

RESPONSE OF BIRDS TO THINNING YOUNG DOUGLAS-FIR FORESTS

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Abstract. Silvicultural practices, such as thinning, are increasingly performed both for commodity production and to help achieve biodiversity goals and promote ecological restoration. However, relatively little research has examined effects of thinning conifer forests on vertebrates. We experimentally manipulated stands using a randomized block design to evaluate influences of two thinning intensities on populations of diurnal breeding birds in western Oregon. We conducted point counts of birds seven times each year in 1994 (prior to treatment) and from 1995 through 2000 (subsequent to treatment). We analyzed data using multiple linear regression and information-theoretic approaches to model selection. Of the 22 species for which we had sufficient data for analysis, detections of nine species decreased and eight species increased in thinned stands relative to controls, and there was no strong evidence that thinning influenced numbers of five species. Of the 17 species that responded to thinning, the magnitude of response of eight species varied with thinning intensity; for each of these species, response was greatest in the more heavily thinned stands. Although no species was extirpated from stands following thinning, detections of Hutton's Vireos (*Vireo huttoni*), Golden-crowned Kinglets (*Regulus satrapa*), Brown Creepers (*Certhia americana*), Black-throated Gray Warblers (*Dendroica nigrescens*), and Varied Thrushes (*Ixoreus naevius*) decreased to less than half of the detections in controls in one or more treatment types, suggesting thinning significantly reduces their numbers. In contrast, American Robins (*Turdus migratorius*), Townsend's Solitaires (*Myadestes townsendi*), and Hammond's Flycatchers (*Empidonax hammondi*) were rare or absent in controls but regularly present in thinned stands, and detections of Western Tanagers (*Piranga ludoviciana*), Evening Grosbeaks (*Coccothraustes vespertinus*), and Hairy Woodpeckers (*Picoides villosus*) increased by threefold or more in thinned stands relative to controls. Only Pacific-slope Flycatchers (*Empidonax difficilis*), Warbling Vireos (*Vireo gilvus*), and Western Tanagers showed strong evidence of temporal trends in response. For these species, differences between numbers in controls and treated stands became more extreme through time. Our findings suggest that thinning densely stocked conifer stands in landscapes dominated by younger stands enhances habitat suitability for several species of birds, but that some unthinned patches and stands should be retained to provide refugia for species that are impacted by thinning.

Key words: birds; Douglas-fir; forest management; habitat; information theory; silviculture; thinning.

INTRODUCTION

As a result of decades of even-aged forest management practices, a large proportion of Douglas-fir forests in western North America are in early stages of forest development (from 20 to 50 years old). Frequently, these stands are structurally simple, and consist of a single canopy layer with one or two species of trees in the overstory and a relatively sparse understory (Hayes et al. 1997). Diversity and structural complexity of vegetative communities have been shown to influence the number and diversity of niches for birds and other species (MacArthur and MacArthur 1961, MacArthur et al. 1966, Willson 1974, Roth 1976, Whelan 2001). The lack of structural complexity typically found in young conifer plantations may limit niche diversity for birds.

Thinning forest stands produces cascading ecological effects by reducing competition among overstory trees and increasing penetration of solar radiation to the forest floor, thereby increasing the growth, size, branch diameter, and crown ratio of remaining overstory trees (Long et al. 1983, Maguire et al. 1991, Marshall et al. 1992, Barbour et al. 1997), and stimulating development of understory vegetation (Tappeiner and Zasada 1993, Messier and Mitchell 1994, Bailey and Tappeiner 1998). As a consequence, thinning, used in conjunction with other practices, may increase structural complexity and improve habitat for several species of vertebrates (McComb et al. 1993, Carey and Curtis 1996, Hayes et al. 1997). In addition, as existing old-growth conifer forests may have developed under lower densities than is typical of contemporary plantations (Tappeiner et al. 1997), thinning may be a tool for ecological restoration in some circumstances. Thinning frequently is used to increase production of wood fiber, and economic benefit is a

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TABLE 1. Pretreatment stand conditions. Values represent means for the four replicates followed by 95% confidence intervals in parentheses.

Characteristic	Control	Moderately thinned stands	Heavily thinned stands
Trees/ha	559 (462–656)	591 (522–660)	574 (452–696)
Basal area (m ² /ha)	41.1 (38.1–44.1)	41.6 (36.4–46.7)	43.7 (39.0–48.5)
Diameter breast height (cm)	31.1 (28.6–33.7)	29.9 (27.4–32.4)	31.6 (29.9–33.3)
Relative density	0.56 (0.50–0.62)	0.57 (0.48–0.65)	0.59 (0.52–0.67)
Percent cover			
Herbs	33.2 (17.0–64.6)	35.7 (18.3–69.5)	38.2 (19.6–74.4)
Slash	9.6 (6.9–13.5)	14.9 (10.6–20.8)	7.3 (5.2–10.2)
Low shrubs	25.6 (12.8–51.2)	11.0 (5.5–21.9)	16.4 (8.2–32.8)
Tall shrubs	18.3 (8.5–39.3)	15.5 (7.2–33.4)	14.9 (6.9–32.0)
Canopy	97.4 (95.8–98.6)	97.7 (96.2–98.8)	97.0 (95.4–98.3)

Note: For additional information on stand conditions and methods used to measure stand characteristics, see Suzuki (2001) and Suzuki and Hayes (2003).

primary motivation for thinning on some lands. Because of the potential ecological and economic benefits, managers plan to thin a large proportion of forested lands in some areas within the next 2–3 decades, and thinning is a cornerstone of some forest management strategies (e.g., Bordelon et al. 2000).

Several studies have examined the influences of forest practices, including clearcutting and partial timber harvest (e.g., Dellasala et al. 1996, Chambers and McComb 1997, Beese and Bryant 1999, Chambers et al. 1999, Lance and Phinney 2001), riparian buffer strips (e.g., Hagar 1999, Pearson and Manuwal 2001), and vegetation management (e.g., Morrison and Meslow 1984, Easton and Martin 1998), on birds in western coniferous forests of North America. However, despite widespread current and future use of thinning in western coniferous forests, understanding of many aspects of the ecological influences of thinning on birds remains poorly developed. To our knowledge, Hagar et al. (1996) published the only account of the influence of commercial thinning on birds in western coniferous forests. In a comparison of unthinned stands to stands thinned 5–15 yr previously, Hagar et al. (1996) found that differences in abundance of birds varied among species, and that most of the apparent influences of thinning were consistent with what is known about the natural history of individual species. Because the work of Hagar et al. (1996) was observational, it is not possible to infer causality from their findings, and apparent relationships between thinning and bird abundance could be related to some confounding factor. However, the study of Hagar et al. (1996) provides an initial framework for our understanding of the responses of birds to thinning, and suggests a number of hypotheses that can be evaluated through experimental manipulations of stands.

We present the results of a 7-yr experimental study evaluating the response of breeding birds to thinning in the northern Oregon Coast Range. Our objectives were to determine if abundance of breeding birds is influenced by thinning, if effects vary in time during

the first six years following thinning, and if influences vary with thinning intensity. We used information-theoretic approaches (Burnham and Anderson 1998) to simultaneously evaluate multiple a priori hypotheses concerning the response of birds to thinning treatments. We assessed the strength of evidence of models representing differing responses to thinning intensity and differing temporal trends.

STUDY AREA

Our study was conducted in the northern Oregon Coast Range in an area known as the “Tillamook Burn.” The area experienced a series of intense fires between 1933 and 1951 covering roughly 140 000 ha (Wells 1999). Most of the area was salvage logged following the fires, and many snags were cut and removed or left on the forest floor to reduce risk of future fires. The area was largely replanted or seeded with Douglas-fir (*Pseudotsuga menziesii*) between 1949 and 1970. The current forest is comprised of even-aged stands dominated by Douglas-fir and red alder (*Alnus rubra*). Western hemlock (*Tsuga heterophylla*), noble fir (*Abies procera*), and western redcedar (*Thuja plicata*) are present, but not common. Common species in the understory include vine maple (*Acer circinatum*), huckleberry (*Vaccinium* spp.), salal (*Gaultheria shallon*), and Oregon-grape (*Berberis nervosa*). The area consists of large tracts of contiguous young forest, thus minimizing potential confounding influences of fragmentation on stand-level responses.

We selected four replicate areas for study. Each area initially consisted of three 26–40-ha stands of 35–45-yr-old unthinned forest. Tree densities before implementation of treatments ranged from 410 to 710 trees/ha. Replicates were selected that minimized differences among stands within a replicate with respect to density of trees, age of stands, and proportion of hardwoods (Table 1). Stands within a replicate were within 500 m of one another, with the exception of one replicate in which one stand was ~1.5 km from the others. Replicates were separated by at least 5 km.

METHODS

Treatments

We randomly assigned each stand within a replicate to one of three treatments: no thinning (control), moderate thinning (thinning to a relative density of 35, or ~240–320 trees/ha), or heavy thinning (relative density of 20, or ~180–220 trees/ha). Relative density is a measure of the number of trees present expressed as a percentage of the theoretical maximum number of trees of the same size that an area could support (Long et al. 1983); relative density is a useful measure of tree density for ecological studies because it corresponds to the availability of solar radiation and other resources used by trees in a stand and the amount available for other species. Stands were thinned “from below” (Smith 1986), removing the smaller suppressed and subdominant trees and leaving the larger codominant and dominant trees. Stands were logged in autumn of 1994 and spring of 1995 using partial suspension cable logging, tractor logging using rubber-tired tractors and skidders, or feller bunchers, depending on slope and access. The moderate thinning treatment was designed to emulate operational commercial thinning that is typically used in the area to achieve wood fiber production goals. The heavy thinning treatment was designed to increase size of canopy openings, accelerate growth of overstory trees, stimulate understory development, and enhance structural complexity of the stands (Hayes et al. 1997). Detailed description of some of the initial changes in vegetation and stand structure to thinning on these study sites is provided in Suzuki and Hayes (2003).

Point counts

We established five point-count stations in each stand. Each station was at least 160 m from all other stations to minimize the chance of double counting individual birds, 50 m from perennial streams to minimize effects of stream noise on our ability to detect birds, and 100 m from stand boundaries. To increase our ability to detect birds at each station, we adjusted locations based on topography. For example, we generally placed stations on ridges rather than just below ridges so that birds on either side of the ridge could be detected.

We visited each point seven times between 10 May and 30 June prior to treatment (1994) and during each of the six years immediately subsequent to treatment (1995–2000). Point counts were conducted between 15 min before and 4 h after sunrise. We conducted bird surveys in all stands within a replicate on the same day or on consecutive days, and did not resurvey a stand within 2 d of a prior survey. After arrival at a point-count station, observers waited quietly for 2 min to minimize influences of any disturbances created while walking to the station. Observers then recorded all birds seen or heard within 80 m of the point-count

station during the following 8 min. To minimize observer bias, schedules of observers were rotated such that each block received roughly the same number of visits from each observer. To minimize temporal bias, the order of sampling among stands and among points within a stand within a replicate was varied.

Data analysis

We conducted statistical analysis on all species of birds that were recorded at least once in each replicate and that were present in at least 70% of the possible year \times replicate combinations. We used the total number of detections over all visits to a stand in a given year as our response variable in all analyses.

Prior to analysis of the effects of thinning, we analyzed the 1994 data to determine if there was any inadvertent bias in the random assignment of treatments to stands that would be expressed as pre-treatment differences in numbers of birds. These data were analyzed as a completely randomized block design with four blocks and three treatments. The hypothesis that the number of detections per visit was equal among treatments was not rejected at $\alpha = 0.05$ level for any species meeting the sample size criteria provided earlier in this section. We interpreted this to indicate a lack of evidence that pre-treatment populations of birds among stands within blocks differed substantially, and thus we could assume that any differences detected subsequent to treatment were the result of treatment. Further analyses focus on comparisons among control and experimentally thinned plots using data collected from 1995 through 2000.

We constructed a set of conceptual models to describe the response of birds to thinning defined in terms of mean treatment differences across years for the post-treatment years, and whether those treatment differences were consistent throughout the post-thinning years. Our models are based on four possible scenarios for mean treatment differences: (1) abundances in controls, moderately thinned stands, and heavily thinned stands were the same (the null model; $C = M = H$); (2) abundances in controls and moderately thinned stands were the same but differed from that in heavily thinned stands ($(C = M) \neq H$); (3) abundances in moderately and heavily thinned stands were the same but differed from that in control stands ($C \neq (M = H)$); and (4) abundances in controls, moderately thinned stands, and heavily thinned stands differed from one another ($C \neq M \neq H$). We did not consider models in which abundances in controls and heavily thinned stands were the same but differed from that in moderately thinned stands ($(C = H) \neq M$). We believe that this response was highly unlikely given the inherent ordering of the treatments and, at these thinning densities, any apparent response of this type would likely be spurious (Anderson et al. 2001).

We then added linear temporal trends to the models to generate our final set of models for analysis. Al-

TABLE 2. Models analyzed and prior probabilities for all species of birds except Hammond's Flycatcher and Townsend's Solitaire.

Model	Treatment effect	Linear temporal effect	Prior probability based on model redundancy
1	$C = M = H$	$C = M = H$	1/4
2	$(C = M) \neq H$	$C = M = H$	1/8
3	$(C = M) \neq H$	$(C = M) \neq H$	1/8
4	$C \neq (M = H)$	$C = M = H$	1/8
5	$C \neq (M = H)$	$C \neq (M = H)$	1/8
6	$C \neq M \neq H$	$C = M = H$	1/16
7	$C \neq M \neq H$	$(C = M) \neq H$	1/16
8	$C \neq M \neq H$	$C \neq (M = H)$	1/16
9	$C \neq M \neq H$	$C \neq M \neq H$	1/16

Note: The prior probabilities for models considered for Hammond's Flycatcher and the Townsend's Solitaire were 1/2 for the null model ($M = H$ for both treatment effect and temporal effect), and 1/4 for each of the other two models ($M \neq H$ for treatment effect and $M = H$ for temporal effect; $M \neq H$ for treatment effect and $M \neq H$ for temporal effect).

though nonlinear temporal trends are conceivable, we restricted our models to linear temporal trends because (1) we believe the potential for nonlinear patterns over the course of the six years of post-treatment study are relatively small, (2) if such patterns exist they would need to be extremely large to be detected given our few years of remeasurement, and (3) the number of potential models including linear and nonlinear trends is very large, exceeding our potential to meaningfully evaluate them using our data. We restricted our final set of potential models to the nine models that we believe to represent ecologically meaningful a priori hypotheses (Table 2). We did not allow models that indicated differing temporal effects for treatments with equal treatment effects. These models would imply that the relative effect of a particular treatment would be reversed over the short period of study; we believe these models to be highly implausible models of reality given the duration and experimental design of our study.

We then constructed and fit a set of quantitative models representing these conceptual models. All quantitative models included terms for categorical effects of blocks and years. Since our response variable (total number of detections per stand per year) was based on count data, before fitting the models we first assessed the data for adequacy of the assumption that these data were generated from a Poisson process. We assessed residuals of the full model ($C \neq M \neq H$ for mean treatment effect and for temporal trend) for outliers and influential points and estimated the overdispersion parameter as the scaled Pearson's χ^2 . We modeled the data as Poisson if the scale parameter (the square root of the overdispersion parameter) was < 1.2 , and as overdispersed Poisson if the scale parameter was between 1.2 and 2.0. A scale parameter ≥ 2 was interpreted as evidence that a Poisson model was inappropriate, in which case the normal and lognormal distributions were assessed. Normality and constancy of the residuals were used to determine which of these two dis-

tributions was the more appropriate. The lognormal distribution was most appropriate for the Hammond's Flycatcher (Latin names for birds are provided in the Appendix) and the Poisson distribution was most appropriate for the Hermit Warbler. All other species were modeled as overdispersed Poisson.

Hammond's Flycatcher and Townsend's Solitaires were rarely or never detected in control stands, thus there was little or no variability among control stands and it was not possible to fit data for these species using the standard set of models used for other species. Consequently, for these species our best estimate of the total number of birds over all visits in control stands was zero with no variance associated with that estimate. Thus, hypotheses that we could statistically evaluate were restricted to comparisons between thinning levels. Our models were: (1) abundance in moderately thinned stands was the same as that in heavily thinned stands ($M = H$) and this was consistent through time ($M = H$); (2) abundance in moderately thinned stands was different than that in heavily thinned stands ($M \neq H$) and this difference was consistent through time ($M = H$); and (3) abundance in moderately thinned stands was different than that in heavily thinned stands ($M \neq H$) and this difference varied through time ($M \neq H$).

As the primary focus of our study was the effect of thinning on numbers of birds, we considered the four basic models describing treatment effects as equally plausible, and thus assigned equal prior probabilities to each. We considered models of temporal variation to be submodels of treatment effects, and gave models of temporal variations equal weight within each set of models of treatment effects (Table 2).

We evaluated the likelihood of each a priori model using an information-theoretic approach as described by Burnham and Anderson (1998). We calculated AIC_c values for models that assumed a lognormal (Hammond's Flycatcher) or Poisson distribution (Hermit Warbler), and $QAIC_c$ values for models based on overdispersed Poisson distributions (all other species).

For each model, we calculated Δ as the difference between AIC_c or $QAIC_c$ of the model under consideration and the lowest AIC_c or $QAIC_c$ value of all models for the species. We calculated the generalized Akaike weight (w_i) of each model, using the unequal prior probabilities described earlier in this section, as an indicator of the strength of evidence in favor of a particular model; w_i ranges from 0 to 1 and models with low w_i values are less plausible than those with higher w_i values (Burnham and Anderson 1998). We also calculated the relative weights as w_0/w_i where w_0 is the generalized Akaike weight of the model with the lowest AIC_c or $QAIC_c$ value, and w_i is the generalized Akaike weight of model i . Relative weight is proportional to the ratio of the likelihood of the model with the lowest AIC_c or $QAIC_c$ relative to the model under consideration (Burnham and Anderson 1998).

We sorted the models by Δ and considered models with $\Delta \leq 2$ to be strongly competing models. We estimated the size of effects of thinning for a species using model averaging techniques outlined by Burnham and Anderson (1998) and made inferences based on the complete set of fitted models. Effects are presented as the estimated number of detections in thinned stands relative to number of detections in control stands expressed as a percentage. We inferred a lack of strong evidence that thinning influences a species when (1) Δ of the null model was ≤ 2 , or (2) the 95% confidence interval of the model averaged parameter estimates of size of effect included 100.

RESULTS

During seven years of observations, we made 19 259 detections of 52 species of birds during 2940 point-count visits (see Appendix). Of these, 18 399 detections were of the 22 species analyzed in this paper; 2193 of these detections were made prior to treatment and 16 206 were made after treated stands were thinned.

Numerical response to thinning

Of the 22 species analyzed, detections of nine species decreased relative to detections in controls following thinning (Table 3). The model representing differences among all treatments ($C \neq M \neq H$) was among the strongly competing models for the Pacific-slope Flycatcher (Fig. 1A), Hutton's Vireo, and Brown Creeper (Table 3), indicating strong evidence that responses of these species varied with intensity of thinning. Numbers of detections of these species decreased in both the moderately thinned and heavily thinned stands, but the decrease was greater in heavily thinned stands than in moderately thinned stands (Table 4). Hermit Warblers, Golden-crowned Kinglets, Swainson's Thrushes, and Black-throated Gray Warblers also decreased in thinned stands, but there was no strong evidence that these species responded to differences in thinning intensity. For each of these species, the model with the lowest AIC_c or $QAIC_c$ value indicated a treatment effect

of $C \neq (M = H)$ (Table 3). Competing models containing $C \neq M \neq H$ occurred for the Hermit Warbler, Golden-crowned Kinglet, and Swainson's Thrush (Table 3), but 95% confidence intervals for estimated magnitudes of effect of moderate and heavy thinning overlapped considerably for each of these species (Table 4), suggesting that evidence that abundance of these species differed in moderately and heavily thinned stands was weak. Steller's Jays and Varied Thrushes appeared to decrease only in heavily thinned stands. The model with the lowest $QAIC_c$ value for each of these species indicated a treatment effect of $(C = M) \neq H$ (Table 3). Strongly competing models contained $C \neq M \neq H$ (Table 3), but the 95% confidence interval for size of effect of moderate thinning overlapped no effect for each of these species (Table 4).

Detections of eight species in thinned stands increased relative to detections in controls following thinning (Table 3). Of these species, responses of Dark-eyed Juncos (Fig. 1B) and Hairy Woodpeckers varied with thinning intensity: all strongly competing models for these species contained $C \neq M \neq H$ for treatment effect (Table 3). Increases in heavily thinned stands were greater than in moderately thinned stands for these two species (Table 4). American Robins, Townsend's Solitaires, Evening Grosbeaks, Western Tanagers, and Hammond's Flycatchers increased in thinned stands, but did not show strong evidence of responding to thinning intensity. For the American Robin, Evening Grosbeak, and Western Tanager, the model with the lowest $QAIC_c$ value indicated a treatment effect of $C \neq (M = H)$ (Table 3). For each of these species, at least one strongly competing model contained $C \neq M \neq H$ (Table 3), but estimated sizes of effects of moderate and heavy thinning were similar and 95% confidence intervals overlapped considerably (Table 4), suggesting very weak support for the hypothesis that thinning intensity influenced numbers of these species. Townsend's Solitaires were never detected in control stands during the post-treatment period, although there were two observations of Townsend's Solitaires during the pre-treatment year (1994) in one of the stands assigned to be moderately thinned. Townsend's Solitaires were detected in moderately and heavily thinned stands each year after treatment, with mean annual number of detections per visit varying from <0.1 to >0.6 in thinned stands. The model for Townsend's Solitaire that had the lowest $QAIC_c$ value contained $M = H$ (Table 3). Hammond's Flycatchers were detected 176 times in thinned stands, but were only detected five times in unthinned forests during the seven years of our study. The model for Hammond's Flycatcher that had the lowest AIC_c value contained $M = H$ (Table 3). Warbling Vireos appeared to respond only to heavy thinning. The only strongly competing model for Warbling Vireos indicated a treatment effect of $(C = M) \neq H$, and this model had a high Akaike weight (0.86; Table 3). The estimated size of effect of moderate thinning for War-

TABLE 3. Strongly competing models (models with $\Delta \leq 2$) and their Δ values, Akaike weights (w), and relative weights.

Species	Treatment	Temporal	Δ	w	Relative weight
Decreased					
Pacific-slope Flycatcher	C \neq M \neq H	C \neq M \neq H	0	0.77	1
	C \neq M \neq H	C = M = H	0	0.35	1
Hutton's Vireo	C \neq M \neq H	C = M \neq H	0.26	0.31	1.14
	C \neq (M = H)	C = M = H	0	0.49	1
Hermit Warbler	C \neq M \neq H	(C = M) \neq H	0.58	0.18	2.67
	C \neq M \neq H	C = M = H	1.97	0.09	5.37
Golden-crowned Kinglet	C \neq M \neq H	C = M = H	0	0.37	1
	C \neq M \neq H	C \neq M \neq H	1.55	0.17	2.17
	C \neq M \neq H	C \neq (M = H)	1.69	0.16	2.32
Steller's Jay	C \neq M \neq H	(C = M) \neq H	1.90	0.14	2.59
	(C = M) \neq H	C = M = H	0	0.52	1
	C \neq M \neq H	C = M = H	0.51	0.20	2.58
Swainson's Thrush	C \neq (M = H)	C = M = H	0	0.32	1
	C \neq (M = H)	C \neq (M = H)	0.48	0.25	1.27
	C \neq M \neq H	C = M = H	1.20	0.09	3.64
	C \neq M \neq H	(C = M) \neq H	1.71	0.07	4.71
Brown Creeper	C \neq M \neq H	C \neq (M = H)	1.77	0.07	4.85
	C \neq M \neq H	C = M = H	0	0.48	1
Black-throated Gray Warbler	C \neq (M = H)	C \neq (M = H)	0	0.45	1
	C \neq (M = H)	C = M = H	0.46	0.36	1.26
Varied Thrush	(C = M) \neq H	C = M = H	0	0.44	1
	C \neq M \neq H	C = M = H	1.08	0.13	3.42
No change					
Chestnut-backed Chickadee	C = M = H	C = M = H	0	0.60	1
	(C = M) \neq H	C = M = H	1.86	0.12	5.1
	(C = M) \neq H	(C = M) \neq H	1.87	0.12	5.1
Winter Wren	C \neq M \neq H	C \neq (M = H)	0	0.21	1
	C \neq M \neq H	C \neq M \neq H	1.01	0.13	1.66
	C \neq (M = H)	C \neq (M = H)	1.16	0.24	0.89
	C \neq M \neq H	(C = M) \neq H	1.41	0.11	2.01
Gray Jay	(C = M) \neq H	(C = M) \neq H	1.86	0.17	1.26
	(C = M) \neq H	C = M = H	0	0.34	1
	C = M = H	C = M = H	1.39	0.34	1
	C \neq M \neq H	C = M = H	1.70	0.07	4.68
Wilson's Warbler	(C = M) \neq H	(C = M) \neq H	1.91	0.13	2.59
	C \neq (M = H)	C \neq (M = H)	0	0.21	1
	C = M = H	C = M = H	0.01	0.43	0.50
	C \neq (M = H)	C = M = H	1.27	0.11	1.89
Red-breasted Nuthatch	(C = M) \neq H	C = M = H	1.44	0.10	2.06
	(C = M) \neq H	(C = M) \neq H	1.94	0.08	2.63
	C \neq (M = H)	C = M = H	0	0.33	1
	C \neq M \neq H	C = (M \neq H)	1.39	0.08	4.00
	C = M = H	C = M = H	1.79	0.27	1.22
Increased					
Dark-eyed Junco	C \neq M \neq H	C = M = H	0	0.54	1
	C \neq M \neq H	C \neq (M = H)	1.76	0.22	2.41
Warbling Vireo	(C = M) \neq H	(C = M) \neq H	0	0.86	1
	C \neq (M = H)	C = M = H	0	0.58	1
American Robin	C \neq M \neq H	C = M = H	1.74	0.12	4.77
	C \neq M \neq H	C = M = H	0	0.44	1
Hairy Woodpecker	C \neq M \neq H	C = M = H	0	0.44	1
	C \neq M \neq H	C \neq (M = H)	1.42	0.22	2.04
	C \neq M \neq H	(C = M) \neq H	1.97	0.17	2.68
Townsend's Solitaire†	C \neq M \neq H	C \neq M \neq H	1.99	0.16	2.71
	M = H	M = H	0	0.99	1
Evening Grosbeak	C \neq (M = H)	C = M = H	0	0.52	1
	C \neq M \neq H	C = M = H	0.54	0.20	2.62
Western Tanager	C \neq (M = H)	C \neq (M = H)	0	0.45	1
	C \neq M \neq H	C \neq (M = H)	0.31	0.19	2.34
	C \neq M \neq H	C \neq M \neq H	1.49	0.11	4.22
	C \neq M \neq H	(C = M) \neq H	1.57	0.10	4.39
Hammond's Flycatcher†	M = H	M = H	0	0.98	1

† Because there were no detections of Townsend's solitaires and few detections of Hammond's flycatchers in control stands, only models comparing responses in moderately thinned stands and heavily thinned stands could be compared.

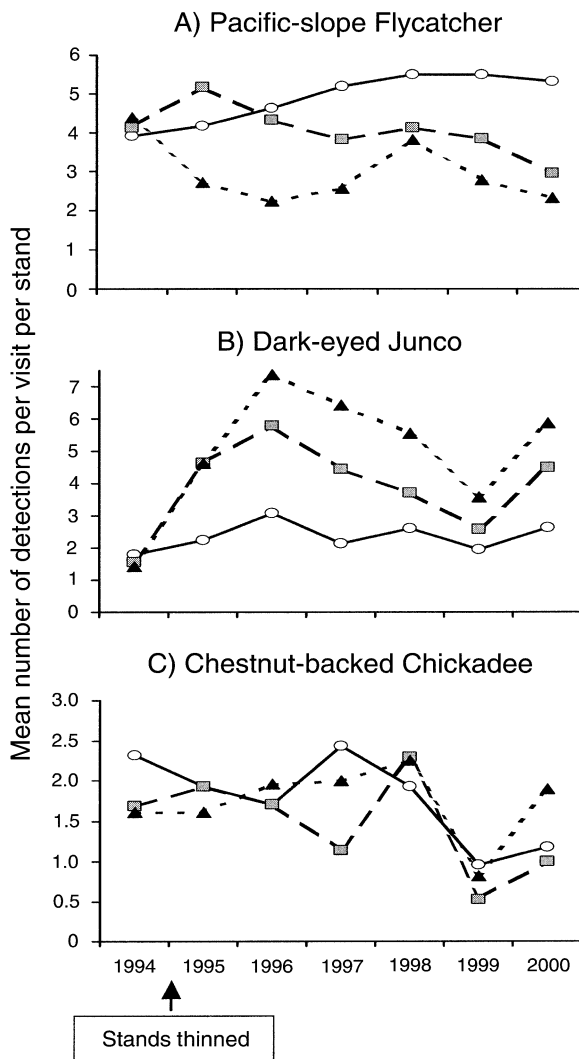


FIG. 1. Examples of responses of birds that (A) decreased in numbers in response to thinning (Pacific-slope Flycatcher), (B) increased in numbers in response to thinning (Dark-eyed Junco), and (C) showed no strong evidence of change in response to thinning (Chestnut-backed Chickadee).

bling Vireos was small and its 95% confidence interval overlapped no effect (Table 4).

Five species (Chestnut-backed Chickadee, Winter Wren, Gray Jay, Wilson's Warbler, and Red-breasted Nuthatch) did not exhibit a strong response to thinning. The null model ($C = M = H$) for numerical response was the model with the lowest QAIC_c value for the Chestnut-backed Chickadee (Fig. 1C), and Wilson's Warbler and was among the strongly competing models for the Gray Jay and Red-breasted Nuthatch (Table 3). Although none of the strongly competing models contained $C = M = H$ for numerical response for Winter Wrens, estimated sizes of effects of thinning were small, and 95% confidence intervals for estimates overlapped no effect for both moderate and heavy thinning

(Table 4), suggesting that there is no strong evidence of a significant influence of thinning on this species.

Temporal patterns

Of the 17 species that showed a numerical response to thinning, the null model for temporal trend ($C = M = H$; $M = H$ for Townsend's Solitaire and Hammond's Flycatcher) was among the set of strongly competing models for 14 species and was the model with the lowest AIC_c or QAIC_c for 12 species (Table 3). The null model for temporal trend was not among the strongly competing models for three species that showed a numerical response to thinning, one of which decreased in numbers following thinning (Pacific-slope Flycatcher), and two of which increased in numbers following thinning (Warbling Vireo and Western Tanager).

For the Pacific-slope Flycatcher, the only model with $\Delta \leq 2$ had a temporal trend of $C \neq M \neq H$ (Table 3). The coefficients for year \times moderate treatment interaction (-0.141 , $SE = 0.038$) and year \times heavy treatment interaction (-0.036 , $SE = 0.043$) suggest that the numbers of Pacific-slope Flycatchers in thinned stands continued to decrease relative to the controls through the duration of the study (Fig. 1A), and that this trend is most pronounced in the moderately thinned stands.

For the Warbling Vireo, the only model with $\Delta \leq 2$ indicated a temporal trend of $(C = M) \neq H$ (Table 3). The positive coefficients for the year \times heavy treatment interaction (0.234 , $SE = 0.069$) and the heavy treatment effect (0.426 , $SE = 0.120$) indicate that numbers of Warbling Vireos in the heavily thinned stands tended to increase relative to numbers in the control and moderately thinned stands over the course of the study.

For the Western Tanager, the model with the lowest QAIC_c value indicated a temporal trend of $C \neq (M = H)$ (Table 3). Although competing models contained temporal trends of $(C = M) \neq H$ and $C \neq M \neq H$ (Table 3), model averaged estimates for coefficients for year \times moderate treatment interaction (0.510 , $SE = 0.231$) and year \times heavy treatment interaction (0.513 , $SE = 0.234$) were very similar, supporting the hypothesis that temporal trends in moderately and heavily thinned stands were similar. The positive coefficients for temporal trends indicate that numbers of Western Tanagers in the thinned stands tended to increase relative to numbers in the control stands over the course of the study.

DISCUSSION

Species response

Our findings demonstrate that thinning influences abundances of several species of diurnal birds during the first few years following thinning. Response of birds to thinning was generally rapid, with patterns for most species evident during the first year following thinning. In addition, patterns of response for most species appeared to be relatively consistent across years, and marked temporal patterns were not common.

TABLE 4. Estimated number of detections and 95% confidence intervals for moderately thinned stands and heavily thinned stands expressed as percentages relative to detections in controls.

Species	Moderate	Heavy
Decreased		
Brown Creeper	55.9 (34.0–91.4)	10.1 (3.7–28.1)
Hutton's Vireo	32.1 (17.6–58.9)	12.9 (4.8–34.3)
Black-throated Gray Warbler	30.8 (18.6–50.7)	29.1 (17.2–49.2)
Varied Thrush	66.0 (39.1–110.5)	45.7 (25.7–81.9)
Golden-crowned Kinglet	67.0 (52.2–85.2)	49.2 (37.2–65.1)
Steller's Jay	133.4 (90.5–197.4)	52.8 (33.0–84.4)
Pacific-slope Flycatcher	81.9 (71.9–93.2)	55.1 (47.7–63.8)
Hermit Warbler	66.5 (52.7–83.5)	64.1 (50.7–81.1)
Swainson's Thrush	74.4 (58.3–95.1)	78.4 (61.3–100.0)
No change		
Gray Jay	123.4 (67.0–229.3)	63.8 (32.3–124.6)
Chestnut-backed Chickadee	93.2 (72.6–120.9)	107.3 (81.9–139.1)
Winter Wren	108.3 (93.2–127.1)	96.1 (81.1–113.4)
Wilson's Warbler	115.0 (91.4–144.8)	115.0 (92.3–144.8)
Red-breasted Nuthatch	166.5 (97.0–285.8)	140.5 (69.8–280.1)
Increased		
Warbling Vireo	96.1 (70.5–131.0)	152.2 (119.7–195.4)
Dark-eyed Junco	175.1 (141.9–213.8)	224.8 (184.0–271.8)
Western Tanager	322.2 (146.2–709.9)	363.3 (166.5–800.4)
American Robin	457.2 (222.6–939.3)	480.7 (234.0–977.7)
Evening Grosbeak	581.2 (285.8–1194.1)	642.4 (315.8–1293.6)
Hairy Woodpecker	366.9 (182.2–738.9)	738.9 (378.1–1429.6)

Notes: Confidence intervals overlapping 100 are interpreted as evidence of no effect. Estimates are based on exponentiated model averaged parameter coefficients. Townsend's Solitaires and Hammond's Flycatchers were not detected in control stands frequently enough to assess models that included control stands; thus the proportion increase in thinned stands relative to the controls cannot be estimated and are not included in this table.

Thinning provided habitat for three species of birds that were rare or absent in unthinned stands. Two of these species, the Townsend's Solitaire (Bowen 1997) and the American Robin (Hansen et al. 1995), are often associated with forests with open canopies. Increased numbers of these species would be expected given the more open habitat conditions resulting from thinning. Consistent with the findings of Hagar et al. (1996), Hammond's Flycatchers were also rare in unthinned stands, but occurred regularly (although in low numbers) in thinned stands. Previously published information on Hammond's Flycatchers presents a number of apparent inconsistencies in habitat associations for this species. Some studies report Hammond's Flycatchers to be present or most abundant in young stands (Carey et al. 1991, Anthony et al. 1996), whereas others have found them to be associated with mature or old-growth forests (Sedgwick 1994, Hansen et al. 1995, McGarigal and McComb 1995). Others have suggested that occurrence of Hammond's Flycatchers depends on the juxtaposition of hardwoods and conifers in an area (Lock and Naiman 1998). Increases in Hammond's Flycatchers may be the result of more open canopy conditions following thinning; Sakai and Noon (1991) found that Hammond's Flycatchers tend to nest in areas with more open canopies. Changes in abundance of Hammond's Flycatchers may also be related to changes in abundance of Pacific-slope Flycatchers, as these two

species may exhibit interspecific competition in the area (see Beaver and Baldwin 1975). Decreased numbers of Pacific-slope Flycatchers in thinned stands may open niches for exploitation by Hammond's Flycatchers in our study sites; alternatively, the increase in numbers of Hammond's Flycatchers in thinned sites may have contributed to decreases in numbers of Pacific-slope Flycatchers.

Detections of Hairy Woodpeckers increased substantially in thinned stands. This finding is also consistent with observations of Hagar et al. (1996). Although primary cavity-nesting birds are often limited by availability of nesting structures, it is unlikely that nest site availability increased in thinned stands. Indeed, D. M. Gomez, R. G. Anthony, and J. P. Hayes (*unpublished manuscript*) documented that snags, the primary nesting structures of Hairy Woodpeckers, were less abundant in these thinned stands than in controls following thinning. This suggests that factors other than nest sites may sometimes limit Hairy Woodpecker populations in young coniferous forests. Weikel and Hayes (1999) concluded that foraging resources are important determinants of the suitability of habitat for Hairy Woodpeckers in young forest stands. Changes in foraging resources following thinning may have been an important factor influencing habitat suitability for Hairy Woodpeckers in this study.

Although no species were extirpated from stands following thinning, detections of some species in one or more of the thinning treatments were 50% or less than detections in unthinned stands. With the exception of the Brown Creeper, all of the species that decreased in abundance following thinning nest or forage in the canopy. Decreases in numbers of these species could be the result of decreased canopy volume, changes in abundance of canopy invertebrates, or increased conspicuousness of nests in the canopy. Some of the species that declined following thinning (the Brown Creeper, Golden-crowned Kinglet, and Varied Thrush) are most abundant in or associated with older forest conditions (Mannan et al. 1980, Carey et al. 1991, Hansen et al. 1995, McGarigal and McComb 1995, Anthony et al. 1996, Hazard and George 1999). Although optimal habitat for these old-forest associates generally does not occur in young forest stands, unthinned stands may provide important refugia for these species in landscapes with little remaining older forest during the period when the canopy is closing in thinned stands.

Scope and limitations

Our study was restricted to 35–45-yr-old Douglas-fir stands in the northern Oregon Coast Range. Our results may not be applicable to substantially different thinning intensities, and should not be applied to much more intensive treatments, such as shelterwood treatments. Strongest inference can be applied to forests of similar structure in the same region. However, as our findings are generally consistent with what is known about the natural history for most of the species that we examined, we believe it is likely that our results can be applied to the same species in other geographic regions with coniferous forests of similar structure. Our work was also restricted to bird response during the first six years following thinning. The lack of evidence of temporal trends in response during this time period suggests that the findings likely apply to somewhat longer time frames, although response of birds to longer term changes following thinning (>10 yr) warrants additional study. The experimental nature of our study allows causal inference, although the mechanisms underlying the responses can not be fully elucidated using our approach. Our study did not examine influences of thinning on demographics, reproduction, or fitness. As abundance is not always a reliable indicator of habitat quality (Van Horne 1983), caution should be used when inferring habitat quality from our findings.

We conducted our research and made our experimental manipulations at a spatial scale of 25–40 ha. Although our point-count stations were at least 100 m from stand boundaries to reduce influences of surrounding stands, characteristics of adjacent stands and the landscape context in which our stands were situated may have influenced our findings. For example, we suspect that the incidental detections of Hammond's Flycatchers in control stands during the latter years of

the study were individuals in transit to nesting habitat in nearby thinned stands; the amount of thinned forest in close proximity to control stands increased substantially during the course of this study. It is conceivable that some of the species that were negatively impacted by heavy thinning, such as the Brown Creeper and Hutton's Vireo, may have persisted in heavily thinned stands only because of their proximity to unthinned or more moderately thinned stands. Most observations of Brown Creepers in heavily thinned stands were made relatively near unthinned stands (within 150 m) or in patches where more trees were retained. Given the size of our stands we suspect that the characteristics of surrounding stands had minimal influences on our overall conclusions, but landscape structure has been demonstrated to influence bird abundance in other studies (e.g., McGarigal and McComb 1995) and we are cognizant of the possibility of larger spatial scale effects influencing our findings.

Although our experience in the area and observations that we made during our study lead us to believe that our sampling protocol was unbiased, we recognize that use of number of detections as a measure of relative abundance can bias results if detectability of birds varied with tree density (Thompson et al. 1998). Such a bias would most likely be expressed as an inverse relationship between detectability and tree density. If this bias existed it would result in conservative estimates of the degree of impact on species whose numbers decreased following thinning, and may have failed to detect negative impacts for species that apparently increased or were not affected by thinning. To evaluate the potential impacts of differences in detectability on the data, we recorded detection distances and examined detection distances of birds for differences among treatment types in 2000. Only the Chestnut-backed Chickadee showed apparent differences in detectability with treatment. This suggests that data for Chestnut-backed Chickadees may be biased, and that we may have failed to detect negative influences of thinning for this species because of our use of fixed-radius counts.

Management implications

Thinning precipitates a number of short- and long-term changes in forest structure, that in turn influence habitat quality and suitability for a variety of species. As neither thinned nor unthinned stands provide habitat for maximum numbers of all species of diurnal birds, to optimize habitat for birds we recommend that landscapes dominated by younger stands be managed to retain a wide diversity of stand types. Maintaining some densely stocked, unthinned stands, such as stands in or entering the stem-exclusion stage of stand development (Oliver and Larson 1996), should provide refugia for species that are impacted by thinning. In addition, our anecdotal observations suggest that small (<0.5 ha), unthinned patches within stands may provide habitat for some species of songbirds, suggesting

that variable-density thinning may be a useful conservation strategy in some situations. However, the short-term consequences of thinning for most bird species evaluated in this study are positive, neutral, or of minor negative impact; this is consistent with previous studies of influences of thinning on birds (Hagar et al. 1996, Haveri and Carey 2000). In addition, moderate and heavy thinning intensities, at least in the short term, appear to be neutral or positive for abundance of flying squirrels (D. M. Gomez, R. G. Anthony, and J. P. Hayes, *unpublished manuscript*), abundance of several species of small mammals (Larson 2002, Suzuki and Hayes 2003), and use by bats (Humes et al. 1999). Because of this and the fact that thinning can be implemented in a way that substantially increases structural complexity of stands over the long term (Barbour et al. 1997), we conclude that most vertebrate populations in landscapes dominated by young, densely stocked plantations would benefit from thinning over a large proportion of the landscape if done in conjunction with management and retention of legacy structures and dead wood, and other conservation measures. Our results do not provide direct guidance concerning the optimal proportions of a landscape that should be thinned or left unthinned to maximize habitat value for birds, but our data provide a foundation for development of conceptual or quantitative models to address this question.

In landscapes managed to emphasize production of wood fiber where providing habitat for wildlife is a secondary or minor consideration, most stands generally will be harvested before many of the long-term benefits of thinning (increased structural diversity) will be fully realized. Conservation of legacy structures may be especially valuable for some species impacted by thinning and other forest management activities in these landscapes. For example, retention of some large trees with deeply furrowed bark may provide preferred foraging habitat for Brown Creepers (Mariani and Manual 1990, Weikel and Hayes 1999) and song posts for Varied Thrush (Beck and George 2000). In these landscapes, thinning young stands still will benefit a number of species, but if thinning is extensively implemented across these landscapes, special attention should be given to species that are strongly negatively impacted by thinning.

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APPENDIX

A summary of detections of birds during the pre-treatment year (1994), post-treatment years (1995–2000), and all years combined, as well as a complete species list is available in ESA's Electronic Data Archive: *Ecological Archives* A013-020-A1.