60	4.55	8
Diptera	51	5.53(0.57)	1.88	22.00	36
Tipulidae	6	5.32 (----)	-	-	1
Lepidoptera (larvae)[4]	43	18.01 (1.28)	11.01	29.28	21
Homoptera	9	6.16 (0.95)	4.51	7.81	3
Cercopidae	4	6.16	-	-	1
Neuroptera	3	-	-	-	-
Collembola (Entomobryidae)	2	2.16 (0.53)	1.63	2.69	2
Hemiptera (Miridae)	2	-	-	-	-
Microcoryphia (Machilidae)	2	-	-	-	-
Orthoptera	2	6.37	-	-	1
Apterygota	1	-	-	-	-

[1] N is the number of fragments in fecal samples used to estimate prey size (length of body from frons to the posterior tip of the abdomen).

[2] Includes Buprestidae, Cantharidae, Carabidae, Cincindelidae, Coccinellidae, Curculionidae, Elateridae, Mordellidae, Scarabidae, Scolytidae, Staphylinidae, Tenebrionidae.

[3] Includes Formicidae, Ichneumonidae, Tenthredididae

[4] Includes Gelechiidae, Pryalidae

Arthropod Prey of Other Species

Eight families within seven orders of arthropods were identified in five fecal samples from MacGillivray's warblers (Table 4.5). Average size of adult arthropods consumed by MacGillivray's warbler was 4.04 mm; average size of larvae consumed was 20.09 mm.

Three families were identified out of six orders of arthropods in four fecal samples from Pacific-slope flycatchers. I was able to estimate size only for beetles consumed by this species (Table 4.6). From the three fecal samples analyzed for Hammond's flycatchers, six orders and one family of arthropods were identified (Table 4.6).

Figure 4.2. Distribution of sizes of A) all arthropod prey and B) beetles consumed by Swainson's thrushes, Oregon Coast Range, 1996, 1997, 1999, 2000.

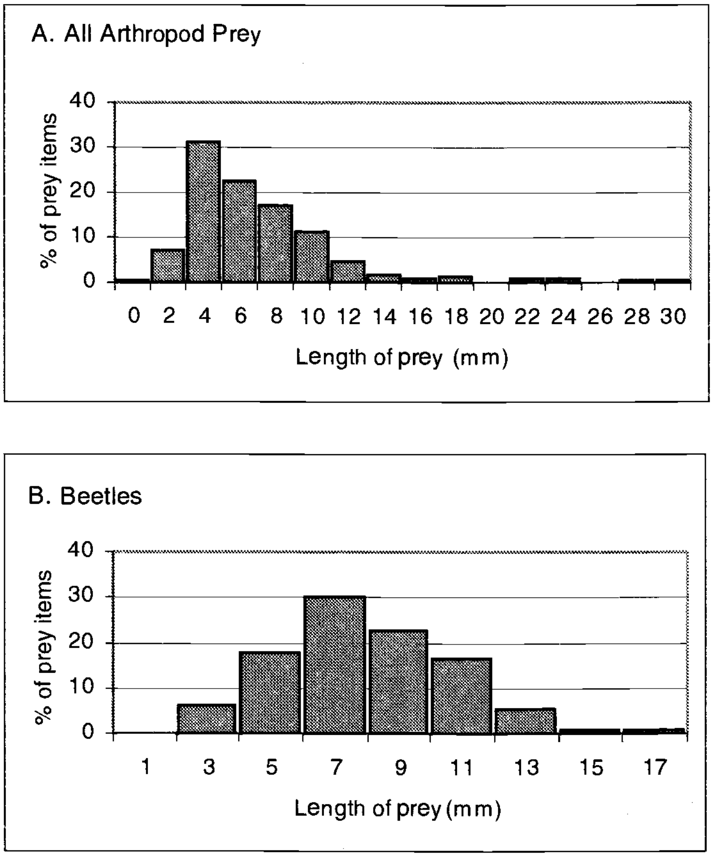


Figure 4.3. Percent of Swainson's thrush fecal samples with seeds from fruiting shrubs by 10-day period, Oregon Coast Range. Combined data from 1997, 1999, 2000 (n = 139 samples).

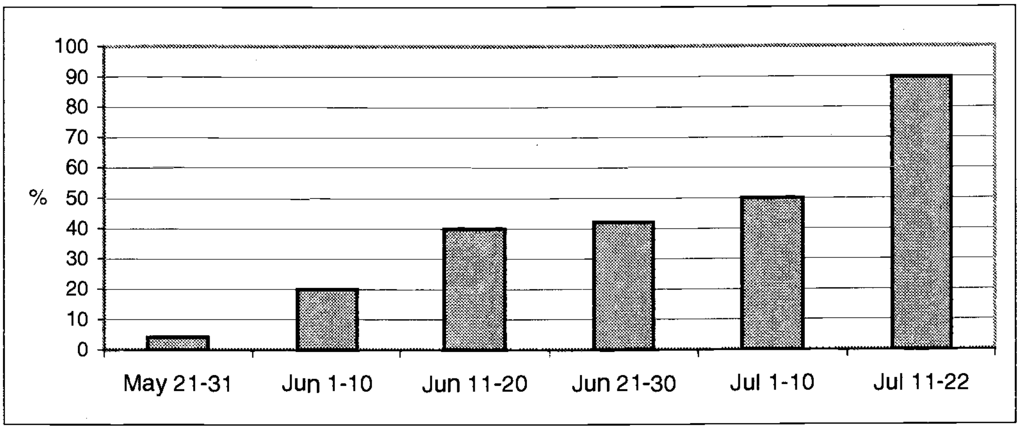


Table 4.5. Frequency of occurrence (number of fecal samples) and sizes (mm) of arthropod prey identified in MacGillivray's warbler fecal samples (n=5), Oregon Coast Range, 1999.

Order	Frequency for Order[1]	Family	Frequency for Family[1]	Size Mean (Range)	N^2
Araneida	5	Linyphiidae	1	.	0
		Unknown spider	5	2.7 (2.6 - 2.8)	2
Coleoptera	5	Coccinellidae	1	.	0
		Curculionidae	1	.	0
		Scarabiidae	1	.	0
		Unknown beetle	5	6.44 (4.3 - 7.9)	4
Diptera	4	Chironomidae	1	.	0
		Unknown fly	4	3.13 (2.4 - 5.1)	8
Hemiptera	2	Tingidae	1	.	0
		Unknown Hemiptera	1	.	0
Homoptera	2	Unknown Homoptera	2	3.94 (2.5 - 5.4)	2
Hymenoptera	4	Diapriidae	1	.	0
		Formicidae	1	.	0
		Symphyta larva	1	19.03	1
		Unknown wasp	2	.	0
Lepidoptera	4	Unknown caterpillar	4	20.31 (11.0 - 27.1)	5
Unknown	4	Unknown	4	5.47 (4.0 - 7.0)	2

[1] Number of fecal samples in which taxa occurred out of five total.

[2] Number of fragments used to calculate length of prey item with regressions of body length as predicted by femur, tibia, or mandible length. Only whole leg segments were used to estimate body length.

Table 4.6. Frequency of occurrence and sizes (mm) of arthropod prey identified in fecal samples of Pacific-slope flycatchers (n=4) and Hammond's flycatchers (n=3), Oregon Coast Range, 1996, 1997, 1999.

	Pacific-slope Flycatcher			**Hammond's Flycatcher**		
Order	**Freq.**[1]	**Size Mean (Range)**	**N**[2]	**Freq.**[1]	**Size Mean (Range)**	**N**[2]
Araneida	3	.	0	1	.	0
Coleoptera	4	.	0	2	.	0
Chrysomelid	1	.	0	0	.	0
Scolytid	1	7.13 (3.4 -10.5)	5	0	.	0
Unknown beetle	4	.		2	8.18 (7.1 - 9.2)	2
Diptera	2	.	0	1	6.73	1
Hemiptera	1	.	0	1	.	0
Homoptera	1	.	0	2	.	0
Cicadellid	1	.		0	.	0
Cercopid	0	.		2	.	0
Hymenoptera (wasp)	1	.	0	2	4.17	1
Lepidoptera	0	.		2	11.53 (8.9 - 14.1)	2
Unknown arthropod	1	.	0	1	.	0

[1] Number of fecal samples in which taxa occurred.

[2] Number of fragments used to calculate length of prey item based on regressions predicting relationship of body length to femur, tibia, or mandible length. Only whole leg segments were used to estimate body length.

Fruit in Bird Diets

Swainson's Thrushes

Forty-one percent of the 139 fecal samples from Swainson's thrushes contained seeds from fruits. Seeds from seven species of plants were identified in the diet. Red huckleberry (*Vaccinium parvifolium*) was the most frequently consumed species, occurring in 18% of all fecal samples. Salal (*Gaultheria shallon*) was the second most frequently consumed, occurring in 12% of the fecal samples. Seeds from elderberry (*Sambucus* spp.) were found in 10% of the fecal samples, and blackberry seeds, including those of Himalayan (*Rubus discolor*) and trailing blackberry (*R. ursinus*), occurred in 9% of samples. The proportion of fecal samples containing seeds from fruits increased throughout the season (Fig. 4.3). Blackberries were the only fruit represented in the Swainson's thrush diet throughout the entire sampling season, from 31 May to 22 July, although salal and red huckleberry were found in all but the first 10-day period.

Other Species

Fecal samples from seven species in addition to Swainson's thrushes were examined for seeds: chestnut-backed chickadee (N=1), wrentit (N=2), hermit thrush (N=1), varied thrush (N=1), spotted towhee (N=2), song sparrow (N=4) and dark-eyed junco (N=15). Salal and *vaccinium* seeds were found in a spotted towhee fecal sample. Salal berries also were consumed by the wrentit. *Vaccinium* seeds were found in the varied thrush sample. Only one of the dark-eyed junco samples contained seeds, which were most likely of herbaceous origin.

Arthropods on Understory Vegetation

Eighteen insect orders, nine non-insect arthropod taxa, and two mollusk taxa were identified from 28,448 individuals collected from 15 understory plant species from 1996 –1999 (Appendix B). The most abundant taxa overall were aphids, collembolans, and two families of web-spinning spiders (Linyphiidae and Theridiidae; Table 4.7). Overall, the dominant taxa by weight included Geometrid caterpillars, and Linyphiid and Araneid spiders. However, the dominant taxa based on biomass varied with stand condition (Table 4.8).

Plant Species Effects on Arthropods

Abundance intensity of all arthropod taxa pooled was ≥5 times higher on bracken fern than on the six other plant species sampled frequently enough to analyze (Fig. 4.4A). Biomass intensity of all arthropod taxa pooled also was high on bracken fern; only oceanspray supported a similar biomass (Fig. 4.4B). Western hemlock and vine maple supported the lowest arthropod prey intensity, in terms of both abundance and biomass.

Table 4.7. Average abundance intensity index (number of individuals/100 g dry plant material) with standard errors by stand age and condition for the three most abundant arthropod taxa sampled on 15 species of understory shrubs across eight sites in four years.

Abundance Rank	Overall	Mature	Group-Selection	Thinned	Unthinned
1	Homoptera: Aphididae 8.93 (2.01)	Collembola: Sminthuridae 7.61 (3.62)	Homoptera: Aphididae 46.76 (11.53)	Homoptera: Aphididae 14.33 (4.36)	Collembola: Entomobryidae 5.70 (0.87)
2	Collembola: Entomobryidae 4.88 (0.48)	Collembola: Isotomidae 5.30 (2.67)	Collembola: Isotomidae 16.30 (8.16)	Collembola: Entomobryidae 4.93 (0.65)	Araneida: Linyphiidae 4.65 (0.74)
3	Araneida: Linyphiidae 3.91 (0.35)	Araneida: Theridiidae 3.97 (0.80)	Araneida: Theridiidae 6.69 (4.07)	Psocoptera 4.00 (1.21)	Psocoptera 3.99 (1.33)

Table 4.8. Average biomass intensity index (mg arthropod / 100 g dry plant material) with standard errors by stand age and condition for the three most abundant arthropod taxa sampled on 15 species of understory shrubs across eight sites in four years.

Biomass Rank	Overall	Mature	Group-Selection	Thinned	Unthinned
1	Lepidoptera: Geometridae (larvae) 14.6 (3.35)	Lepidoptera: Geometridae 29.0 (13.26)	Homoptera: Aphididae 90.8 (52.80)	Homoptera: Aphididae 14.9 (4.17)	Araneida: Linyphiidae 16.1 (2.11)
2	Araneida: Linyphiidae 11.9 (1.07)	Spirobolida 20.3 (13.72)	Lepidoptera: Geometridae 64.7 (20.58)	Araneida: Theridiidae 12.2 (1.99)	Araneida: Araneidae 15.1 (2.25)
3	Araneida: Araneidae 10.9 (1.13)	Araneida: Araneidae 11.4 (2.21)	Raphidioptera: Raphidiidae 42.5 (18.44)	Homoptera: Cercopidae 11.6 (3.50)	Lepidoptera: Geometridae 11.9 (3.28)

Intensity of large Lepidoptera larvae (>6 mm) differed among plant species (abundance: $P = 0.01$, biomass: $P = 0.04$, Kruskal-Wallis test). Oceanspray and hazel had the highest mean scores for both intensity variables; the sum of scores for vine maple and western hemlock also were higher than expected under a null hypothesis of no difference among plant species (Table 4.9). The two fern species and salal scored lower than expected for both intensity variables, with sword fern scoring the lowest of all seven plant species.

Abundance intensity of Homoptera (>2 mm) was 17 times higher on bracken fern than on the shrub species with the next highest abundance, hazel (Fig. 4.5A). Biomass intensity of Homoptera was almost 10 times higher on bracken fern than on the shrub with the next highest biomass, salal (Fig. 4.5B).

Intensity of large Diptera (>3 mm) varied among plant species ($P \leq 0.01$, Kruskal-Wallis test). Bracken fern and oceanspray supported the greatest abundance and biomass intensity of large Diptera, whereas hemlock and hazel had the lowest scores (Table 4.10).

Abundance intensity of adult beetles (>3 mm) differed significantly among plant species ($P = 0.003$, Kruskal-Wallis test.) Oceanspray, vine maple, bracken fern, and sword fern all scored higher than expected under a null hypothesis of no difference among plant species, whereas hazel scored close to expected (Table 4.11). In contrast, hazel had the highest score for biomass intensity. Vine maple, oceanspray, bracken fern, and sword fern also scored higher than expected for biomass intensity of beetles. Salal and western hemlock scored lower than expected for both intensity variables of beetles.

Figure 4.4. A) Median abundance intensity index (number of individuals/ 100 g dry plant material) and B) biomass intensity index (mg / 100 g dry plant material) with 90% confidence limits of arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) for seven understory plant species in the Oregon Coast Range. Two plant species differ significantly in intensity if 90% confidence limits of one do not overlap the median of the other. Plant species and sample size are: ACCI = vine maple (51), COCO = California hazel (10), GASH= salal (49), HODI = oceanspray (11), POMU = sword fern (34), PTAQ = bracken fern (24), and TSHE = western hemlock (32).

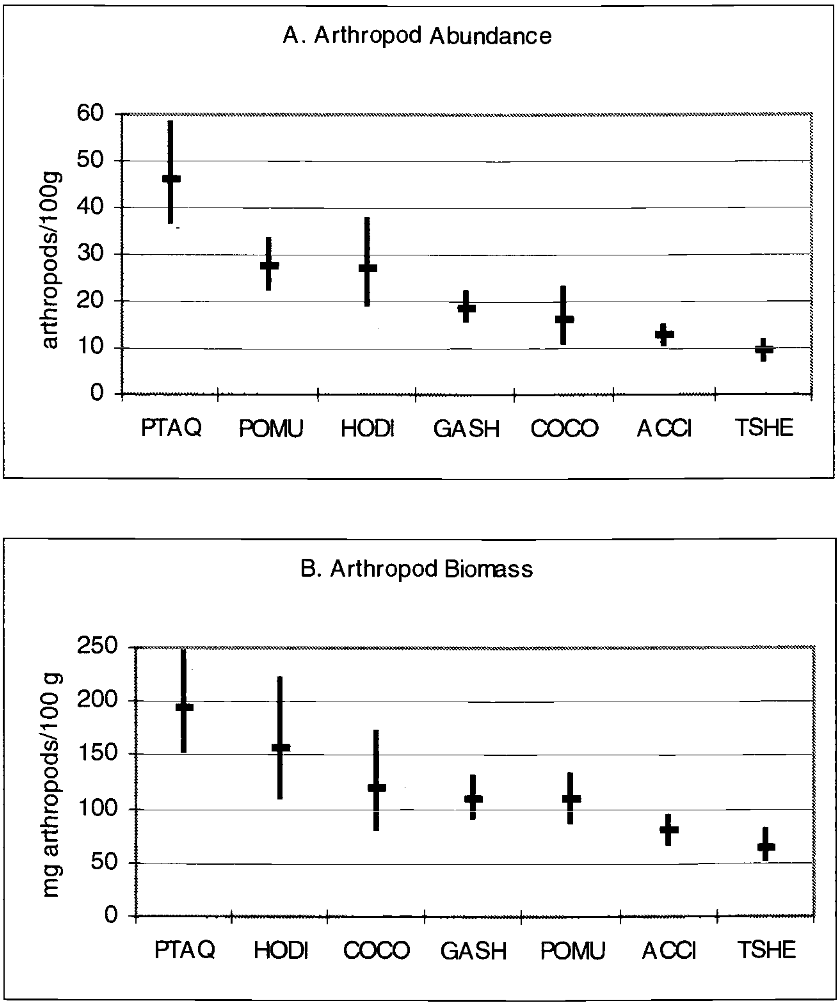
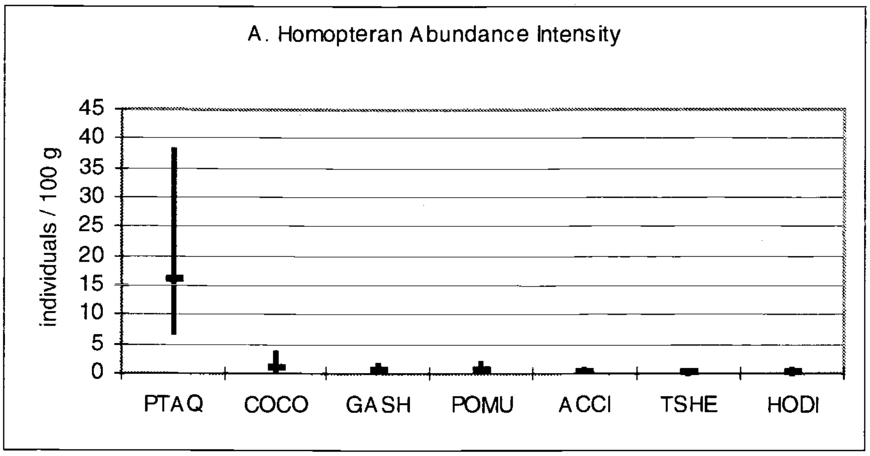


Figure 4.5. A) Median abundance intensity (number of individuals / 100g plant weight) and B) biomass intensity indices (mg arthropod/100 g plant weight) with 90% confidence limits for **Homoptera** on seven species of understory vegetation in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range. Plant species and sample size are: ACCI = vine maple (51), COCO = California hazel (10), GASH= salal (49), HODI = oceanspray (11), POMU = sword fern (34), PTAQ = bracken fern (24), and TSHE = western hemlock (32).



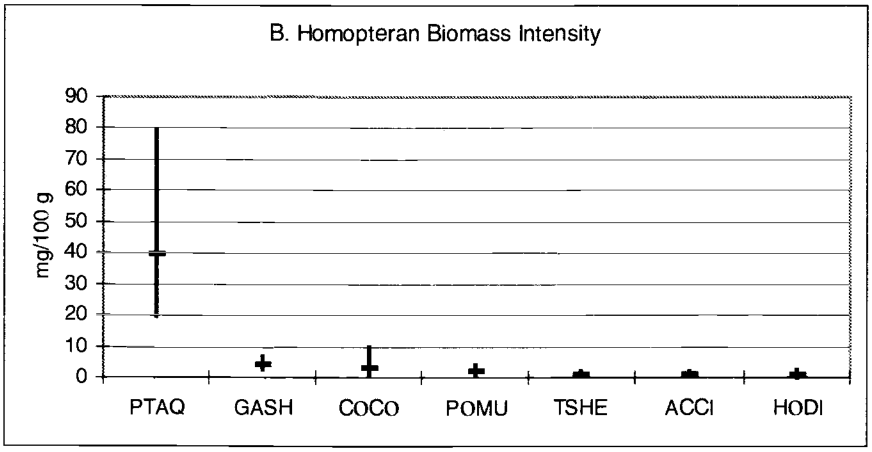


Table 4.9. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **lepidoptera larvae** >6 mm in length on seven understory plant species. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

		Abundance Index			Biomass Index		
Plant Species	N[1]	Sum of Scores	Expected Under H_0	Mean Score	Sum of Scores	Expected Under H_0	Mean Score
Oceanspray	11	1606	1160	**146**	1523	1160	**138**
California hazel	10	1330	1055	**133**	1309	1055	**131**
Vinemaple	50	5506	5275	**110**	5461	5275	**109**
Western hemlock	32	3475	3376	**109**	3541	3376	**111**
Bracken fern	24	2484	2532	103	2462	2532	103
Salal	49	4900	5169	100	4997	5169	102
Sword fern	34	2854	3587	84	2862	3587	84

[1] N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

Table 4.10. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **flies** >3 mm on seven understory plant species, in descending order of mean score. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

		Abundance Index			Biomass Index		
Plant Species	N[1]	Sum of Scores	Expected Under H_0	Mean Score	Sum of Scores	Expected Under H_0	Mean Score
Bracken fern	24	3202	2532	**133**	3171	2532	**132**
Oceanspray	11	1329	1160	**121**	1264	1160	**115**
Vinemaple	50	5503	5275	**110**	5579	5275	**112**
Salal	49	5386	5169	**110**	5207	5169	**106**
Sword fern	34	3513	3587	103	3645	3587	**107**
Western hemlock	32	2499	3376	78	2595	3376	81
California hazel	10	721	1055	72	692	1055	69

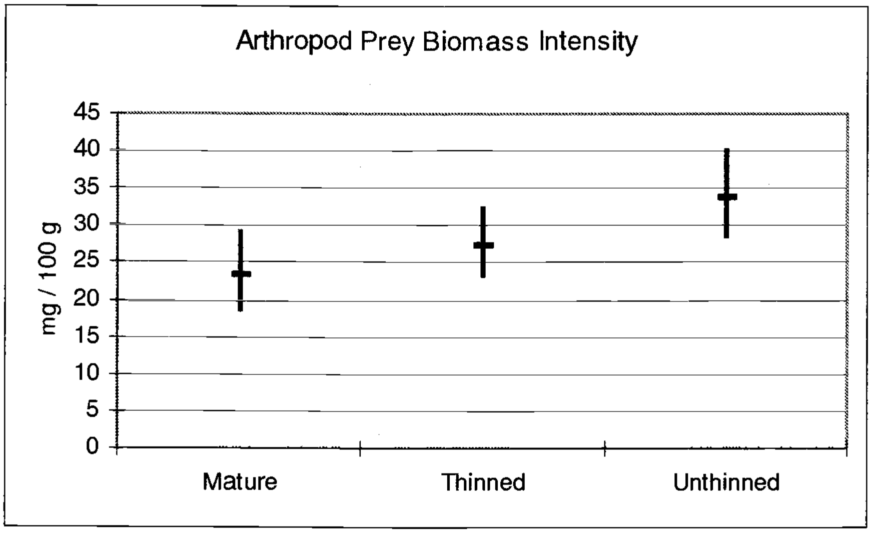
[1] N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

Table 4.11. Wilcoxon Scores (Rank Sums) for abundance and biomass intensity of **beetles** >3 mm on seven understory plant species, in descending order of mean score. Mean scores in bold were higher than expected under the null hypothesis of no difference in intensity among plant species (Kruskal-Wallis test).

		Abundance Index			Biomass Index		
Plant Species	N[1]	Sum of Scores	Expected Under H_0	Mean Score	Sum of Scores	Expected Under H_0	Mean Score
Oceanspray	11	1369	1160	**124**	1245	1160	**113**
Vinemaple	50	6031	5275	**121**	6195	5275	**124**
Bracken fern	24	2878	2532	**120**	2645	2532	**110**
Sword fern	34	4017	3587	**118**	3779	3587	**111**
California hazel	10	1054	1055	105	1319	1055	**132**
Salal	49	4587	5169	94	4435	5169	90
Western hemlock	32	2217	3376	69	2535	3376	79

[1] N is the number of samples for each plant species pooled across four years and eight sites (not all sites were sampled each year).

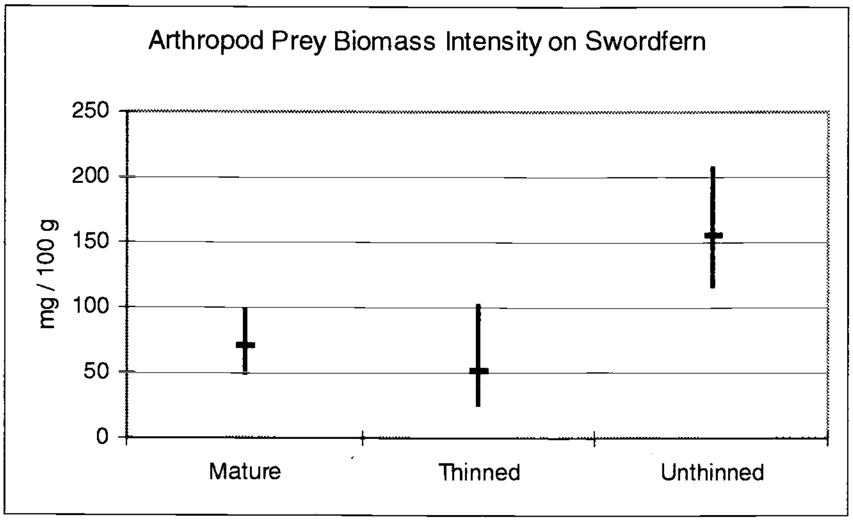
Figure 4.6. Median biomass intensity index with 90% confidence limits (mg arthropod /100g dry plant weight) for arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larvae >6 mm, and all other taxa >2 mm) on understory vegetation in three Douglas-fir stand types in the Oregon Coast Range.



Stand Condition Effects on Arthropods

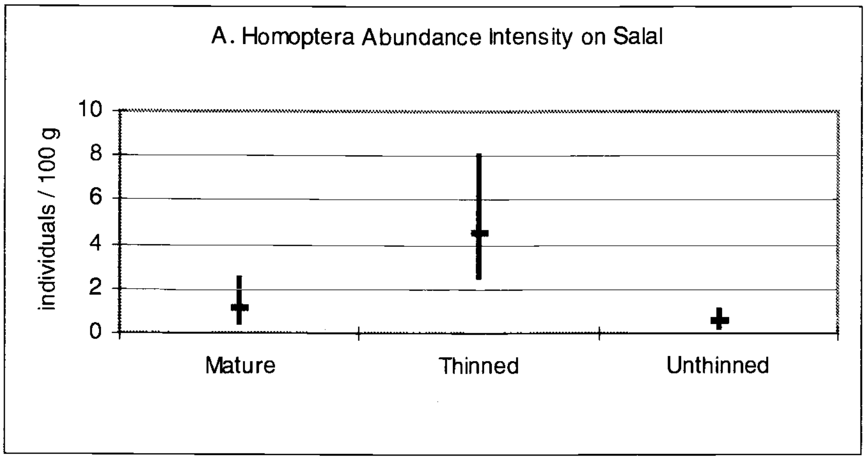
Abundance intensity of arthropods did not differ among mature, young thinned, and young unthinned stand conditions for all plant species pooled (P = 0.27, ANOVA), nor for any of the four plant species adequately sampled in each stand condition (vine maple, salal, oceanspray, sword fern; P > 0.10, ANOVA). Biomass intensity of all arthropod prey for Wilson's warblers pooled differed among stand conditions for all plant species pooled (P = 0.08, ANOVA; Fig. 4.6). Arthropod biomass intensity on sword fern was 2.2 times greater (P = 0.005, ANOVA) in unthinned than mature stands and 3 times higher in unthinned than in thinned (Fig. 4.7).

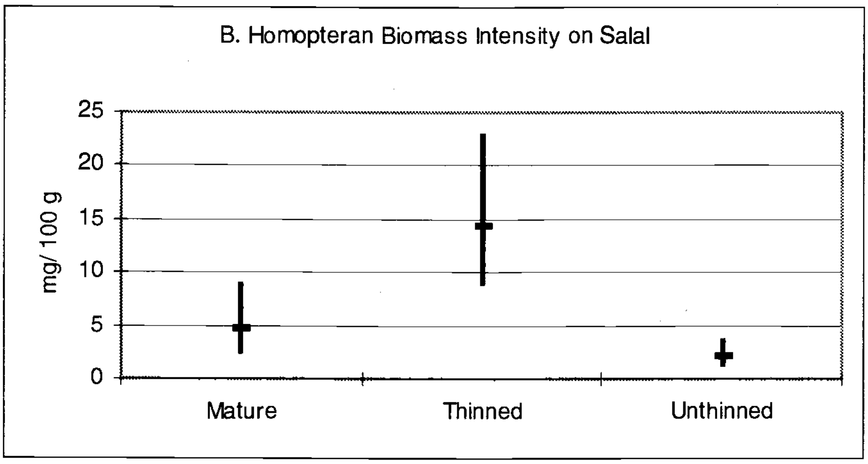
Figure 4.7. Arthropod biomass intensity index with 90% confidence limits (mg arthropod/100 g dry plant weight) for arthropod prey for Wilson's warblers (Coleoptera and Diptera >3 mm, larva >6 mm, and all other taxa >2 mm) on **sword fern** in three Douglas-fir stand types in the Oregon Coast Range.



Neither abundance nor biomass intensity of Lepidoptera larvae differed among stand conditions for all plant species pooled ($P > 0.28$, Kruskal-Wallis test), nor for vine maple, salal, oceanspray, or sword fern ($P \geq 0.65$, Kruskal-Wallis test). Homoptera intensity in terms of both abundance and biomass was greater on salal in thinned stands than on salal in mature or unthinned stands ($P < 0.04$, Kruskal-Wallis test; Fig. 4.8).

Figure 4.8. A) Median abundance intensity (number of individuals / 100g plant weight) and B) biomass intensity indices (mg arthropod/100 g plant weight) for **Homoptera** on salal in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range.





Ranked abundance intensity of large Diptera did not differ among mature, thinned, and unthinned stand conditions for all plant species pooled. Abundance intensity of Diptera was greater in unthinned than in thinned and mature stands for sword fern ($P = 0.02$, Kruskal-Wallis test) and salal ($P = 0.03$, Kruskal-Wallis test). Biomass intensity of Diptera did not differ among stand conditions ($P = 0.31$, Kruskal-Wallis test). Beetle abundance intensity was greatest in unthinned stands for all plant species pooled ($P = 0.08$, ANOVA; Fig. 4.9A). Abundance intensity of beetles on salal was 6.25 times higher in unthinned stands than in thinned. Similarly, median beetle abundance intensity on sword fern was more than 10 times greater in unthinned than in thinned and mature. Biomass intensity of beetles showed a similar pattern to abundance, and was greatest in unthinned stands (Fig. 4.9B). When tested separately by plant species, biomass intensity of beetles was 5.3 times greater on salal in unthinned than thinned stands. On sword fern, beetle biomass intensity was 24 times higher in unthinned than in thinned stands, and 8.7 times higher in unthinned than mature stands.

Although intensity of some arthropod prey groups was greatest on individual plants in unthinned stands, accounting for shrub cover at the stand level resulted in greater estimates of overall abundance in thinned than in unthinned and mature stands (Fig. 4.10A). Cover-weighted biomass also was greatest in thinned stands, although the slight overlap of the upper confidence interval for unthinned stands with the mean of that in thinned provided only weak evidence for a statistical difference (Fig. 4.10B). No consistent relationship between stand condition, shrub cover, and stand-level arthropod abundance or biomass was evident across individual study sites (Table 4.12).

Figure 4.9. A) Median abundance (number of individuals / 100g plant weight) and B) biomass indices (mg arthropod / 100 g plant weight) for Coleoptera on salal, swordfern, and across pooled plant species in thinned, unthinned, and mature Douglas-fir stands in the Oregon Coast Range.

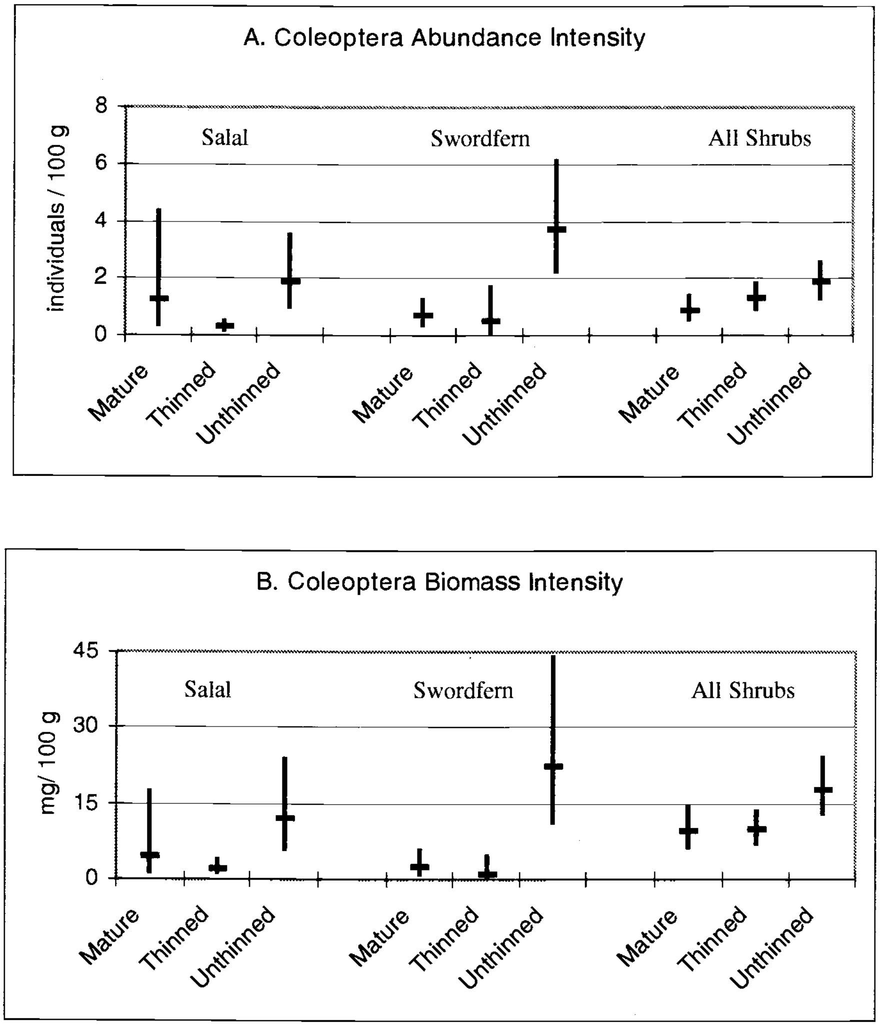


Figure 4.10. Median cover-weighted abundance (A) and biomass (B) indices with 90% confidence intervals for arthropod prey on understory shrubs in three stand conditions in the Oregon Coast Range.

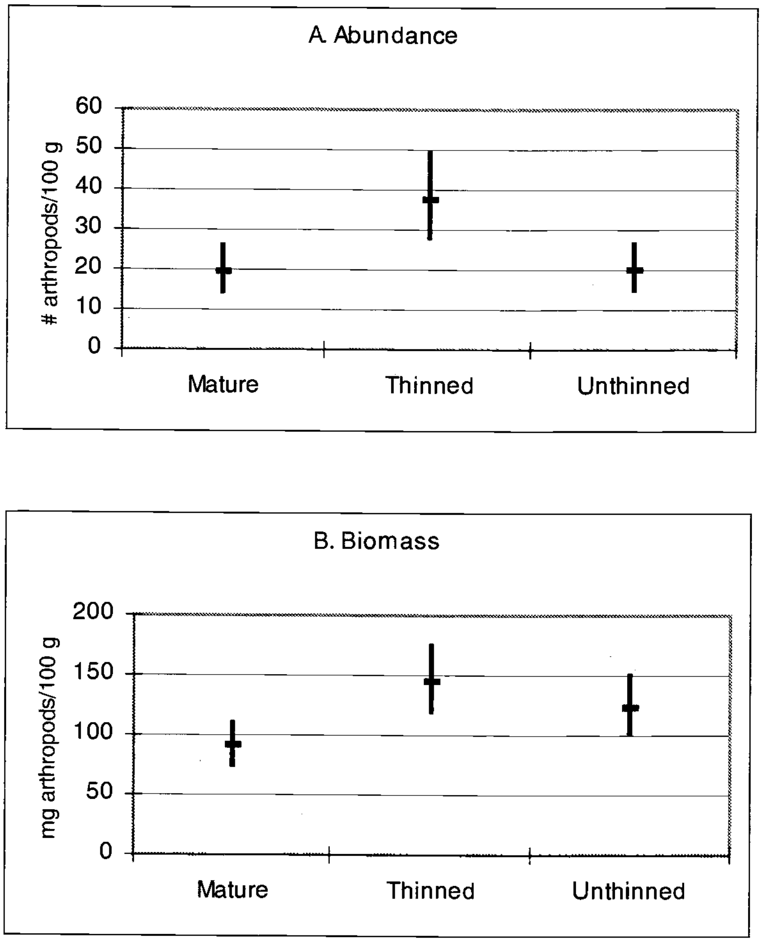


Table 4.12. Average abundance (number of individuals/ 100 g dry plant material) and biomass (mg arthropod/ 100 g dry plant material) indices weighted by shrub cover, and average cover of low shrubs and tall, deciduous shrubs in 13 Douglas-fir stands in the Oregon Coast Range.

Site	Condition	Abundance	Biomass	Low Shrub (%)	Tall Shrub (%)
D-Line	Mature	29.04	85.66	56	10
	Thinned	52.70	178.77	99	20
	Unthinned	21.40	113.52	57	8
Mary's Peak	Mature	69.11	329.86	45	13
	Thinned	69.62	218.38	41	16
	Unthinned	16.17	87.84	70	65
Sand Creek	Mature	25.98	113.91	98	40
	Thinned	18.40	138.60	18	28
	Unthinned	59.76	327.01	72	34
Lewisburg Saddle	Group Selection	59.67	377.48	57	40
	Mature	15.13	122.33	49	15
Peavy	Group Selection	68.52	180.81	52	6
	Mature	18.35	116.33	46	5

DISCUSSION

Bird Diets

Many insectivorous passerines prefer certain taxa, but will prey on a wide range of arthropod orders (Beaver and Baldwin 1975, Sample et al. 1993). This appeared to be true for Wilson's warblers, which are known to eat a relatively large variety of insect taxa (Beal 1907, Raley and Anderson 1990), but most frequently consumed caterpillars, homopterans, flies, and beetles. The number of arthropod orders (>6) found in relatively small samples for MacGillivray's warblers, Pacific-slope and Hammond's flycatchers is consistent with the literature indicating their lack of prey specificity (Beaver and Baldwin 1975, Pitocchelli 1995). Regardless of taxa, arthropods ≤2 mm in length were infrequently found in the diets of the birds I examined, even though this size class was very abundant on understory vegetation. Arthropods <2 mm in length are seldom taken even by winter wrens (Van Horne and Bader 1990), one of the smallest of the avian insectivores that feeds in the forest understory. Wilson's warblers select prey >3 mm (Raley and Anderson 1990). Arthropods >24 mm in length also occurred rarely in diets of the birds I studied. However, arthropods that exceeded the maximum lengths found in bird diets were rare on the vegetation I sampled.

Wilson's Warblers

The complexity of forest vegetation hampers the ability to accurately quantify food resources that are actually available to birds (Morrison et al. 1990). I attempted to minimize this problem by focusing on understory vegetation and the birds primarily associated with this vertical layer in forests. Wilson's warblers are known to forage to the maximum height of the available vegetation (Stewart et al. 1977), and 25% of the foraging activity I observed occurred above the layer of vegetation that I sampled for arthropods (Chapter 3). Thus, I did not measure all prey available to Wilson's warblers. High abundance in mid-story or canopy vegetation of any taxa that appeared to be used more than expected based on availability in the understory (forage ratio >1 in Table 4.2) would belie their selection as prey.

In addition, my sampling method may have underestimated some arthropod prey. Beating foliage to dislodge arthropods was an adequate method for sampling free-living, sedentary prey items available to birds, but organisms such as miners and borers would have been inadequately sampled because I did not visually inspect for organisms that may have been attached to vegetation. However, these organisms offer less food value to many species of insectivorous birds because of their relative inaccessibility (Holmes and Schultz 1988). Arthropod eggs also may not have been well sampled with the method of beating shrubs. However, the low frequency of occurrence of arthropod eggs in both diet ($\leq$15%) and shrub samples may indicate that Wilson's warblers foraged opportunistically on arthropod eggs when encountered, but did not necessarily select for them. I recommend a combination of shrub beating and aerial insect traps to sample food resources for Wilson's warblers and other species that use perch- and hover- gleaning foraging strategies.

In spite of these limitations, I believe that Wilson's warblers were selectively consuming Lepidoptera larvae, Diptera, and Coleoptera. Most species of Lepidoptera are generally uncommon in coniferous forests in the Pacific Northwest (Parsons et al. 1991), including the canopy of old-growth Douglas-fir (Voegtlin 1982, Schowalter and Ganio 1988), so it is unlikely that their abundance increased above the layer of vegetation I sampled. Furthermore, Lepidoptera larvae are known to be especially important prey for many neotropical migrant species that breed in temperate forests (Holmes et al. 1979, Graber and Graber 1983, Sample et al. 1993). Lepidopteran and sawfly larvae also were consumed by MacGillivray's warblers, Swainson's thrushes, and Hammond’s flycatchers. As the largest food items consumed by Wilson's warblers and other birds, and the dominant arthropod prey group by weight across all sites and stand conditions, Lepidoptera larvae probably represented a critical source of energy for birds on my study sites. In addition, caterpillars and sawfly larvae have high calcium concentrations relative to many other arthropod groups (Schowalter and Crossley 1983), providing insectivorous birds with an essential resource for egg-laying.

The importance of Diptera in the diet that I observed is supported by the foraging strategy of Wilson's warblers and by published accounts. A large proportion of flies in the diet reflects the hover-gleaning and aerial fly-catching foraging strategy frequently used by Wilson's warblers (Bent 1963, Stewart et al. 1977). Active, flying insects such as adult flies and wasps likely were under-sampled with the foliage beating method I used to estimate available arthropod prey. If flies were indeed under-sampled, in both understory and overstory vegetation, they may have been more available than estimated, and therefore may not have been selected as prey by Wilson's warblers. However, the selection of Diptera by Wilson's warblers that I observed is consistent with the findings of Raley and Anderson (1990) for Wilson's warblers foraging in montane willow habitats.

A high frequency of Coleoptera in the diet relative to that on shrubs is consistent with a preferential selection of Coleoptera as prey by Wilson's warblers reported by Raley and Anderson (1990). Raley and Anderson (1990) collected stomachs from birds and were able to identify Cantharidae as a large proportion of the Coleoptera eaten. Using fecal analysis, I was not often able to identify arthropods to the family level. Nonetheless, I also identified Cantharidae, as well as Mordellidae, in Wilson's warbler diets. Adult Cantharids are common on foliage, soft-bodied, and mostly 5 – 15 mm in length (Borror et al. 1989). These characteristics make them an optimal prey item for Wilson’s warblers. Mordellids also are common on foliage, but unlike Cantharids, they tend to move rapidly or take flight when alarmed (Borror and White 1970), possibly making them a less efficient prey item. I identified fragments of Mordellids in only 2 out of 96 Wilson's warbler fecal samples.

Although Homoptera occurred more frequently in Wilson's warbler diets than on understory shrubs, there is little evidence to support the selection of this insect group as prey. Homoptera are common to abundant throughout forest canopies (Parsons et al. 1991, Schowalter and Ganio 1998), and could have been consumed opportunistically as they were encountered. Raley and Anderson (1990) found that Homoptera ranked lowest in preference of all prey groups consumed by Wilson's warblers in a montane willow habitat. However, Homoptera and other arthropod groups that were not used disproportionately to their availability by Wilson's warblers in my study, such as spiders and adult hymenoptera, should not be considered unimportant as prey. These taxa occurred in ≥40% of the Wilson's warbler fecal samples I examined, and may function as staples in the diet. Furthermore, birds may rely more heavily on non-preferred prey items when preferred taxa are scarce (Sample et al. 1993).

Swainson's Thrushes

The generalized diet that I recorded for Swainson's thrushes, including fruit as well as many arthropod taxa, has been documented for this species from various parts of the breeding range (Mack and Yong 2000). The variety of arthropod taxa in the diet reflects the varied foraging strategies used by Swainson's thrushes. The inclusion in the diet of ground-dwelling taxa, such as carabid beetles, indicates the tendency of this species to spend a significant amount of foraging time on the ground. The methods I used to sample arthropod prey did not include ground-dwelling arthropods. However, some prey, such as Homopterans and sawfly larvae, were most likely gleaned from foliage while foraging throughout the vertical profile of the forest (Holmes and Robinson 1988).

Although I was unable to adequately sample prey availability for Swainson's thrushes, the importance of beetles and ants is evident from my observations and is supported by the findings of others (Mack and Yong 2000). Several beetle taxa that were preyed on by Swainson's thrushes, including Buprestidae and Elateridae, and some species of ants are associated with dead and dying wood (Borror et al. 1989). The presence of crane flies, another taxa often associated with decaying wood, in Swainson's thrush diets also was recorded by Beal (1915) from stomach samples. Woody debris may therefore be an important habitat element for Swainson's and other thrushes with similar foraging habits and diets (e.g., hermit and varied thrushes).

Fruit becomes an increasingly important food for Swainson's thrushes, as well as many other species of omnivorous passerines, late in the breeding season as birds prepare for migration from breeding to wintering grounds (Parrish 1997, Mack and Yong 2000). Increased availability (Fire Effects Information System [online], personal observation) and consumption (Fig. 4.3) of fruit was apparent by mid-July in my study area, with red huckleberry, salal, elderberry, and blackberry as the primary sources of mast for thrushes. An increase in fruit availability coincides with decreasing abundance of insects, so fruit may function as an alternative food resource to preferred insect prey. For some long-distance migrants however, fruit may actually be required in order to acquire sufficient energy reserves for successful migration (Martin 1985, Blake and Loiselle 1992). A dietary shift from primarily insects to fruit may confer an energetic advantage because frugivory facilitates energy storage in the form of fat reserves (Parrish 1997). The importance of fruit and fruit-bearing shrubs to the survival of Swainson's thrushes and other frugivorous migrants should therefore not be underestimated.

Distribution of Food Resources

Effect of Plant Species

Common understory plant species varied in abundance and biomass of arthropod prey for songbirds. Herbivorous insect species often are associated with a narrow range of plant taxa, thus defining characteristic assemblages of arthropods on each plant species (Schowalter 2000). Even though I was not able to identify most arthropods below the taxonomic level of family, I found differences among plants species even for the much coarser prey categories I analyzed. Many of the differences I found can be explained by a dichotomy between deciduous and evergreen plant species. In general, deciduous species supported a higher intensity of the arthropods that were important prey for birds than did evergreen species.

Tall deciduous shrubs were important sources of arthropod prey, particularly Lepidoptera larvae. While conifers may support high abundances of lepidopteran larvae, especially during outbreaks (Furniss and Carolin 1977) a large proportion of the lepidopteran diversity in western forests is associated with deciduous trees and shrubs (Hammond and Miller 1998). Because populations of forest insect species can fluctuate dramatically among generations, prey diversity provides a stable resource for generalist insectivores over time (Jackson 1979). I was unable to assess lepidopteran diversity on the plants I sampled, but I found that tall, deciduous shrubs such as oceanspray, California hazel, and vine maple supported the highest intensity of lepidopteran larvae of the understory plant species I sampled. Although western hemlock in the forest understory also was a potential source of lepidopteran larvae for birds, it supported low levels of all other prey categories. Oceanspray may be particularly important in supporting prey for birds because it supports both a high diversity and a high abundance of Lepidoptera (Muir et al. 2002). Oceanspray also supported relatively high intensity of all prey taxa pooled, a high abundance of beetles, and the highest abundance of flies.

Vine maple has not been noted for a high diversity of Lepidoptera larvae (Oboyski 1996, Muir et al. 2002). However, Braun et al. (2002) calculated that folivory by 22 lepidopteran taxa on vine maple in western Washington was equal to 66% of the folivory on the three overstory conifers. This high rate of folivory on a shrub that is common throughout the Pacific Northwest suggests that vine maple may support a significant prey resource for insectivorous birds in the region. On my study sites, vine maple supported a relatively high intensity of prey taxa important in the diet of Wilson's warblers: Lepidoptera larvae, beetles and flies. The high frequency of foraging on vine maple by Wilson's and MacGillivray's warblers (Chapter 3) provides further evidence of the value of this shrub as a source of prey.

Bracken, a fern that grows new fronds each spring from perennial rhizomes, supported a notably high intensity of flies, beetles, and all prey taxa pooled relative to other understory plants. Bracken fern supports a high abundance of herbivores and their associated predators (Lawton 1976), especially where it grows in large, dense patches in sunlit areas (Doolittle 2000). Bracken fern was distinguished from other understory species by exceptionally high abundance intensity of several arthropod groups found in diets of Wilson's warblers and other bird species: aphids, ants, coccinellid beetles, Tenthredinidae (sawfly) larvae, and Cercopidae (Homoptera) (Doolittle 2000). A relatively high abundance but low biomass of arthropods on swordfern reflected an arthropod assemblage dominated by small detritivores such as Pscoptera and Collembola (Doolittle 2000) that were not important in bird diets.

Effect of Stand Condition/ Management History

Because forest management influences the structure and composition of vegetation communities, it was difficult and unrealistic to completely separate the effects on arthropods of plant species composition from those of management history. Abundance and cover of many of the understory species I studied are known to respond to management-induced changes in the density and cover of overstory trees. By increasing resource availability, partial removal of the overstory favors several of the shrubs that supported the most arthropod prey (Bailey et al. 1998, Thomas et al. 1999), whereas the light-depauperate understory of unthinned stands tends to be dominated by species that were less important in providing food resources for birds. For example, bracken fern, a species that supported high arthropod prey loads, can become abundant following disturbances such as thinning (Crane 1990). As a shade-intolerant pioneer and seral species, bracken fern has been proposed as an indicator of light intensity (Emmingham 1972). In western Oregon, cover of bracken fern is more extensive in thinned stands than in unthinned and mature stands, where cover is typically low or negligible (Bailey et al. 1998, Doolittle 2000, Muir et al. 2002). In contrast, sword fern tends to be most abundant in young unthinned stands compared to thinned and mature conditions (Bailey et al. 1998). While probably not an important source of arthropods that are prey for birds, sword fern is used for nesting by some species that are associated with the understory, including Wilson's warblers (Chambers, pers. comm.), rufous hummingbirds, and varied thrushes (pers. obs.).

The tall, deciduous shrubs that were an important source of arthropod prey (oceanspray, hazel, and vine maple) are moderately shade tolerant and frequently occur under closed canopy. However, they can achieve greater cover and density under incomplete canopy and generally respond positively to reduction of overstory cover (O'Dea et al. 1995, Thomas et al. 1999, Thysell and Carey 2000). O'Dea et al. (1995) found higher rates of vine maple clone expansion and vegetative reproduction in thinned than unthinned Douglas-fir stands, and concluded that thinning can potentially increase vine maple density. Bailey et al. (1998) described vegetation at 28 sites in western Oregon, including two of the triads I sampled (see Methods), and found that tall shrub cover, density, and leaf area index was greater in thinned than in unthinned stands. Oceanspray and hazel supported more prey than vine maple and were more influential in habitat selection by Wilson's and other shrub-associated warblers (Chapter 3). On my study sites, oceanspray cover was significantly greater in thinned and hazel cover was greater in GS compared to unthinned stands (Chapter 2). Thinned stands are therefore more likely than unthinned stands to provide suitable foraging habitat for Wilson's and MacGillivray's warblers, and dense thickets used by Swainson's thrushes for foraging and nesting (Dowlan 2003a, Hagar 2003a, 2003b).

The significantly greater intensity of arthropods on some species of understory plants in unthinned stands indicated that concentrations of some arthropod groups were greater on individual plants in unthinned stands relative to thinned and mature forest (Figs. 4.6, 4.7, 4.9), but did not mean that prey abundance was greater in unthinned stands. My indices of abundance and biomass intensity were standardized by unit weight of foliage, so significantly greater density, cover, and leaf area index of shrub foliage in thinned stands (Bailey et al. 1998, Chapter 2) translated to greater overall prey abundance and biomass (Fig. 4.10). One or a combination of the following hypotheses may best explain high arthropod intensity on shrubs in unthinned stands. First, some of the understory shrubs I sampled in unthinned stands may have been stressed as a result of competition for light and other resources. Greater physiological stress of plants may have made them more susceptible to herbivores (Schowalter 1985). Plants experiencing physical stress may be prone to high abundances and outbreaks of leaf-feeding insects (Stoszek et al. 1981, Berryman 1986). Arthropod predators can respond to high herbivore abundance with increased density (Halaj et al. 1998, Schowalter 2000:199), creating high overall arthropod abundance. Secondly, some herbivores are positively affected by density and patch size of host plants and negatively affected by diversity of surrounding plants (Strong and Lawton 1984). Thus, the relatively low richness of understory plant species in unthinned stands compared to thinned stands (Bailey et al. 1998) may have fostered high herbivore intensity. Sword fern and salal were dominant shrubs in unthinned stands and tended to occur in large, continuous patches. In the other stand types, small patches of these species were scattered throughout a more diverse plant community. This distribution may have influenced the higher arthropod intensity in unthinned stands. Doolittle (2000) found negative relationships between surrounding shrub diversity and abundance of arthropods on salal. Thirdly, predation rates on insects may have been different among stand types. Predation by birds has significant effects on population dynamics of forest insects (Holmes et al. 1979, Otvos 1979). Wilson's, MacGillivray's, and orange-crowned warblers were the main foliage-gleaning species on understory vegetation, but they were virtually absent from unthinned stands (Chapter 2, Chapter 3). A lack of predation pressure from these species may have permitted greater intensity of prey species such as aphids (Doolittle 2000). Habitat in unthinned stands was probably unsuitable for understory foliage-gleaners because of sparse cover of tall deciduous shrubs that are used for foraging (Chapter 3) and nesting (Dillingham 2003, Dowlan 2003a, Hagar 2003a, 2003b). Finally, shrubs growing in the understory of unthinned stands may have had higher nutritional quality for herbivorous arthropods than those in the higher light environment of partially harvested stands. Under conditions of limited carbon availability (e.g., heavy shade), tannin production may be decreased (Coley et al. 1985) whereas nitrogen and water concentrations in plant tissues may increase (Barry and Foss 1983, Fales 1984). Increased tannin production by understory plants in clear-cuts compared to old-growth stands was associated with lower availability of crude protein for ungulate herbivores (Happe et al. 1990).

Cover and productivity of fruit- and seed-bearing understory plants also are influenced by characteristics of forest overstory structure (Alaback and Herman 1988, O'Dea et al. 1995, Klinka et al. 1996, Huffman and Tappeiner 1997). For example, by increasing resources available to understory plants, commercial thinning may result in an increase in their cover and biomass (Bailey et al. 1998, Thomas et al. 1999). Kerns et al. (in press) examined huckleberry abundance on some of the same sites I studied in the Oregon Coast Range, and found that thinned stands had significantly greater density of red huckleberry than unthinned. Furthermore, fruit production by huckleberry can increase where overstory cover is reduced (Minore 1984) or removed (Vance et al. 2001). Similarly, Bunnell (1990) found that salal seldom flowered under forest canopy cover >33%, leading him to suggest that salal growing under a canopy is unlikely to provide food for frugivorous wildlife. Red elderberry also decreases in cover with increasing conifer overstory cover, rarely fruits under a forest canopy, and is favored by thinning (Crane 1989). Increased availability of mast from understory vegetation in thinned stands may explain the positive response of several bird species that include fruit in their diet (e.g., Swainson's thrush, Townsend's solitaire, western tanagers, and spotted towhees) to thinning (Muir et al. 2002, Hayes et al. 2003, Hagar and Howlin, submitted).

Conclusions and Management Implications

Traditionally, understory vegetation, particularly woody shrubs, has not been favored in management practices aimed at timber production. Instead, the goal of standard vegetation management, using herbicides or manual methods, is to reduce cover of understory vegetation in order to minimize competition with crop trees (Burhill et al. 1989). Indeed, forest practice regulations require landowners to control non-conifer vegetation as a means of ensuring successful conifer regeneration after clear-cut harvests (Oregon Department of Forestry 2001). Even commercial thinning has been conventionally implemented at sufficiently low intensities to discourage response by the understory. As a result of these and other management practices, shrub and hardwood tree cover in the Oregon Coast Range has declined over the past five decades, and is likely to decrease further on federal forest lands as a result of reduced harvesting (Kennedy and Spies, submitted). However, a change in forest management goals on public lands and an evolving awareness of the importance of diversity in achieving sustainable resource outputs is driving a new appreciation for the value of understory vegetation.

Understory vegetation is a significant component of floristic and structural diversity in conifer-dominated forests (Halpern and Spies 1995). Although conifer regeneration and shrubs each contribute to vertical structure, there are important functional difference, particularly between conifers and deciduous shrubs and trees. Some obvious differences include different growth forms, leaf chemistry, phenology, and reproductive strategies. The presence of shrubs and deciduous trees increases habitat heterogeneity in conifer-dominated forests, contributing to the diversity of niches available for birds and resulting in greater bird species diversity (Willson 1974, Willson and Comet 1996a, Hobson and Bayne 2000). Therefore, a forest stand that has multiple layers of coniferous foliage does not support as diverse a bird assemblage as one that has both deciduous and coniferous layers.

My findings illustrate the importance of understory vegetation, particularly tall, deciduous shrubs, in supporting arthropod prey and mast for songbirds. Vine maple, hazel, and oceanspray also provide resources for other wildlife species. Vine maple is a preferred food of deer and elk, and small mammals as well as birds consume its seeds, buds and flowers (Uchytil 1989). California hazel provides browse for big game, its nuts are a staple of food of several small mammal species and Steller's jays, and birds eat catkins and buds (Zimmerman 1991). Consumption of hazel pollen by white-footed voles, a species endemic to western Oregon and northwestern California, explained a strong association between capture rates and hazel cover (Manning et al. 2003). Oceanspray provides cover and browse for big game, and is used by dusky-footed woodrats in Oregon (Carey 1991).

Management activities that promote development and maintenance of understory vegetation can positively influence songbird diversity by maintaining habitat for shrub-associated species. Commercial thinning can favor the establishment and expansion of many shrub species, leading to the development of a vigorous understory (Tappeiner and Zasada 1993, Huffman et al. 1994). Group selection harvests in rotation age stands also can promote understory development in and adjacent to harvested patches (Chapter 2). However, modifications to conventional thinning may be required to achieve desired shrub cover, including wider spacing, uneven spacing, and protection of shrubs during harvest operations. Stand characteristics in addition to overstory cover and stem density also may affect understory vegetation. Nurse logs and decaying wood are important for the establishment of salal (Huffman et al. 1994, Huffman and Tappeiner 1997), red huckleberry (Pojar and MacKinnon 1994, Klinka et al. 1989), and western hemlock (Harmon and Franklin 1986) in forest understories. Swainson's thrushes consumed ants and beetles that may be associated with large woody debris. Therefore, in addition to providing foraging habitat for bark-gleaning bird species, woody debris also plays a role in trophic pathways that support other songbirds. In general, managed forests have a deficit of decaying wood relative to natural forests, and the management of woody debris is a major issue in Pacific Northwest forests (Rose et al. 2001). As more information is revealed on the ecological importance of decaying wood, it is becoming apparent that current guidelines for augmenting volumes of woody debris in managed forests may be inadequate to sustain all the functions it fulfills in natural forests (Rose et al. 2001).

Although the seedlings of many shrubs establish readily following thinning, older shrubs have unique ecological values that are worth preserving. Larger, older shrubs are more likely to flower and produce seeds than smaller, younger shrubs (Harrington et al. 2002). Larger shrubs provide more vertical structure, and support more epiphytes (Rosso 2000). Forest epiphytes (lichens and bryophytes) are known to support diverse arthropod communities (Gerson and Seaward 1977, Neitlich 1993) and invertebrates inhabiting epiphytic lichens are an important food source for some birds Pettersson et al. 1995). Thinning may increase diversity and abundance of macrolichens on shrubs, but harvesting operations that result in the loss of old shrub stems may have negative effects on some epiphytes in the short term (Rosso 2000).

Management of habitat for any one species or group of species involves tradeoffs with other species. Promoting the development of understory shrubs in managed forests is likely to enhance floristic, invertebrate, and vertebrate diversity. However, some bird species, such as golden-crowned kinglet and hermit warbler, are closely associated with conifer canopies, and others such as hermit and varied thrushes, dwell primarily in the understory of closed-canopy conifer stands (Marshall et al. 2003). Stands that are managed to develop dense understories may not provide suitable habitat for these species. To ensure habitat availability for all species, a range of forest structural conditions should be represented on the landscape.

Chapter 5

VARIATION IN AERIAL ARTHROPOD ABUNDANCE AND TAXONOMIC RICHNESS WITH STAND STRUCTURE AND VEGETATION COMPOSITION IN THE OREGON COAST RANGE

INTRODUCTION

Aerial insects are important prey for several species of birds that breed in Pacific Northwest coniferous forests. Some aerial insectivores, such as swifts, swallows, and nighthawks, forage entirely on the wing, usually in open habitats or above the forest canopy. Other bird species, such as Hammond's flycatcher, western tanager, Townsend's solitaire, and Wilson's warbler, forage within or below the forest canopy by making brief sallies from perches to catch airborne insects. For species that use any type of aerial foraging strategy, stand structure may influence the suitability of foraging habitat. For example, open spaces within and below the canopy provide suitable foraging habitat for Hammond's flycatcher, western tanager, and Townsend's solitaire (Dowlan 2003b, Hagar 2003c, Nehls 2003). Commercial thinning harvests create such canopy openings in dense conifer stands, at least temporarily, and all of these species were more abundant in recently thinned than in unthinned 50-year-old Douglas-fir (*Pseudotsuga menziesii*) stands (Hagar et al. 1996, Hayes et al. 2003, Hagar and Howlin, submitted). Clearly, the configuration of open spaces and perch sites is an important aspect determining suitability of foraging habitat for these species, but availability of prey theoretically should be at least as important. Indeed, increases in the density of insectivorous birds have been associated with increases in the abundance of flying insect prey (Brush and Stiles 1986, Whitaker et al. 2000). However, the influence of forest structure on availability of aerial insect prey has not been well studied in western coniferous forests. A basic understanding of habitat characteristics that influence aerial arthropod abundance is prerequisite to assessing both their response and the response of their predators to changes in forest structure that result from management practices.

Forest overstory cover may directly influence the taxonomic composition and abundance of aerial arthropod prey. Some insect taxa may be most abundant in areas with high light intensity, while others may be correlated with foliage density in tropical forests (Koike et al. 1998). In temperate forests, insect species richness and diversity has been negatively correlated with canopy cover (Humphrey et al. 1999). A positive relationship between amount of light penetration through forest canopy and primary productivity was cited as a possible explanation for higher abundances of aerial insects in gaps than under forest canopies (Blake and Hoppes 1986). However, insect abundance in relation to canopy cover and gap size has not been well studied in temperate coniferous forests, providing little basis for prediction of the response of aerial arthropods to partial canopy removal such as thinning or group selection harvests.

Forest overstory conditions also have effects on the cover and composition of ground vegetation (Klinka et al. 1996, Bailey et al. 1998), which in turn may influence abundance of flying insects. Cover of vegetation, particularly deciduous shrubs, in the shrub layer of forests has been positively correlated with abundance of flying arthropods (Jokimaki et al. 1998) and fly diversity (Humphrey et al. 1999). In a western Oregon study, higher abundance of flying insects in commercially thinned young conifer stands than in similar unthinned stands may have been related to greater herbaceous cover in thinned than unthinned stands (Hagar 1992), but empirical evidence for this relationship was lacking. Cover of both herbaceous and woody ground vegetation in gaps may create suitable habitat for arthropods by minimizing negative effects of surface heat buildups and moisture deficits (Oliver and Larson 1990, Shure and Phillips 1991).

The relationship between the abundance of aerial arthropods and understory vegetation cover and composition may be particularly relevant to management of habitat for the Wilson's warbler. A predominance of flies and other winged insects in the diet of Wilson's warblers (Chapter 4) reflects the hover-gleaning and aerial fly-catching foraging strategy frequently used by this species (Bent 1963, Stewart et al. 1977). This strategy enables Wilson's warblers to prey on small, winged insects found on or near the tips of branches and twigs too small to support the weight of a perched bird. Wilson's warblers are associated with deciduous vegetation in forest understory (Hagar 2003b), and have responded positively to commercial thinning in Pacific Northwest conifer forests (Muir et al. 2002). A greater abundance of Wilson's warblers in thinned than unthinned stands and their association with deciduous shrubs may be related to abundance of sedentary prey on shrub foliage (Chapters 2, 3, and 4), but it is not known if abundance of aerial arthropods also may be important.

Given the importance of airborne arthropods as prey for birds, I wanted to understand habitat characteristics that influenced their abundance in Douglas-fir forests in the Oregon Coast Range. Specifically, I addressed three questions: 1) Does abundance of aerial arthropods differ among stands with different management histories? 2) Do gaps created by group selection harvesting support higher abundances of aerial arthropod prey than the unharvested matrix surrounding the gaps? 3) Is abundance of aerial arthropod prey related to forest canopy cover and the cover and composition of understory vegetation? In the analyses, I focused on flies >3 mm in length and adult Lepidoptera, because they were prey for Wilson's warblers (Chapter 4) but were not adequately sampled by beating shrubs. I also was interested in total abundance of all airborne arthropods and all airborne arthropods >3 mm in length because these could represent coarse estimates of available prey for fly-catching bird species in general.

STUDY SITES

I sampled aerial arthropods in a subset of the study sites described in Chapter 2 (sites 1, 2, 5, and 6 in Fig. 2.1), chosen to represent a range of variability in understory structure. I used two pairs of young thinned and unthinned stands (Mary's Peak and D-Line), and two unmanaged, mature stands each paired with stands of the same age that had been partially harvested with a group selection method (hereafter referred to as GS stands), for a total of eight stands. The young stands (thinned and unthinned) regenerated naturally following clear-cut harvesting and were 55 - 65 years old. A single age cohort dominated the overstory, with very few large trees and well-decayed snags (<1/ ha) persisting from previous stands. Unthinned stands were in the stem-exclusion stage of forest development (Oliver and Larson 1990), and were characterized by a dense, uniform overstory of Douglas-fir, and a sparse understory. Clumps of tall shrubs, mainly vine maple (*Acer circinatum)* and oceanspray (*Holodiscus discolor*), that occurred in unthinned stands tended to be scattered, and were primarily composed of a few tall stems with sparse foliage. Thinned stands had been thinned to uniform spacing 19 – 27 years prior to this study. Residual tree densities were typical for standard thinning operations meant to optimize timber yield. In other words, the goal of thinning at the time it was performed did not include the fostering of structural and biological diversity. In contrast, GS stands were part of an experiment to assess wildlife response to alternatives to clear-cutting aimed at maintaining biodiversity in managed forests (Chambers et al. 1999). In these 120-year-old stands, one-third of the volume was removed in 0.2-ha circular patches. All sites were located in forests dominated by Douglas-fir on the east side of the Oregon Coast Range, in the Western Hemlock Vegetation (*Tsuga heterophylla*) forest zone (Franklin and Dyrness 1988). Regional climate is characterized by mild, wet winters and dry summers.

METHODS

Sticky traps were intended to capture aerial insects that are potential prey for fly-catching birds and consisted of a 46- x 46-cm piece of hardware cloth coated with tanglefoot insect trap, stapled to the top of a 2.4-m long wooden stake driven into the ground. Thus, traps sampled insects approximately 2 m above ground. In each of the eight stands, ten traps were haphazardly placed within 10 – 25 m of mist-net locations, where birds were captured to sample diets (see Chapter 4). In the GS stands, five traps were placed in gaps, and five in adjacent forested matrix.

Aerial arthropods were sampled at the same trap locations during two periods in 2000: (1) 6 June to 4 July, and (2) 12 – 31 July. Trapped arthropods were identified in the field seven days after traps were placed. Arthropods >2 mm in length were identified to the lowest possible taxonomic level in the field and measured to the nearest mm. Arthropods >10 mm in length and those we were unable to identify in the field were removed from traps, mounted on index cards, and identified in the laboratory. I did not attempt to identify arthropods <2 mm in length. Used screens were replaced with fresh ones at the beginning of the second sampling period.

Methods of vegetation sampling

I ocularly estimated overall cover of live vegetation and cover of deciduous vegetation within a 5-m radius of each trap in four height classes: <1.5 m, 1.5- to 4 m, 4.1- to 15 m, and >15 m. Height classes were based on approximate natural breaks in the vegetation. Most herbs and low shrubs fell into the lowest height class; tall shrubs were represented by the 1.5- to 4 m class, and the highest classes represented mid- and overstory cover, respectively.

Data Analysis

I assumed that the number and taxa of arthropods caught on each screen trap represented the local abundance and community composition of aerial arthropods. Therefore, I summed the number of arthropods on each trap within each sampling period to derive an index of abundance. I calculated this abundance index for three arthropod categories: all arthropods, all arthropods >3 mm in length, and Diptera >3 mm in length. I summed the number of orders and families on each trap within each sampling period to derive two indices of taxonomic richness. I assumed that each trap location was independent because individual arthropods respond to microsite characteristics (Schowalter 2000), causing variation in arthropod communities within a stand. Therefore, each screen trap represented an experimental unit (N = 80).

I used analysis of variance (ANOVA) to test the null hypotheses that mean abundance of the three categories of arthropod prey did not differ among stand conditions and between matrix and gap plots within the GS stands only. I included an interaction term for sampling period because arthropod abundance can fluctuate over the time period represented by my sampling effort, introducing variability in the data. I log-transformed the response variables to meet the statistical assumptions of normally distributed residuals with constant variance.

I used an information-theoretic approach to selecting the "best" model from a set of pre-defined candidate regression models (Burnham and Anderson 2002) to explain variation in aerial arthropod response variables as a function of vegetation cover. I used this method to explain variation in five response variables: abundance of all arthropods, abundance of arthropods >3 mm, abundance of Diptera >3 mm, ordinal richness and family richness. I modeled each response variable separately for each sampling period. Candidate models were selected from the variables describing overall cover and deciduous cover in each of the four height categories. I examined plots of predictor versus response variables and log-transformed variables that appeared to have non-constant variance. Variables that did not conform to statistical assumptions following transformation were not used in analyses. Strongly correlated variables were not included in any of the candidate models. I included a null model in the set of candidates to ensure the final model performed better than a model based solely on average arthropod abundance or taxonomic richness. The model with the lowest Akaike Information Criteria (AIC) score was considered the "best" in the set if it met assumptions of constant variance and normal distribution of residuals. For each of the remaining models in the set, I calculated Δ as the difference between the AIC score of the best model and that of the model under consideration. Models within 2 Δ units of best model were considered equally plausible as long as they met model assumptions. I calculated the Akaike weight (w_i) to evaluate the strength of evidence supporting the best models. Models with w_i values close to 1 are more plausible than those with values close to 0 (Burnham and Anderson 2002).

Because adult Lepidoptera were captured on only 22% of the screen traps, multiple regression could not be used to model the association between their abundance and vegetation cover. Instead, I used ANOVA to test the hypothesis that the mean percent cover at traps where adult Lepidoptera were caught did not differ from that at traps where they were not caught for three cover variables: total vegetation cover <4 m, cover of woody deciduous shrubs <4 m, and total vegetation cover >4 m.

I compared overall vegetation cover at the three lowest height categories between gap (N=10) and matrix plots (N=10) within the GS stands using ANOVA. By definition, gaps did not have any overstory cover in the highest height category.

RESULTS

Thirteen orders of arthropods were identified from the 18,492 specimens captured on screen traps. The order Diptera dominated the collection numerically, representing 42% of all captures (Table 5.1). Coleoptera was the second most abundant order. Both Diptera and Coleoptera were captured on 99% of the traps. Eighty percent of the arthropods captured were $\leq$5 mm in length. Arthropods <3 mm in length composed 49% of the sample.

Differences in ordinal and family richness among stand conditions depended on the sampling period ($P_{interaction}$ <0.001, ANOVA; Fig. 5.1). During the early sampling period, the average number of orders / trap was significantly greater ($P < 0.001$, least squares means test) in thinned stands than in any of the other stand types (Fig. 5.1A), while the number of families was higher ($P < 0.02$, least squares means test) in GS and thinned stands than in mature and unthinned stands (Fig. 5.1B). During the later sampling period both ordinal and family richness was highest in GS and lowest in unthinned stands, but lower in thinned relative to mature stands.

Differences in abundances of all arthropods and arthropods >3 mm among stand types did not vary with sampling period ($P_{interaction} \geq$0.18, ANOVA). For aerial arthropods of all sizes, median abundance was 1.6 to 2.1 times lower in unthinned stands than in the other three stand types ($P \leq 0.007$, least squares means test; Fig. 5.2A). For aerial arthropods >3 mm, median abundance was 1.8 to 2.6 times higher (approximately 24 – 38 arthropods/trap) in mature and GS stands than in young thinned and unthinned stands ($P < 0.001$, least squares means test). Abundance in thinned stands averaged 25% greater than in unthinned stands (Fig. 5.2B), but this difference was not statistically significant.

Table 5.1. Frequency of occurrence of arthropods on 155 sticky traps and total numbers of captures by taxonomic group in Douglas-fir stands in the Oregon Coast Range, 2000. Only arthropods >2mm in length were identified to order.

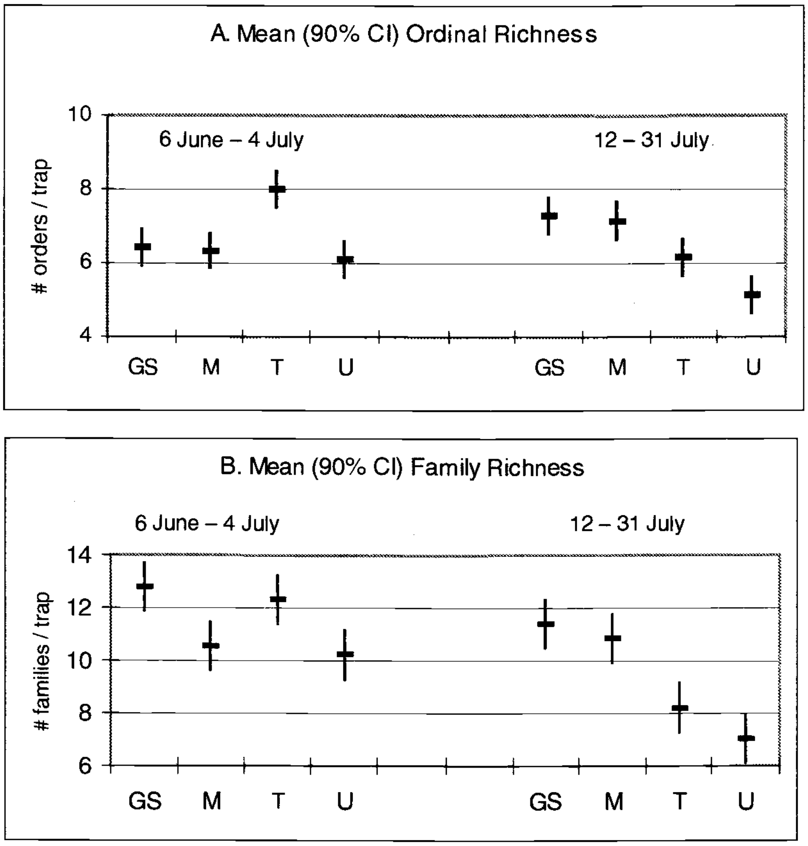
Arthropod Taxa	Frequency of occurrence [1]	total #	% of total
Diptera	0.99	7774	0.420
Coleotera	0.99	1912	0.103
Hymenoptera	0.92	745	0.040
Psocoptera	0.45	480	0.026
Araneida	0.74	269	0.015
Homoptera	0.54	165	0.009
Hemiptera	0.39	117	0.006
Neuroptera	0.38	86	0.005
Lepidoptera - Adults	0.22	42	0.002
Lepidoptera - Larvae	0.09	16	0.001
Plecoptera	0.05	12	0.001
Tricoptera	0.05	10	0.001
Ephemeroptera	0.05	9	0.000
Opiliones	0.01	2	0.000
Unknown >2 mm in length	0.04	11	0.001
Unknown <2 mm in length	0.72	6842	0.370

[1] Number of traps on which taxa was recorded / 155 total traps

Differences in abundance of flies >3 mm among stand conditions depended on sampling period ($P_{interaction}$ <0.008, ANOVA; Fig. 5.3). During Period 1, median abundance was 2.8 to 8.4 times higher in mature than in any other stand condition (P<0.10, least squares means test). Abundance was 2.1 to 4.7 times higher in GS stands than in thinned and unthinned stands (P < 0.03, least squares means test). Median fly abundance was 2.25 times higher in thinned than unthinned stands (P = 0.02, least squares means test). Overall median fly abundance was 3.7 times lower during sampling

Period 2 compared to Period 1. Within Period 2, median abundance in GS stands was 1.8 to 4.7 times higher than in any other stand condition (P < 0.08, least squares means test).

Figure. 5.1. Mean (90% confidence intervals) number of arthropod (A) orders and (B) families per trap in four stand conditions (GS = Group Selection harvest, M = unmanaged mature, T = young, commercially thinned, U = young, unthinned), during two sampling periods, Oregon Coast Range, 2000.



Within GS stands, ordinal richness was greater in gaps than matrix plots (P= 0.02, ANOVA); traps in gaps had on average 0.3 to 1.8 (90% CI) more orders than traps in matrix (mean difference = 1.05 orders/trap). Average number of families/trap did not differ between gap and matrix plots (P= 0.12, ANOVA). Total abundance of all sizes of arthropods did not differ between gap and matrix plots during the first sampling period, but was almost three times greater in gaps than in matrix locations during Period 2 (P = 0.001, ANOVA; Fig. 5.4). Arthropods >3 mm in length were almost twice as abundant in gap as in matrix plots regardless of sampling period (P = 0.008, ANOVA; Fig. 5.5). Abundance of arthropods >3 mm was 1.9 times greater during Period 1 than Period 2 (P = 0.03, ANOVA). Similarly, flies >3 mm were more than twice as abundant in gap (median = 34/trap, 90% CI: 21, 54) as in matrix plots (median = 15/trap, 90% CI: 9, 24; P = 0.04, ANOVA), but about half as abundant during Period 2 (median = 15/trap, 90% CI: 9, 24) compared to Period 1 (median = 33/trap, 90% CI: 20, 53; P = 0.06, ANOVA; data not graphed).

Regression models explained 12 to 31% of the variation in abundance of the arthropod prey categories that I analyzed, and 8 to 28% of the variation in family and ordinal richness (Table 5.2). Associations between response variables and understory cover (≤4 m from forest floor) were uniformly positive. Deciduous understory cover explained the most variation for every response variable in at least one of the sampling periods. Except for abundance of Diptera during Period 1, responses were negatively associated with mid- and overstory cover (>4 m).

Adult Lepidoptera were captured at 43.5% (37 of 85) of the screen trap plots during both sampling periods combined. Cover of deciduous shrubs <4 m and cover of all vegetation <4 m was significantly greater (P < 0.10, ANOVA) on plots where adult Lepidoptera were captured than where they were not captured. Cover of deciduous vegetation <4 m was estimated to be on average 12.8% greater at traps where adult Lepidoptera were caught (mean = 58.5%, 90% CI: 49.1, 67.9) than where no adult Lepidoptera were caught (mean = 45.7%, 90% CI: 37.4, 53.9). Cover of all vegetation <4 m was estimated to be on average 14.3% greater at traps where adult Lepidoptera were caught (mean = 98.2%, 90% CI: 90.2, 106.2) than where no adult Lepidoptera were caught (mean = 83.9%, 90% CI: 76.9, 91.0). A difference in overstory cover (>4 m) was not detected between plots with and without Lepidoptera (P = 0.55, ANOVA).

Cover of vegetation differed significantly between gap and matrix plots within GS stands for three height categories (Fig. 5.6). Cover in the lowest layer (<1.5 m) was greater in gaps than matrix by an average of 24% (P = 0.007, ANOVA). Cover from 1.5 – 4.0 m was greater in matrix plots by an average of 18% (P = 0.034, ANOVA). Cover above 4.0 m also was greater in matrix than gap plots (P < 0.001, ANOVA).

Figure 5.2. Comparison of mean number of captures on sticky traps (90% confidence intervals) for A) all sizes of arthropods, and B) arthropods >3 mm in four stand conditions (GS = Group Selection harvest, M = unmanaged mature, T = young, commercially thinned, U = young, unthinned), Oregon Coast Range, 2000.

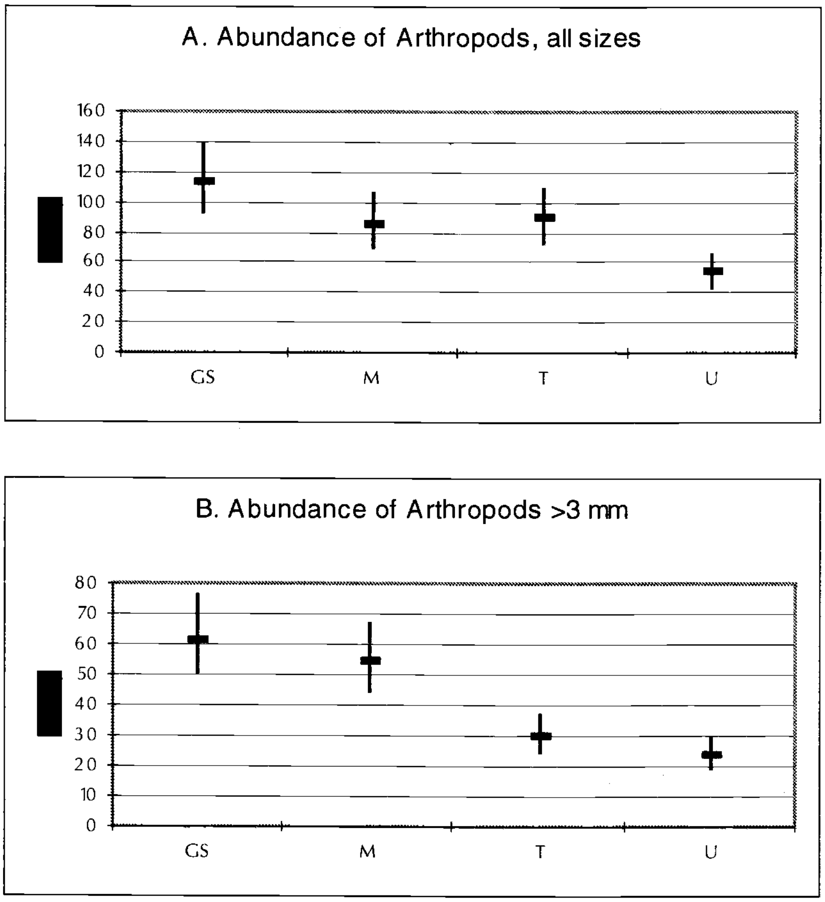


Figure 5.3. Comparison of mean number of captures (90% confidence intervals) of **flies** on sticky traps, during two sampling periods in four stand conditions (GS = Group Selection harvest, M = unmanaged mature, T = young, commercially thinned, U = young, unthinned), Oregon Coast Range, 2000.

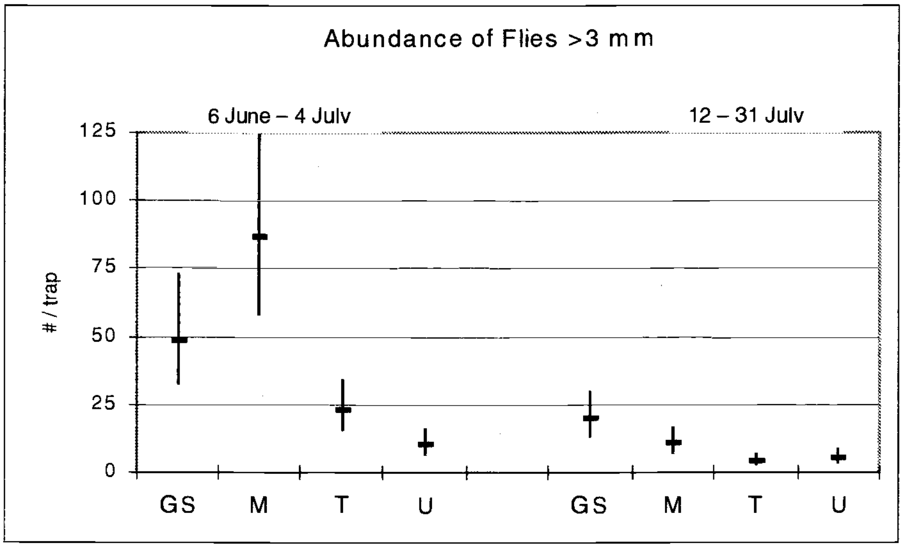


Figure 5.4. Comparison of median number of captures (90% confidence intervals) of **all arthropods** on sticky traps in gaps and matrix of group selection stands during two sampling periods in the Oregon Coast Range, 2000.

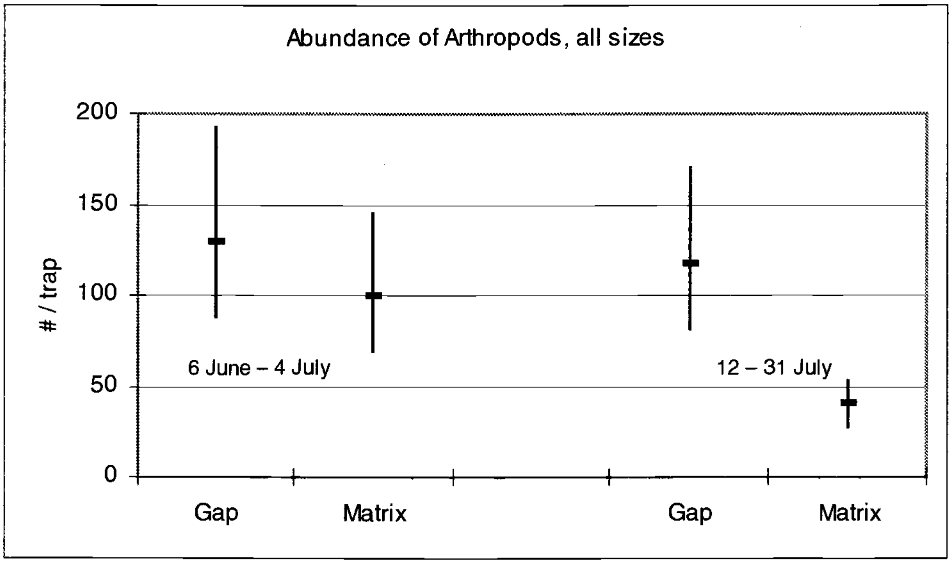


Figure 5.5. Comparison of median number of captures (90% confidence intervals) of arthropods >3 mm on sticky traps between gap and matrix plots averaged over two group selection stands and sampling periods in Oregon Coast Range, 2000.

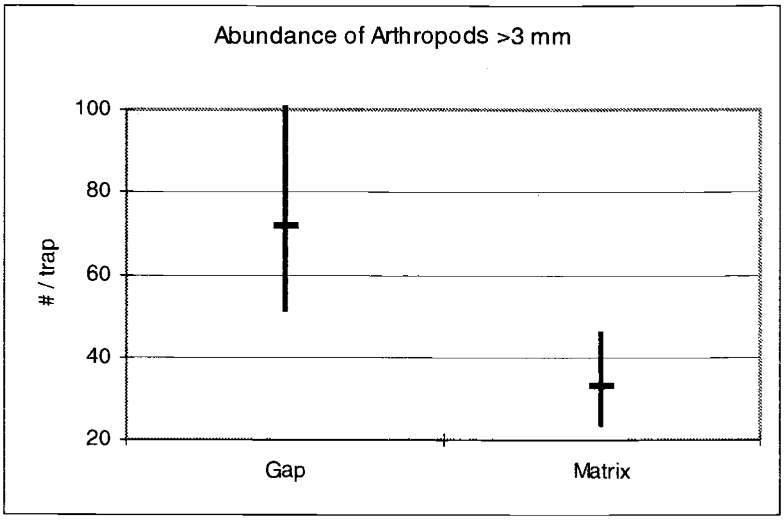


Figure 5.6. Comparison of average vegetation cover (95% confidence intervals) in three height categories between gap and matrix plots in two group-selection stands in the Oregon Coast Range.

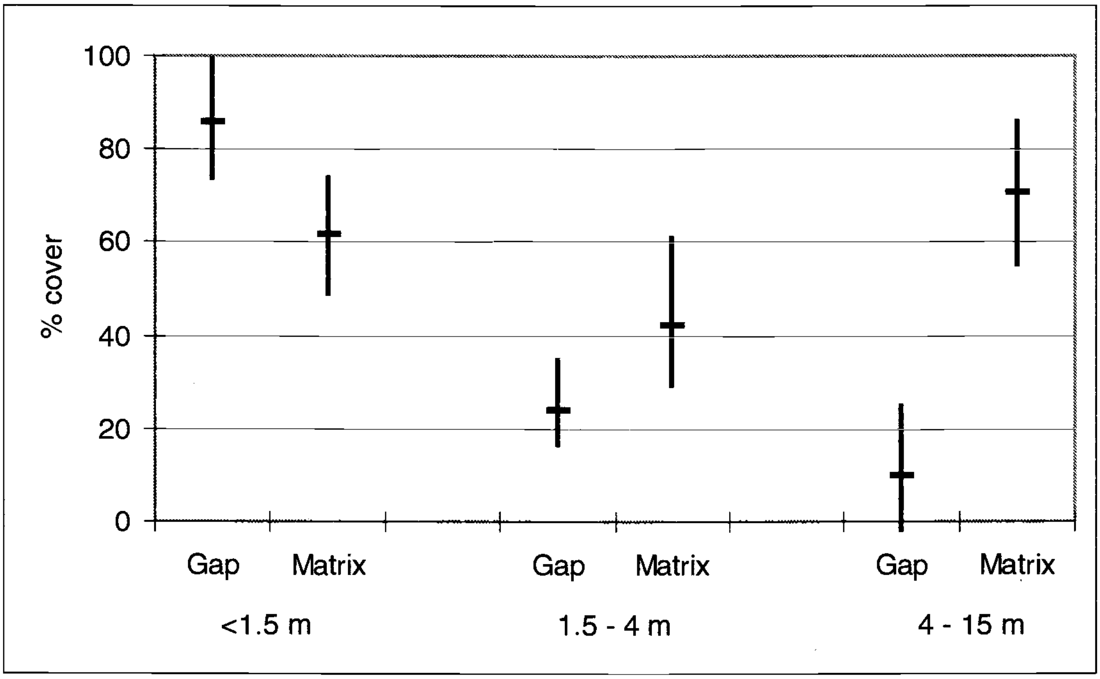


Table 5.2. Best models for explaining variation in abundance of aerial arthropod prey as a function of habitat variables in Douglas-fir forests, Oregon Coast Range. Potential values of Akaike Weight range from 0 to 1, with greater values indicating stronger evidence in support of the best model.

Response	Model Variables	Parameter Estimate	Akaike Weight	Adjusted Model R^2
Arthropods, All Sizes				
Period 1	log (vegetation cover 4 - 15 m)	0.802	0.97	0.14
Period 2	deciduous cover ≤4 m	0.009		
	vegetation cover ≥4 m	-0.005	0.99	0.31
Arthropods >3 mm				
Period 1	log (deciduous cover <1.5 m)	0.319	0.83	0.12
Period 2	deciduous cover ≤4 m	0.009		
	vegetation cover ≥4 m	-0.004	0.92	0.25
Diptera >3 mm				
Period 1	log (deciduous cover <1.5 m)	0.481	0.67	0.12
Period 2	deciduous cover <4 m	0.012	0.57	0.15
Ordinal Richness				
Period 1	log (vegetation cover 4 – 15 m)	-0.286	0.34	0.08
Period 2	log (deciduous cover <1.5 m)	0.598	0.46	0.21
Family Richness				
Period 1	log (vegetation cover 1.5 – 4 m)	0.132	0.72	0.11
Period 2	deciduous cover <4 m)	1.005	0.60	0.28

DISCUSSION

Taxonomic richness and abundance of aerial arthropods varied among stands with different silvicultural histories and were associated with amount and composition of cover in different vertical strata of forest vegetation. Cover of deciduous shrubs in particular was important in explaining variation in the abundance of several arthropod groups (Table 5.2), and was greater in thinned and GS stands than in mature and unthinned stands (Chapter 2). Within GS stands, the greater cover of vegetation within 1.5 m of the forest floor in gaps was associated with greater abundance of aerial arthropods in gaps relative to matrix. Some arthropods that birds catch on the wing may be dispersing, but many may be associated with local vegetation, using it for feeding, resting, or hiding. For example, Lepidoptera are particularly important prey for many songbirds, and the adults are commonly consumed by fly-catching bird species (Beaver and Baldwin 1975; Chapter 4). A diversity of understory vegetation may benefit some species of Lepidoptera that use different host plants during phytophagous larval stages than during nectivorous adult stages (i.e., some butterflies; Opler et al. 1995). Other actively flying insects that are prey for insectivorous birds also may be influenced by local plant community characteristics. Wilson's warblers preyed on cantharid and mordellid beetles, which are common on flowers (Borror et al. 1989). Pollinating insects, including members of the orders Hymenoptera and Diptera also were prey for warblers and flycatchers (Chapter 4). The light-rich environment of gaps may provide more flowers for pollinators and nectarivores than the shaded matrix. Similarly, plants in the understory of thinned stands may produce more flowers than those under a more closed canopy (Harrington et al. 2003).

Structural and species diversity of vegetation correlates positively with the variety of habitats and resources available for invertebrates (Schowalter 1995, Lawton 1983, Southwood et al. 1979). Therefore, it is not surprising that taxonomic richness of arthropod prey increased with cover of understory vegetation. Furthermore, the relationship between vegetation and availability of habitats for arthropods may explain why taxonomic richness was consistently lowest in young unthinned stands, which are relatively simple in structure and plant species composition (Muir et al. 2002, Bailey and Tappeiner 1998). In contrast, consistently high taxonomic richness of aerial arthropods in GS stands may have been related to high plant and structural diversity characteristic of this stand type (Chambers 1996). Old-growth Douglas-fir forests also typically have high structural and plant diversity (Spies 1991, Spies and Franklin 1991), which has been associated with arthropod diversity (Schowalter 1995), although not for airborne arthropods in particular. In my study, richness of arthropod groups was not consistently higher in mature relative to young and GS stand types, but it did appear to be more stable throughout the season (Fig. 5.1). Prey diversity may be an important attribute of prey availability for birds because higher diversity may equate with more foraging opportunities for more species of birds. The positive association between taxonomic richness of aerial prey and cover of deciduous shrubs that I found may contribute to a positive relationship between deciduous shrubs and bird species richness (Muir et al. 2002; Willson and Comet 1996a, 1996b).

All measures of abundance of aerial arthropod prey that I analyzed were positively associated with cover of understory vegetation. Development of understory vegetation can be profuse in naturally created gaps (Franklin and Spies 1991). Partial removal of the overstory by thinning or group selection also can promote development of understory vegetation by increasing the availability of light and other resources. On my study sites, greater abundance of aerial arthropods corresponded with greater cover of understory vegetation in small (0.2 ha) gaps relative to matrix, and in thinned compared to unthinned young stands (Chapter 2). Cover of deciduous shrubs was a particularly important correlate for all measures of aerial prey abundance and diversity. The abundance of both aerial (Jokimaki et al. 1998) and sedentary arthropod taxa (Chapter 4) in temperate coniferous forests has been positively correlated with deciduous shrubs. In coniferous forests in western Oregon, 57% of all lepidopteran species richness and 69% of the abundance of moths are associated with hardwoods (Hammond and Miller 1998). The positive correlation that I found between cover of deciduous shrubs and Lepidoptera captures is consistent with this pattern. Herbs and grasses also support a significant proportion of Lepidoptera species in western Oregon

(31%; Hammond and Miller 1998) and have been positively associated with arthropod abundance in general (Blenden et al. 1986). Thinned Douglas-fir stands support greater species richness and abundance of herbs and grasses than unthinned and old-growth stands (Bailey et al. 1998).

Microenvironmental characteristics, including temperature and moisture, influence the abundance and activity of aerial arthropods and are mediated by vegetation. Because insects are poikilotherms, a minimum temperature is required for flight, but the small size of most insects makes them vulnerable to desiccation. Thus, forest gaps may provide habitats where elevated light and temperature promotes activity of flying insects while vegetation minimizes the negative effects of heat buildups and moisture deficits. A tradeoff likely exists between gap size and the ability of surrounding vegetation to mediate temperature and humidity (Shure and Phillips 1991). Furthermore, the larger a gap becomes the more likely that the spatial distribution of flying insects will be influenced by wind (Whitaker et al. 2000). Gaps in the forest canopy large enough to increase insolation to the understory, but small enough to be undisturbed by wind may be ideal foraging habitat for insectivores that use sallying maneuvers to capture aerial prey because they support concentrations of flying insects near perches. Natural treefall gaps, such as those in old-growth Douglas-fir stands, and gaps created by partial harvesting, as in the thinned and group selection stands that I sampled, seem to fit these criteria.

In conclusion, the abundance of aerial arthropod prey for birds was positively associated with forest understory cover, particularly of deciduous vegetation. Understory cover, in turn, is influenced by forest management practices that manipulate overstory cover. Small gaps in the canopy of commercially thinned stands, and larger gaps created by group selection harvests appear to promote conditions favorable to aerial arthropods and some of the insectivorous bird species that prey on them.

Chapter 6

GENERAL CONCLUSIONS

In this work, I have shown how vegetation structure and composition in the understory of coniferous forests in western Oregon influences food resources for several species of birds. Wilson's, MacGillivray's, and orange-crowned warblers selected habitat patches with a high percent cover of tall deciduous shrubs, and foraged extensively on these species. Swainson's thrush abundance also was associated with deciduous shrub cover. Tall deciduous shrubs, particularly oceanspray, supported greater abundances of arthropod prey than evergreen shrub species. The positive associations among cover of deciduous shrubs, abundance of both foliage-dwelling and aerial arthropod prey, and the abundance of Wilson's warblers, MacGillivray's warblers, and Swainson's thrushes, suggests that abundance of these birds reflects habitat quality (Whitaker et al. 2000, Brush and Stiles 1986). Furthermore, the presence and amount of deciduous vegetation in the forest understory may indicate habitat quality for these bird species. However, more extensive research, based on larger sample sizes than in this study, would be needed to more accurately quantify relationships among bird populations and vegetation characteristics. For example, my data do not allow quantification of the patch size or volume of deciduous vegetation understory required to support sufficient arthropod prey for a pair of breeding warblers. In addition, habitat quality is influenced by other factors besides food resources that influence survival and productivity. Although my study was not designed to measure these parameters, recaptures of some birds on the same sites over several (>2) years and captures of fledglings (unpubl. data) suggest that survival and productivity may have been good at the sites where birds were most abundant.

Of the more than 400 species of vertebrate wildlife in the Pacific Northwest (Johnson and O'Neil 2000), I looked at the ecology and habitat associations of only four. However, my results link the habitat associations of these four species with those of understory shrub species and arthropods. Understory vegetation provides the foundation for food webs that contribute to diversity at multiple trophic levels in conifer-dominated forests. Based on these results, the following suggestions are aimed at helping managers achieve goals related to the maintenance of biodiversity in managed forests.

- Management of density with pre-commercial and commercial thinning starting early in stand development will promote the retention and growth of understory vegetation. However, the intensity of thinning should vary across the landscape, ranging from no thinning to very heavy thinning. Conifer stands with dense, closed canopies and little understory do provide habitat for some species, and should be retained at various spatial scales.

- Thinning prescriptions should explicitly address goals for understory vegetation structure and composition as well as the traditional attention to overstory characteristics.

- In forests managed under long rotations or an uneven-aged system, group selection or other partial harvests may help maintain understory vegetation by creating gaps in the forest canopy. Allowing shrubs to develop in at least some of these gaps, rather than intensive management for the next cohort of conifer trees, will promote diversity of understory vegetation, arthropods, and songbirds.

- Although I have highlighted the habitat associations of species that are more abundant in young forests that have a well-developed understory, my results in no way suggest that harvesting in old-growth stands should be considered as a strategy for fostering biodiversity! On the contrary, given the scarcity of old-growth conifer forests on the landscape, I do not recommend any harvesting in residual stands to create habitat for species associated with younger forests.

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APPENDICES

APPENDIX A

LENGTH – WEIGHT REGRESSIONS OF ARTHROPODS FROM FOREST UNDERSTORY VEGETATION IN THE OREGON COAST RANGE

Introduction

An assessment of arthropod prey availability for songbirds requires estimates of both density and biomass of potential prey. However, weighing all arthropods in a reference collection is not always practical or economical because it can be time-consuming and require specialized equipment (e.g., electrobalances) for weighing small specimens. An alternative to directly weighing all specimens is to relate body length to weight with regression equations developed from a sample of arthropods (Rogers et al. 1977, Hodar 1996). Such regression equations are available in the literature for many taxonomic groups of arthropods, but length-weight regressions from arthropods of Pacific Northwest forests are not currently available. Equations made with specimens from one zone may not be accurate for estimating biomass of specimens from a different zone (Schoener 1980, Gowing and Recher 1984). I developed equations to estimate the biomass of arthropods collected from shrubs in the Oregon Coast Range in order to compare food resources for insectivorous songbirds among shrub species and silvicultural treatments.

Methods

Collection A: I collected arthropods by beating shrubs in the understory of young thinned, young unthinned, and mature/old-growth Douglas-fir stands, from May to July, 1996 – 1999. Arthropods were stored in alcohol until they were identified, 1 to 22 months after collection. I used an ocular micrometer to measure the length of each specimen from the frons to the posterior tip of the abdomen.

Collection B: I used this separate collection of arthropods to build regression equations that were used to estimate the weight of arthropods in Collection A. Andy Moldenke (Oregon State University) and B. Marcot (USDA Forest Service) collected these arthropods by beating understory shrubs in old-growth conifer stands in western

Washington. I randomly sub-sampled from Collection B ten groups of arthropods that commonly occurred in the diets of songbirds associated with forest understory vegetation. I measured length of these specimens with a ruler to the nearest 0.5 mm. I also measured the width of the abdomen at the widest point for spiders. I used arthropods from Collection B that comprised a similar range of lengths to those in Collection A to build regression equations. Arthropods had been stored in glycol; I blotted them on paper towel until no wet spots remained, and weighed to 10^{-3} mg with an electronic balance.

Data Analysis

I used a power model (Rogers et al. 1977) to quantify the relationship between length and weight for ten arthropod orders or groups of orders. I included abdomen width in the model for spiders because it was a measurement I had recorded for spiders at the time of identification, and because it greatly improved the predictive ability of the model. I used the general Hemiptera equation to predict biomass of Berytids, but developed another model that excluded Berytids for use with all other Hemipteran families. Berytids biased the Hemipteran equation because their long, but very narrow, shape was uncharacteristic of the other common Hemipterans in our collection. I lumped Diptera and Pscocoptera because of their similarity in body shape. I lumped all larvae because body shape was similar across the orders I most commonly encountered. I separated ants from winged Hymenoptera because of their dissimilarity in body shape.

Results

Table A1. Length-weight regressions for Coast Range arthropods.

Arthropod Group	N[1]	Length Range[2]	Regression Equation	R^2
Araneida	42	2 – 12.5	ln(weight) = -2.7416 + 1.6624*ln(length) + 1.1607ln(width).	0.91
Coleoptera	34	2.7 – 16	ln(weight)=-4.6200 + 2.6172*ln(length)	0.82
Diptera and Psocoptera	27	1.0 – 13	ln(weight) = -4.1095 + 2.2708*ln(length)	0.86
Hemiptera	33	2 – 10	ln(weight) = -3.6541 + 1.8739*ln(length)	0.75
Hemiptera without Berytids	30		ln(weight) = -4.2252 + 2.3478*ln(length)	0.91
Homoptera: Aphids and others	23	1.3 – 3.4	ln(weight) = -4.0841 + 2.3693*ln(length)	0.90
Hymenoptera (non- Formicid)	23	1.8 – 15	ln(weight) = -6.1987 + 3.3979*ln(length)	0.91
Formicidae	20	1.5 – 14	ln(weight) = -4.4891 + 2.5791*ln(length)	0.94
Larvae	29	3 – 29	ln(weight) = -5.1939 + 2.5151*ln(length)	0.94
All Arthropods	235	1 – 29	ln(weight) = -4.1595 + 2.3898*ln(length)	0.81

[1] Number of individuals used in regression.
[2] Minimum and maximum length (mm) of arthropods used in regression.

Appendix B. Frequency of occurrence of arthropods on 15 species of understory plants in Oregon Coast Range Douglas-fir forests. Number in parantheses indicate sample size for each plant species. Plant species are salal (*Gaultheria shallon*; GASH), vine maple (*Acer circinatum*; ACCI), sword fern (*Polystichum munitum*; POMU), western hemlock (*Tsuga heterophylla*; TSHE), bracken fern (*Pteridium aquilinum*; PTAQ), oceanspray (*Holodiscus discolor*; HODI), California hazel (*Corylus cornuta* var. Californica; COCO), salmonberry (*Rubus spectabilis*; RUSP), Douglas-fir (*Pseudotsuga menziesii*; PSME), Oregon-grape (*Berberis nervosa*; BENE), Snowberry (*Symphoricarpos* spp., SYMPH), red huckleberry (*Vaccinium parvifolium*; VAPA), Pacific dogwood (*Cornus nuttallii*; CONU), Indian plum (*Oemleria cerasiformis*; OECE), and thimbleberry (*Rubus parviflorus*; RUPA).

	GASH	ACCI	POMU	TSHE	PTAQ	HODI	COCO	RUSP	PSME	BENE	SYMPH	VAPA	CONU	OECE	RUPA
	(257)	(252)	(187)	(156)	(132)	(61)	(47)	(20)	(8)	(7)	(3)	(3)	(1)	(1)	(1)
INSECTA															
ARCHAEOGNATHA															
Machilidae	0.004	0.016	0.032	0.045	0.008	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EPHEMEROPTERA	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ORTHOPTERA	0.012	0.000	0.005	0.006	0.008	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Rhaphidophorinae	0.004	0.000	0.005	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gryllacrididae	0.000	0.000	0.005	0.006	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gryllidae	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PLECOPTERA	0.000	0.008	0.016	0.013	0.015	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Perlidae	0.000	0.000	0.011	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Perlodidae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PSOCOPTERA	0.502	0.258	0.267	0.667	0.326	0.213	0.106	0.150	0.250	0.143	0.000	0.000	0.000	0.000	0.000
THYSANOPTERA	0.016	0.008	0.000	0.019	0.023	0.000	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Phloeothripidae	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Thripidae	0.016	0.008	0.000	0.019	0.023	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HEMIPTERA	0.144	0.163	0.134	0.160	0.242	0.311	0.234	0.200	0.000	0.000	0.000	0.333	0.000	0.000	1.000
Aradidae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Berytidae	0.008	0.004	0.005	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Cimicidae	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Coreidae	0.000	0.000	0.000	0.000	0.000	0.066	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Corimelaenidae	0.004	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lygaeidae	0.000	0.000	0.000	0.006	0.008	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Miridae	0.086	0.087	0.107	0.141	0.129	0.131	0.106	0.150	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Nabidae	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pentatomidae	0.016	0.012	0.000	0.006	0.008	0.000	0.021	0.050	0.000	0.000	0.000	0.333	0.000	0.000	0.000
Reduviidae	0.000	0.000	0.000	0.000	0.030	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HOMOPTERA	0.553	0.500	0.540	0.365	0.955	0.230	0.532	0.650	0.125	0.143	1.000	1.000	1.000	1.000	1.000
Achilidae	0.000	0.024	0.027	0.032	0.053	0.016	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Adelgidae	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aleyrodidae	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Aphididae	0.397	0.444	0.476	0.224	0.932	0.197	0.383	0.450	0.000	0.000	1.000	1.000	0.000	1.000	1.000
Cercopidae	0.265	0.024	0.032	0.160	0.394	0.016	0.085	0.150	0.000	0.000	0.000	0.333	1.000	0.000	1.000
Cicadellidae	0.035	0.012	0.037	0.038	0.061	0.000	0.021	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cixiidae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Eriosomatidae	0.000	0.012	0.016	0.000	0.000	0.000	0.128	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Psyllidae	0.004	0.000	0.005	0.013	0.015	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
NEUROPTERA	0.058	0.087	0.043	0.064	0.159	0.082	0.021	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chrysopidae	0.039	0.063	0.011	0.013	0.129	0.066	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Coniopterygidae	0.008	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Hemerobiidae	0.012	0.024	0.032	0.032	0.038	0.016	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Raphidiidae	0.000	0.004	0.005	0.006	0.008	0.000	0.064	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
COLEPTERA	0.545	0.623	0.540	0.494	0.659	0.639	0.447	0.300	0.750	0.143	0.667	0.333	1.000	1.000	0.000
Alleculidae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
Anobiidae	0.004	0.004	0.005	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Brentidae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Byrrhidae	0.000	0.000	0.000	0.000	0.008	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cantharidae	0.342	0.413	0.310	0.218	0.409	0.459	0.128	0.050	0.625	0.000	0.667	0.000	0.000	0.000	0.000
Malthodes	0.257	0.298	0.225	0.167	0.356	0.361	0.064	0.050	0.625	0.000	0.333	0.000	0.000	0.000	0.000
Cerambycidae	0.004	0.016	0.000	0.000	0.008	0.033	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chrysomelidae	0.008	0.036	0.027	0.032	0.015	0.049	0.149	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Coccinellidae	0.152	0.159	0.118	0.077	0.348	0.213	0.043	0.100	0.250	0.000	0.000	0.333	0.000	1.000	0.000
Psyllobora	0.074	0.099	0.064	0.058	0.144	0.016	0.000	0.100	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Stethonus	0.047	0.008	0.027	0.000	0.121	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
Curculionidae	0.078	0.056	0.016	0.064	0.023	0.033	0.021	0.050	0.000	0.143	0.000	0.333	0.000	0.000	0.000
Dascillidae	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Elateridae	0.016	0.079	0.070	0.090	0.091	0.033	0.000	0.000	0.250	0.000	0.000	0.000	1.000	0.000	0.000
Eucnemidae	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lathridiidae	0.019	0.008	0.027	0.013	0.008	0.000	0.021	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Lucanidae	0.000	0.004	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Melandryidae	0.000	0.000	0.005	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Meloidae	0.004	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Melyridae	0.004	0.016	0.021	0.013	0.015	0.033	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mordellidae	0.023	0.040	0.016	0.032	0.030	0.098	0.021	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Phalacridae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pselaphidae	0.000	0.004	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ptiliidae	0.004	0.000	0.000	0.013	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Salpingidae	0.004	0.000	0.005	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scolytidae	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scydmaenidae	0.004	0.000	0.000	0.006	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Staphylinidae	0.012	0.012	0.027	0.045	0.030	0.000	0.043	0.000	0.000	0.000	0.333	0.000	0.000	1.000	0.000
Tenebrionidae	0.012	0.004	0.000	0.006	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Throscidae	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
MECOPTERA															
Panorpidae	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TRICHOPTERA	0.008	0.000	0.005	0.026	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
LEPIDOPTERA	0.113	0.167	0.075	0.192	0.114	0.213	0.362	0.200	0.250	0.286	0.000	0.000	0.000	0.000	0.000
Geometridae	0.058	0.135	0.043	0.160	0.083	0.197	0.277	0.150	0.125	0.143	0.000	0.000	0.000	0.000	0.000
Erannis tiliaria	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Neoalcis californiaria	0.000	0.004	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pero mizon	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Thallophaga taylorata	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Hesperiidae															
Hesperumia sulphurana	0.000	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lasiocampidae	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Unknown Microlepidoptera	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lycaenidae															
Habrodais grunus	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Noctuidae	0.004	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Anomogyna sp.	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tortricidae	0.000	0.004	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
DIPTERA	0.638	0.631	0.684	0.731	0.811	0.443	0.596	0.550	0.500	0.714	0.333	0.667	0.000	1.000	1.000
Anthomyzidae	0.004	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Bibionidae	0.000	0.000	0.000	0.006	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cecidomyiidae	0.183	0.187	0.235	0.314	0.174	0.131	0.128	0.200	0.000	0.286	0.000	0.000	0.000	0.000	0.000
Ceratopogonidae	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chironomidae	0.214	0.246	0.257	0.397	0.326	0.066	0.106	0.100	0.125	0.143	0.000	0.333	0.000	0.000	1.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Chloropidae	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Culicidae	0.004	0.000	0.011	0.013	0.008	0.016	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Cyclorrhapha	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Dolichopodidae	0.000	0.000	0.000	0.006	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dixidae	0.000	0.000	0.000	0.000	0.008	0.016	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Drosophilidae	0.004	0.004	0.000	0.006	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Empididae	0.012	0.028	0.032	0.019	0.053	0.000	0.021	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lonchaeidae	0.000	0.000	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Mycetophilidae	0.004	0.008	0.021	0.013	0.023	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Otitidae	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Phoridae	0.027	0.024	0.011	0.019	0.030	0.000	0.043	0.000	0.000	0.000	0.333	0.000	0.000	0.000	1.000
Rhagionidae	0.000	0.000	0.005	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sciaridae	0.346	0.310	0.299	0.269	0.439	0.344	0.277	0.250	0.000	0.571	0.333	0.333	0.000	1.000	0.000
Simuliidae	0.000	0.000	0.005	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000
Tabanidae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Therevidae	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Tipulidae	0.016	0.004	0.021	0.006	0.008	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
SIPHONAPTERA	0.000	0.004	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HYMENOPTERA	0.482	0.472	0.471	0.462	0.848	0.164	0.426	0.300	0.625	0.143	1.000	0.667	1.000	0.000	0.000
Apocrita	0.004	0.004	0.005	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ceraphronidae	0.004	0.008	0.000	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Chalcidoidea	0.117	0.214	0.166	0.269	0.152	0.049	0.043	0.100	0.000	0.000	0.000	0.333	0.000	0.000	0.000
Encyrtidae	0.012	0.004	0.000	0.006	0.015	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Eulophidae	0.012	0.012	0.011	0.026	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000
Eupelmidae	0.000	0.000	0.005	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pteromalidae	0.023	0.091	0.027	0.083	0.015	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Torymidae	0.000	0.000	0.005	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Cynipidae	0.004	0.012	0.000	0.006	0.008	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Diapriidae	0.019	0.012	0.048	0.013	0.008	0.000	0.021	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.000
Diprionidae	0.004	0.008	0.000	0.032	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Formicidae	0.296	0.194	0.283	0.103	0.705	0.082	0.319	0.000	0.250	0.000	0.667	0.333	0.000	0.000	0.000
unknown ant egg	0.000	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Formicinae	0.140	0.107	0.150	0.090	0.553	0.049	0.213	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000
Myrmicinae	0.156	0.087	0.118	0.013	0.303	0.049	0.128	0.000	0.125	0.000	0.667	0.000	0.000	0.000	0.000
Ichneumonidae	0.086	0.067	0.075	0.090	0.038	0.016	0.064	0.050	0.000	0.143	0.333	0.000	1.000	0.000	0.000
Braconidae	0.043	0.036	0.027	0.045	0.023	0.000	0.043	0.000	0.000	0.000	0.333	0.000	1.000	0.000	0.000
Mymaridae	0.000	0.008	0.005	0.000	0.008	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Platygasteridae	0.004	0.012	0.005	0.013	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Proctotrupidae	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scelionidae	0.019	0.016	0.016	0.026	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000
Tenthredinidae	0.023	0.024	0.037	0.019	0.477	0.000	0.000	0.200	0.375	0.000	0.000	0.000	0.000	0.000	0.000
Tiphiidae	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Trichogrammatidae	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Xyelidae	0.000	0.000	0.005	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
COLLEMBOLA	0.739	0.460	0.818	0.679	0.765	0.393	0.511	0.650	0.500	1.000	1.000	1.000	0.000	0.000	1.000
Entomobryidae	0.661	0.353	0.690	0.628	0.712	0.328	0.149	0.450	0.500	0.143	0.000	0.000	0.000	0.000	0.000
Isotomidae	0.054	0.040	0.139	0.019	0.023	0.049	0.255	0.000	0.000	0.857	1.000	0.333	0.000	0.000	1.000
Sminthuridae	0.389	0.175	0.348	0.269	0.348	0.131	0.128	0.450	0.000	1.000	0.333	1.000	0.000	0.000	1.000
DIPLOPODA	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PSELAPHOGNATHA															
Polyxenidae	0.265	0.048	0.316	0.122	0.045	0.016	0.085	0.000	0.125	0.429	0.000	0.000	0.000	0.000	0.000
SPIROBOLIDA	0.016	0.004	0.048	0.026	0.000	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CHILOPODA															

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
LITHOBIOMORPHA	0.004	0.004	0.000	0.000	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Henicopidae	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PAUROPODA	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ARACHNIDA															
OPILIONES															
Phalangidae	0.082	0.032	0.150	0.192	0.098	0.016	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
ARANEIDA	0.949	0.825	0.941	0.987	0.947	0.852	0.766	0.950	1.000	0.857	1.000	0.333	1.000	1.000	1.000
Agelenidae	0.012	0.000	0.005	0.019	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Amaurabiidae	0.008	0.000	0.005	0.006	0.000	0.000	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Anyphaenidae															
Anyphaena sp.	0.086	0.075	0.053	0.147	0.098	0.148	0.043	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Araneidae	0.319	0.345	0.422	0.705	0.424	0.393	0.426	0.500	0.625	0.286	0.000	0.000	0.000	0.000	1.000
Araniella displicata	0.008	0.032	0.005	0.064	0.038	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Araneus sp.	0.039	0.036	0.118	0.115	0.076	0.049	0.128	0.300	0.500	0.000	0.000	0.000	0.000	0.000	0.000
Araneus gemmoides	0.016	0.024	0.005	0.032	0.030	0.049	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Cyclosa conica	0.012	0.016	0.021	0.051	0.008	0.016	0.000	0.050	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nuctenea sp.	0.012	0.000	0.043	0.058	0.030	0.033	0.149	0.050	0.250	0.000	0.000	0.000	0.000	0.000	0.000
Nuctenea patagiata	0.187	0.254	0.219	0.500	0.197	0.180	0.106	0.100	0.000	0.143	0.000	0.000	0.000	0.000	1.000
Archaeidae	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Clubionidae	0.183	0.135	0.198	0.231	0.356	0.115	0.106	0.050	0.375	0.429	0.000	0.333	0.000	0.000	0.000
Clubiona canadensis	0.152	0.103	0.144	0.224	0.326	0.098	0.106	0.050	0.000	0.286	0.000	0.000	0.000	0.000	0.000
Dictynidae	0.047	0.036	0.032	0.128	0.053	0.033	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dictyna sp.	0.047	0.036	0.027	0.128	0.053	0.033	0.000	0.200	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dirksia sp.	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Linyphiidae	0.751	0.389	0.679	0.776	0.697	0.475	0.277	0.300	0.500	0.714	1.000	0.333	0.000	0.000	1.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Micryphantinae	0.323	0.095	0.230	0.199	0.182	0.049	0.085	0.000	0.000	0.429	1.000	0.000	0.000	0.000	1.000
Neriene sp.	0.148	0.020	0.080	0.051	0.053	0.000	0.000	0.100	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Pityohyphantes rubro	0.027	0.020	0.016	0.058	0.015	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Pityohyphantes brachygynos	0.008	0.016	0.005	0.096	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Pityohyphantes sp.	0.086	0.032	0.086	0.314	0.076	0.082	0.043	0.100	0.125	0.143	0.000	0.000	0.000	0.000	0.000
Prolinyphia sp.	0.074	0.052	0.080	0.103	0.053	0.098	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.000
Spirembolus mundus	0.132	0.036	0.118	0.026	0.144	0.049	0.000	0.000	0.375	0.000	0.000	0.000	0.000	0.000	0.000
Philodromidae	0.093	0.159	0.193	0.109	0.273	0.082	0.128	0.050	0.000	0.286	0.333	0.000	1.000	1.000	1.000
Philodromus spectabilis	0.019	0.012	0.080	0.032	0.030	0.016	0.064	0.000	0.000	0.000	0.000	0.000	1.000	0.000	1.000
Philodromus sp.	0.019	0.012	0.011	0.026	0.008	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Philodromus rufus	0.027	0.087	0.075	0.045	0.182	0.049	0.064	0.050	0.000	0.143	0.333	0.000	0.000	1.000	1.000
Salticidae	0.105	0.071	0.118	0.103	0.038	0.082	0.106	0.000	0.375	0.143	0.333	0.000	0.000	0.000	1.000
Tetragnathidae	0.000	0.008	0.000	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Theridiidae	0.716	0.381	0.545	0.481	0.591	0.508	0.447	0.600	0.125	0.857	1.000	0.000	0.000	1.000	0.000
Achaearanea sp.	0.023	0.000	0.021	0.006	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Dipoena sp.	0.008	0.000	0.011	0.006	0.023	0.016	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Enoplogantha ovata	0.008	0.008	0.048	0.000	0.023	0.000	0.043	0.050	0.000	0.000	1.000	0.000	0.000	0.000	0.000
Theridion aurantium	0.019	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Theridion californicum	0.074	0.020	0.021	0.006	0.023	0.016	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000
Theridion differens	0.078	0.000	0.021	0.045	0.015	0.016	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Theridion lawrencei	0.019	0.020	0.011	0.051	0.023	0.066	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

	GASH (257)	ACCI (252)	POMU (187)	TSHE (156)	PTAQ (132)	HODI (61)	COCO (47)	RUSP (20)	PSME (8)	BENE (7)	SYMPH (3)	VAPA (3)	CONU (1)	OECE (1)	RUPA (1)
Theridion murarium	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Theridion sexpunctatum	0.160	0.056	0.166	0.090	0.136	0.033	0.064	0.250	0.000	0.571	0.000	0.000	0.000	0.000	0.000
Theridion sp.	0.424	0.206	0.230	0.212	0.212	0.230	0.085	0.150	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Thomisidae	0.051	0.036	0.059	0.032	0.136	0.066	0.043	0.000	0.375	0.143	0.667	0.333	0.000	0.000	0.000
Misumena sp.	0.004	0.020	0.032	0.019	0.045	0.016	0.021	0.000	0.250	0.000	0.667	0.000	0.000	0.000	0.000
Xysticus sp.	0.031	0.000	0.021	0.013	0.045	0.033	0.021	0.000	0.125	0.000	0.000	0.000	0.000	0.000	0.000
Uloboridae															
Hyptiotes gertshci	0.012	0.008	0.059	0.186	0.030	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ACARI															
ACARINA	0.268	0.163	0.401	0.256	0.318	0.049	0.064	0.300	0.000	0.286	0.000	0.000	0.000	0.000	0.000
ORABATIDA	0.074	0.032	0.091	0.032	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CHELONETHIDA	0.004	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MOLLUSCA	0.043	0.008	0.032	0.006	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SLUG	0.004	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SNAIL	0.039	0.004	0.032	0.006	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
no arthropods in sample	0.000	0.004	0.000	0.000	0.000	0.016	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000