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 3 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.

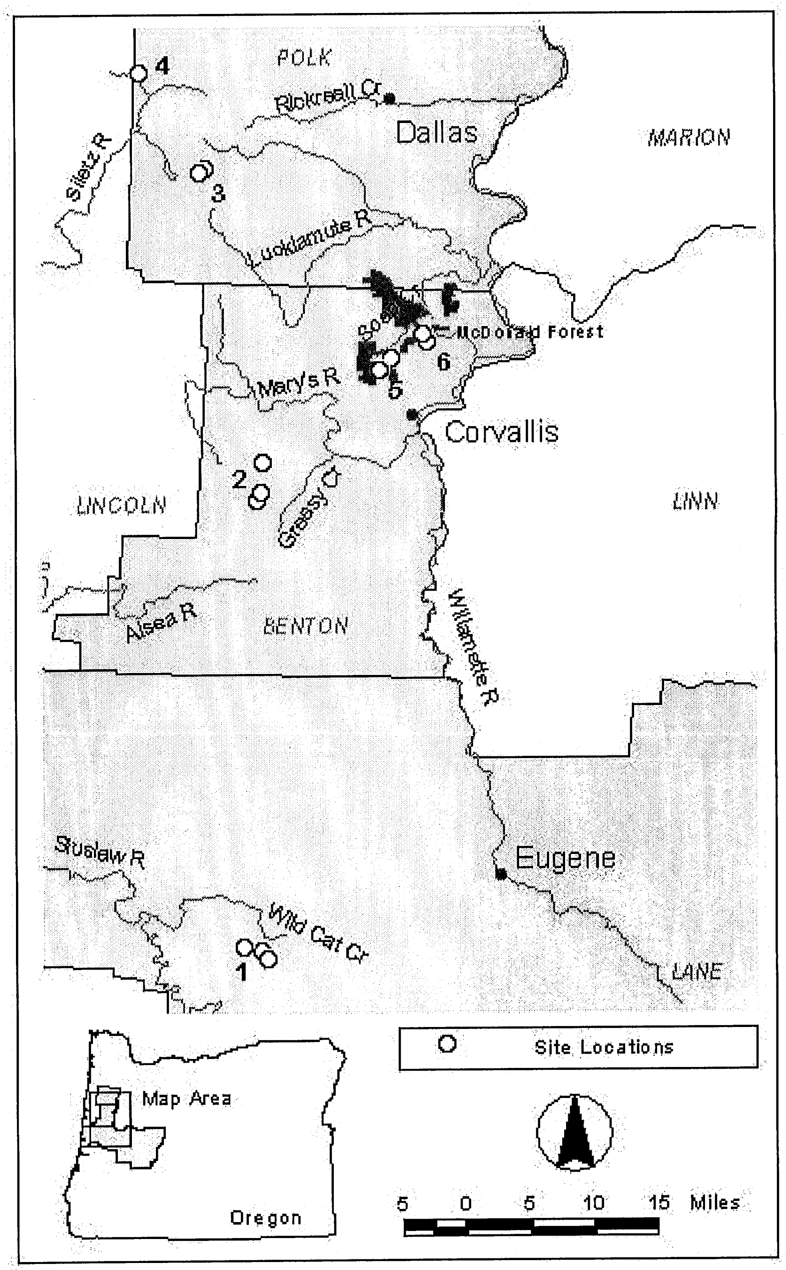


Table 2.1. Description of study stands.

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 ≥250 m from any other station and ≥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*)

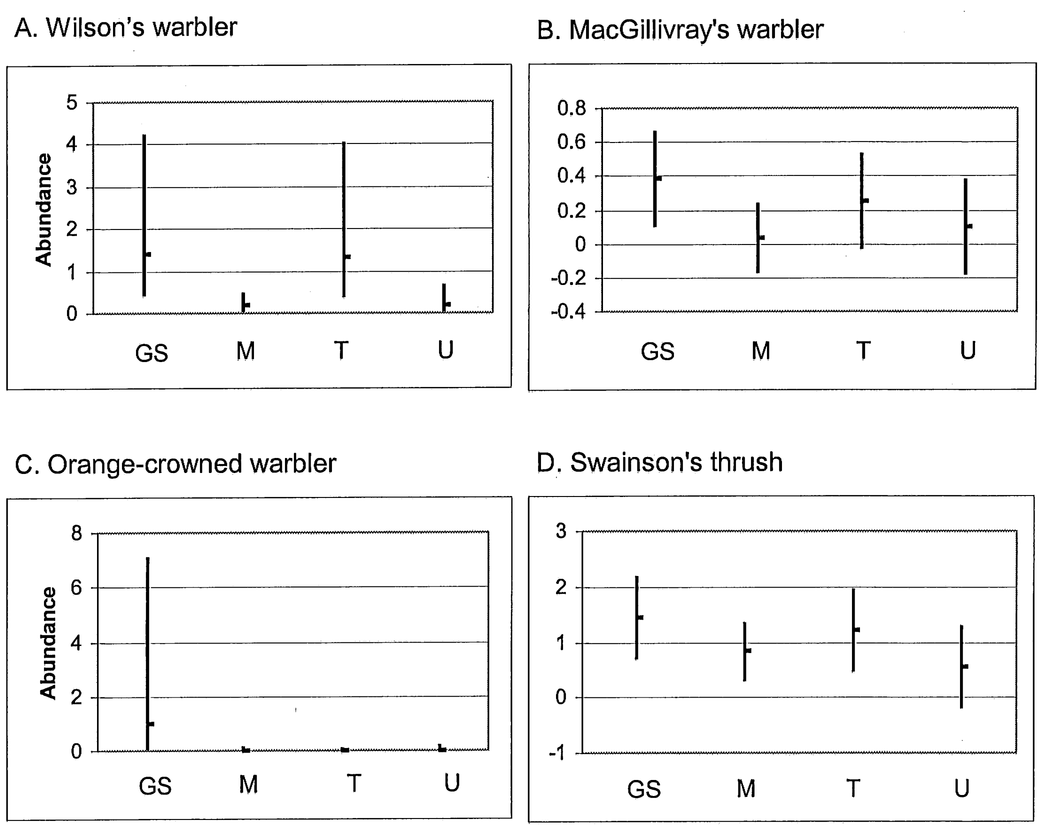
Deciduous Trees and Tall Shrubs
- Vine maple (*Acer circinatum*)
- Bigleaf maple (*Acer macrophyllum*)
- Red alder (*Alnus rubra*)
- California hazel (*Corylus cornuta*)
- Dogwood (*Cornus nuttalli*)
- Oceanspray (*Holodiscus discolor*)
- Indian plum (*Oemleria cerasiformis*)
- Bitter Cherry (*Prunus 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.



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.

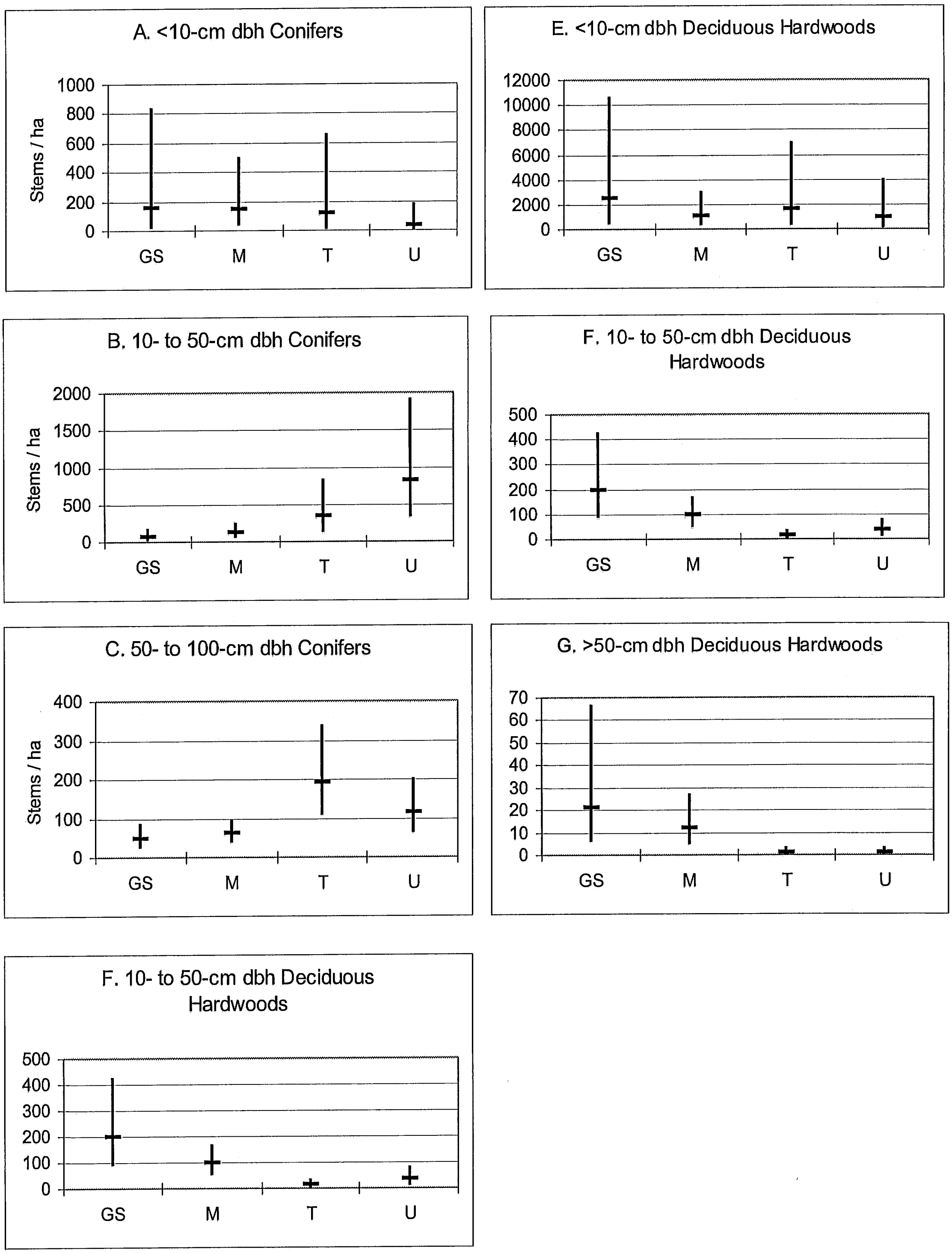


Figure 2.4. Median cover with 90% confidence intervals for understory vegetation (within 3 m of forest floor) in four silvicultural conditions (GS: group selection, M: mature, T: young thinned, and U: young unthinned) in the Oregon Coast Range, 1999.

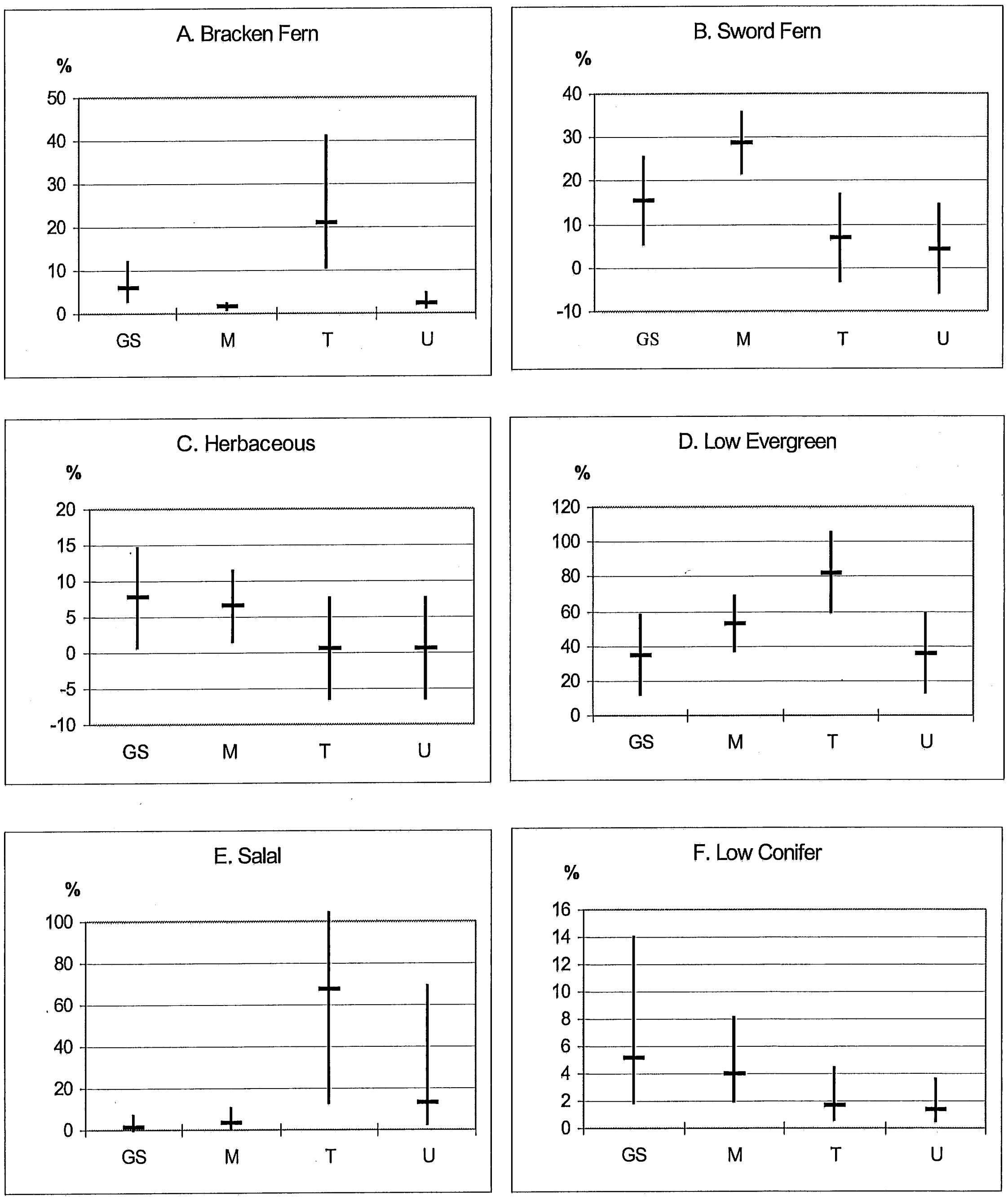
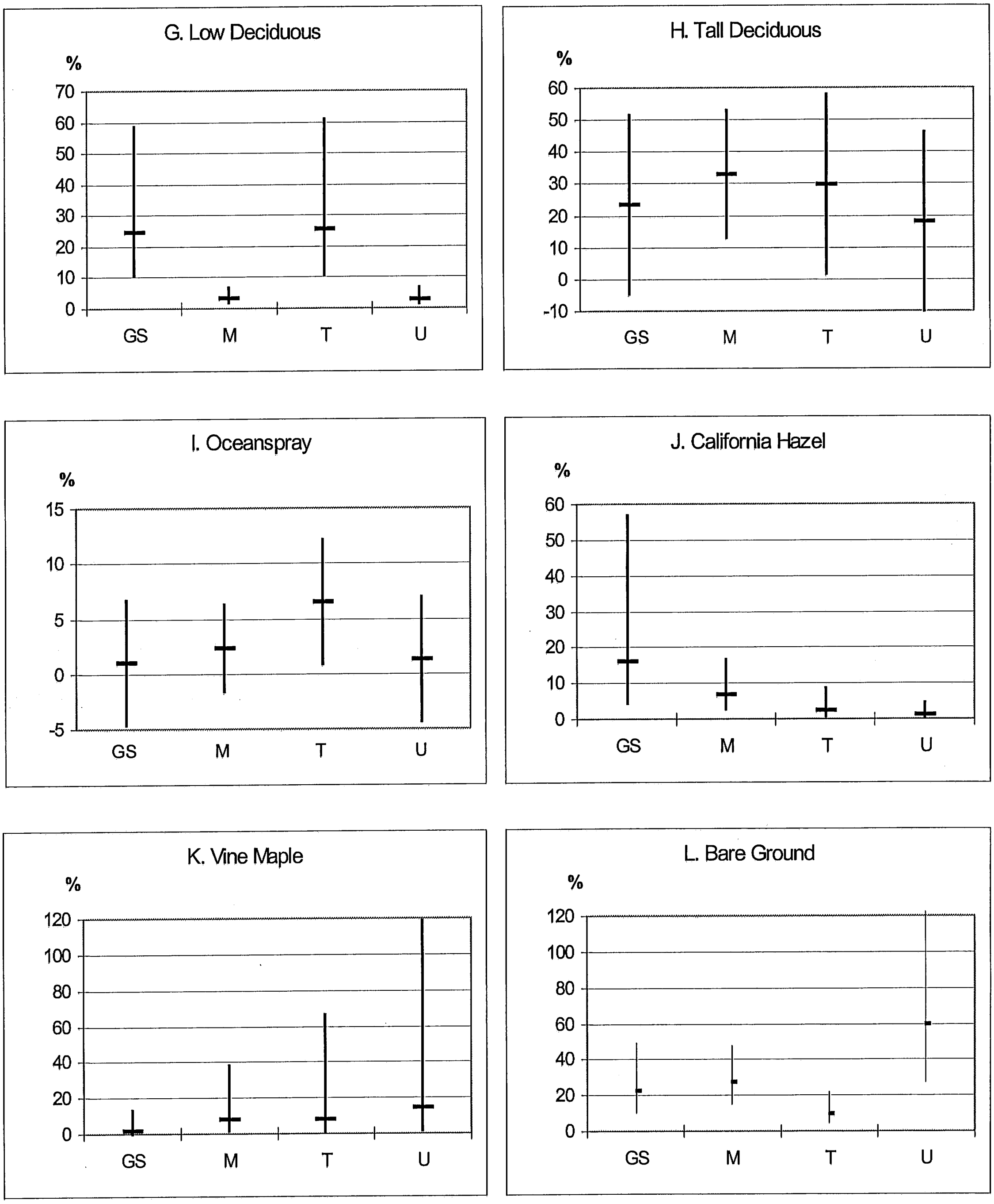


Figure 2.4. Continued.



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.