

## 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 (*Pseudotsuga 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  $\geq 250$  m from any other station and  $\geq 100$  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  $\frac{1}{2}$  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.

$$\text{Manly's Alpha} = \frac{r_i}{\sum_{i=1}^m r}$$

*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  $\geq 1\%$  cover; shrub species with  $< 1\%$  cover were included if they were used for foraging  $\geq 1$  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  $\geq 1$  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 &gt;3 m above forest floor by bird species and vegetation type, Oregon Coast Range, 1999.

Foraging Height Class	Plant Species	Number of Observations by Bird 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 (%)	<b>2 (50)</b>	<b>1 (50)</b>	<b>7</b>	<b>18 (45)</b>
	<i>Prunus</i> 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 ( <i>Alnus rubra</i> )	0	0	0	3
Oregon White Oak ( <i>Quercus garryanna</i> )	0	0	0	1	
Hardwood Total (%)	<b>2 (50)</b>	<b>1 (50)</b>	<b>6</b>	<b>22 (55)</b>	
<b>3-10 m Height Class Total</b>		<b>4</b>	<b>2</b>	<b>13</b>	<b>40</b>
>10 m	Pacific Yew	0	0	0	0
	Douglas-Fir	4	2	3	14
	Grand Fir	0	0	0	0
	Conifer Total (%)	<b>4 (100)</b>	<b>2 (67)</b>	<b>3</b>	<b>14 (67)</b>
	<i>Prunus</i> 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 (%)	<b>0 (0)</b>	<b>1 (33)</b>	<b>0</b>	<b>7 (33)</b>	
<b>&gt;10 m Height Class Total</b>		<b>4</b>	<b>3</b>	<b>3</b>	<b>21</b>

### 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 ( $\leq 3$  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").

Plant Species	Wilson's Warbler		MacGillivray's Warbler		Orange-crowned Warbler	
	# Obs. (%)	Sel. Index	# Obs. (%)	Sel. Index	# Obs. (%)	Sel. Index
<b>Conifers</b>						
Douglas-fir	11 (6.0)	<b>0.22</b>	9 (15.0)	<b>0.21</b>	5 (13.5)	<b>0.04</b>
Grand fir	4 (2.2)	<b>0.15</b>	2 (3.3)	<b>0.47</b>	0 (0.0)	-0.05
Pacific yew	3 (1.6)	<b>0.21</b>	0 (0.0)	nc	0 (0.0)	nc
West. Hemlock ( <i>Tsuga heterophylla</i> )	0 (0.0)	-0.05	1 (1.7)	-0.06	0 (0.0)	-0.05
<b>Deciduous</b>						
Bigleaf maple	18 (9.8)	<b>0.03</b>	2 (3.3)	<b>0.02</b>	5 (13.5)	<b>0.03</b>
Bitter cherry	3 (1.6)	<b>0.12</b>	1 (1.7)	-0.04	1 (2.7)	<b>0.07</b>
Cascara	1 (0.6)	<b>0.09</b>	0 (0.0)	-0.05	2 (5.4)	<b>0.11</b>
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)	<b>0.17</b>
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.

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

Table 3.4. Comparison of mean (90% CI) understory cover ( $\leq 3$  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  $\leq 3$  m above the ground.

	% Cover (90% CI)	
	Occupied (n=5)	Not Occupied (n=5)
<b>a. Wilson's Warbler</b>		
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>b. MacGillivray's Warbler</b>		
	(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
<b>c. Orange-crowned Warbler</b>		
	(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 <sup>1</sup>	# 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 <sup>1</sup>	# 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 <sup>1</sup>	# 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		

<sup>1</sup> 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.