Long-Term Effects of Group-Selection Timber Harvesting on Abundance of Forest Birds

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Abstract: *Relatively few studies have examined the ecological effects of group-selection timber harvesting, and nearly all have been short-term and have lacked experimental manipulations that allow pre- and posttreatment comparisons. We have been documenting the effects of a group-selection timber harvest on bird abundance in a Maine forest for 24 years (preharvest, 1983–1987; postharvest, 1988–2006). Here we characterized the trends in bird abundance over the first 20 years of the study in the managed and control halves of the 40-ha study area. Species responses to the group-selection harvest were idiosyncratic, but in general the mature-forest bird community was retained and species dependent on early successional habitat temporarily (≤8 years) benefited. The Eastern Wood-Pewee (Contopus virens), Winter Wren (Troglodytes troglodytes), Pine Warbler (Dendroica pinus), and White-throated Sparrow (Zonotrichia albicollis) increased in abundance in the managed half of the study area following timber harvest, whereas the Veery (Catharus fuscescens) decreased. The Black-and-White Warbler (Mniotilta varia), Nashville Warbler (Vermivora ruficapilla), and Common Yellowthroat (Geothlypis trichas) responded positively to harvesting, as indicated by decreases in abundance in the control area and more protracted declines or stable abundances in the managed area. This study constitutes the longest experimental investigation to date of the effects of a group-selection harvest on birds and thus provides important information on the strength, direction, and duration of temporal changes in bird populations following forest management.*

Keywords: bird abundance, forest birds, group-selection timber harvest

Efectos de Largo Plazo de la Cosecha Selectiva de Madera sobre la Abundancia de Aves Forestales

Resumen: *Relativamente pocos estudios han examinado los efectos ecológicos de la cosecha selectiva de madera, y casi todos han sido de corto plazo y carecen de manipulaciones experimentales que permitan comparaciones pre y post tratamientos. Hemos documentado los efectos de la cosecha selectiva de madera sobre la abundancia de aves en un bosque de Maine durante 24 años (precosecha, 1983–1987; poscosecha, 1988–2006). Aquí, caracterizamos las tendencias en la abundancia de aves en los primeros 20 años del estudio en las mitades del área de estudio de 40 ha bajo manejo y control. Las respuestas de las especies a la cosecha selectiva de madera fueron idiosincrásicas, pero en general la comunidad de aves de bosque maduro fue retenida y las especies dependientes de hábitat en sucesión temprana (≤8 años) fueron beneficiadas. La abundancia de* Contopus virens, Troglodytes troglodytes, Dendroica pinus *y* Zonotrichia albicollis *incrementó en la mitad del área de estudio bajo manejo, mientras que la de* Catharus fuscescens *disminuyó.* Mniotilta varia, Vermivora ruficapilla *y* Geothlypis trichas *respondieron positivamente a la cosecha, como lo indican la disminución en abundancia en el área control y las declinaciones más extensas o abundancias estables en el área bajo manejo. A la fecha, este estudio constituye la investigación experimental más larga de los efectos de la cosecha selectiva sobre las aves y, por lo tanto, proporciona información importante sobre la intensidad, dirección y duración de los cambios temporales en poblaciones de aves posteriormente al manejo del bosque.*

Palabras Clave: abundancia de aves, aves forestales, cosecha selectiva de madera

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Introduction

As the global harvest of wood products continues to rise, it is important to understand how forest vegetation is changed by different silvicultural practices and in turn how these changes affect animal populations. The effects of even-aged management such as clearcutting on bird populations has been the focus of much research (e.g., Conner & Adkisson 1975; Thompson et al. 1992; Hagan et al. 1997). Nevertheless, growing opposition to clearcutting has led to an increase in the use of alternatives such as selection cutting, a form of uneven-aged management that removes trees as scattered individuals (single-tree selection) or in small groups (group selection) at relatively short intervals (Smith et al. 1997). Despite the increasing reliance on selection harvesting, comparatively few researchers have examined its effects on populations of forest birds (e.g., Annand & Thompson 1997; Robinson & Robinson 1999; Moorman & Guynn 2001; Gram et al. 2003).

The reliability of knowledge gained from studies of the effects of forest management on bird populations has been questioned recently (Marzluff et al. 2000; Sallabanks et al. 2000; Thompson et al. 2000). A primary concern is that most studies have been short-term (<4 years). Given the interannual variability in bird populations (e.g., Holmes & Sherry 2001), short-term studies can detect changes that are unrelated to the management practices under investigation (Sallabanks et al. 2000; Collins 2001). Another major concern is the lack of manipulative experiments with pre- and posttreatment data (Sallabanks et al. 2000). Although statistical inference can be generated from carefully designed observational studies, inference is strongest when based on manipulative experiments with randomly assigned treatments (James & McCulloch 1995).

Here we present the results of a long-term experimental study on the effects of a group-selection timber harvest on birds that is being conducted as part of a long-term (24 years to date) ecosystem study of an oak-pine forest at the Holt Research Forest in Arrowsic, Maine (Witham et al. 1993). Specifically, we examined the first 20 years of data on bird abundance (5 years of pretreatment data and 15 years of posttreatment data) to describe the strength, direction, and duration of the response of bird populations to the small openings created by the first cycle of a group-selection harvest.

Methods

Study Area

The Holt Research Forest is a 120-ha tract of forest on Arrowsic Island in the Kennebec River of Maine (43°52′N, 69°46′W) (Fig. 1). It occurs within the transition zone between oak-pine forest to the west and south and coastal
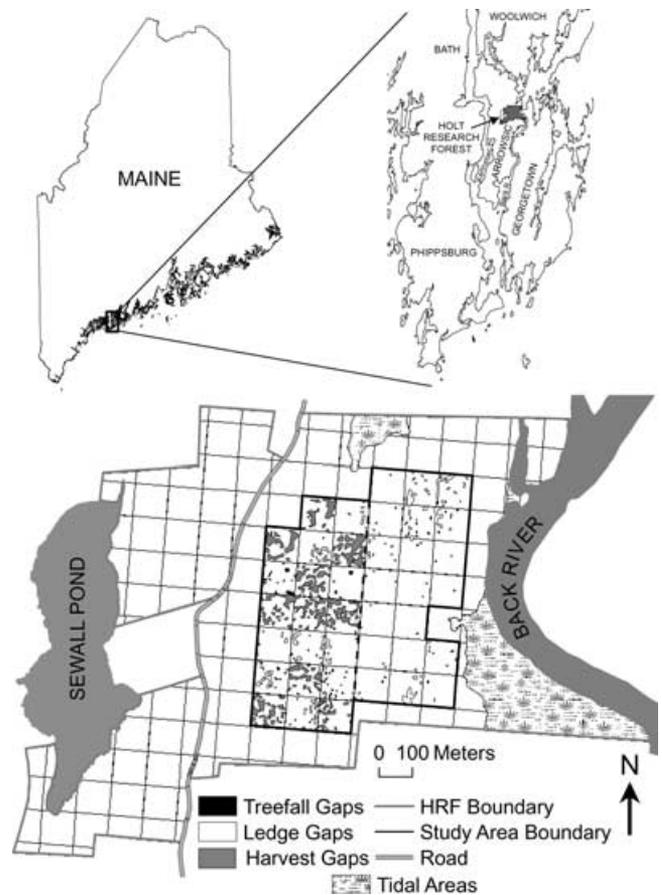

Figure 1. Map of the Holt Research Forest and the 40-ha study area in the year following the experimental treatment (1988). Dashed line separates western managed half from eastern control half. Two types of natural gaps were also in the study area: tree-fall gaps were openings caused by the death or windthrow of canopy trees, and ledge gaps were openings caused by the absence of canopy trees over very shallow soils or exposed bedrock.

spruce-fir to the east and north (McMahon 1990). The principal tree species in decreasing order of trees per hectare and total stand basal area are eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), northern red oak (*Quercus rubra*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*) (Kimball et al. 1995). The forest developed following the abandonment of agricultural land 70–110 years ago (Moore & Witham 1996).

The 40-ha study area is buffered by an average of 90 m (range 17–185 m) of forest from adjacent forests, a narrow road, and an estuarine river (Fig. 1). The study area is divided into a grid of forty 1-ha (100 × 100 m) blocks. The western 20 ha were designated as the managed half of the study area and the eastern 20 ha as the control half in which no silvicultural treatments have occurred or are planned.

Experimental Design

After 5 years (1983–1987) of baseline data collection on the entire study area, 10, 1-ha blocks within the managed half of the study area were partially harvested in the winter of 1987–1988 (Fig. 1). These harvested areas were chosen by randomly selecting one block from each of 10 pairs of adjacent blocks. The harvest removed an average of 44% (13.6 m^2/ha, SD = 6.7) of the basal area and 26% (SD = 7.5) of the forest cover from harvested blocks. The gaps averaged 210.2 m^2 (SE = 32.0, $n = 126$) and ranged from single tree gaps <25 m^2 to one gap that exceeded 3000 m^2 (Kimball et al. 1995). The total area of the gaps was distributed proportionally to the area of soil drainage classes and types of forest cover (Kimball et al. 1995; see Schumann et al. [2003] for postharvest vegetation in gaps).

This design, although adequate for our less-vagile study taxa, was not ideal for birds. The small size of the blocks relative to the territory size of birds made it difficult to ascribe territories to one block. Moreover, some bird species responded to the harvest-created gaps by shifting their distribution away from harvested blocks into control blocks and vice versa (S.P.C. et al., unpublished data). Thus, control blocks also showed treatment effects. To minimize the effects of these shifts, we counted territories at the scale of the managed and control halves of the study area. Nevertheless, aggregating control and managed blocks in the managed half diminished the effect of the harvest in our comparisons and therefore our findings are conservative. In addition, by aggregating blocks, the design was reduced from a true experimental design to a multiple-time-series design (sensu Campbell & Stanley 1966), which is still a strong alternative to a true experiment (James & McCulloch 1995).

Territory Mapping

One observer (J.W.W.) conducted territory mapping (International Bird Census Committee 1969; Witham et al. 1993) for all 20 years. Territory maps were based on 16 visits during the breeding season (late May through early July) each year. Each visit consisted of sampling the entire length of all transect lines (i.e., north–south lines through block centers) or all north–south grid lines of the study area between 04:30 and 10:30 (Fig. 1). All positional data (e.g., singing males, females, and nests) and interactions between observations (e.g., concurrent singing and movements) were digitized into a geographic information system (Witham & Kimball 1996). Composite maps were made for all visits for each species in each year.

Territory numbers were determined from the maps in all years by J.W.W. A minimum of five records of occurrence was required to denote a territory, and an emphasis was placed on observations of countersinging males. Territories that straddled the inner boundary between the control and managed halves of timber study area or the outer boundary of the study area were counted where a majority of their points fell.

Data Analysis

We characterized the response of birds to the harvest by describing changes in the community and in individual species occurring in each of the 20-ha managed and control halves of the study area and by comparing these changes between the two halves. To describe community-wide changes we examined species richness and the combined abundances of all species. Species richness included all species that had at least one observation within the boundary of the study area and that were known to breed on the island. Combined abundance included all species that could be accurately counted by territory mapping (Table 1) and excluded species that had territories larger than the study area (e.g., Pileated Woodpecker [*Dryocopus pileatus*]), occurred in flocks (e.g., Cedar Waxwing [*Bombycilla cedrorum*]) or family groups (e.g., Blue Jay [*Cyanocitta cristata*]), or had vocalizations not indicative of a territory (e.g., Great Crested Flycatcher [*Myiarchus crinitus*]).

For the abundance of individual species, we examined species that averaged more than one territory per year and three species that can have negative effects on the productivity of bird populations: the American Crow (*Corvus brachyrhynchos*), Blue Jay, and Brown-headed Cowbird (*Molotrus ater*). The latter three species could not be sampled reliably with territory mapping, so we used average number of detections per visit as an abundance index.

We characterized changes in abundance with one of three possible responses: no response to the disturbance (i.e., no change in the predisturbance trend); a positive or negative response to the disturbance (i.e., a single change in the predisturbance trend); and a positive or negative response followed by a return to predisturbance levels (i.e., two subsequent and opposite changes in the predisturbance trends). The first type of response can be modeled with a simple linear regression and the latter two types can be modeled with one- and two-breakpoint piecewise regression models, respectively (Seber & Wild 1989).

We fit all three models to the 20-year time series of each species in each half of the study area with nonlinear regression (PROC NLIN; SAS Institute 2003). To meet model assumptions, abundances were log transformed (ln[territories/20 ha + 0.5]). We used the Gauss-Newton iterative method to search the parameter space for the least-squares estimates that minimized the residual sums of squares of each model. Convergence occurred when the relative offset convergence measure of Bates and Watts was $<10^{-5}$ (SAS Institute 2003). Initial parameter estimates for the breakpoints (x_0 for the one-breakpoint model and x_0 and x_1 for the two-breakpoint model) were

Table 1. Frequency (Freq) of occurrence and mean, standard deviation (SD), coefficient of variation (CV), median, and range of territory numbers for 28 bird species breeding on the 40-ha study area at the Holt Research Forest, 1983–2002.

Bird species	Freq*	Mean	SD	CV	Median	Range
Downy Woodpecker (*Picoides pubescens*)	3	0.2	0.37	244.23	0.0	0–1
Hairy Woodpecker (*P. villosus*)	18	1.5	0.76	52.36	1.5	0–3
Eastern Wood-Pewee (*Contopus virens*)	20	6.6	2.44	37.22	6.5	3–10
Blue-headed Vireo (*Vireo solitarius*)	18	4.0	2.50	62.30	4.0	0–9
Red-eyed Vireo (*V. olivaceus*)	8	0.5	0.61	134.40	0.0	0–2
Tufted Titmouse (*Baeolophus bicolor*)	6	0.5	0.83	183.46	0.0	0–3
Black-capped Chickadee (*Poecile atricapilla*)	20	9.2	2.12	23.02	9.0	6–13
Brown Creeper (*Certhia americana*)	20	5.9	1.48	25.14	6.0	4–9
White-breasted Nuthatch (*Sitta carolinensis*)	9	0.7	0.92	131.91	0.0	0–3
Red-breasted Nuthatch (*S. canadensis*)	20	4.7	1.53	32.45	4.0	2–8
Winter Wren (*Troglodytes troglodytes*)	8	1.1	1.67	158.99	0.0	0–5
Golden-crowned Kinglet (*Regulus satrapa*)	19	2.8	1.74	61.97	3.0	0–6
Veery (*Catharus fuscescens*)	20	3.6	1.98	55.12	3.5	1–7
Hermit Thrush (*C. guttatus*)	20	10.2	2.96	29.17	10.5	6–15
Nashville Warbler (*Vermivora ruficapilla*)	10	1.8	2.55	145.83	0.5	0–8
Yellow-rumped Warbler (*Dendroica coronata*)	20	12.2	2.67	21.87	12.0	6–16
Black-and-white Warbler (*Mniotilta varia*)	20	4.6	1.43	31.47	5.0	2–8
Black-throated Blue Warbler (*D. caerulescens*)	7	0.6	0.88	147.10	0.0	0–2
Blackburnian Warbler (*D. fusca*)	20	11.8	2.31	19.56	11.0	8–17
Black-throated Green Warbler (*D. virens*)	20	27.7	4.78	17.30	26.0	23–40
Pine Warbler (*D. pinus*)	20	2.7	1.59	58.99	3.0	1–6
Canada Warbler (*Wilsonia Canadensis*)	15	0.9	0.59	69.08	1.0	0–2
Ovenbird (*Seiurus aurocapillus*)	20	27.2	4.12	15.18	27.0	21–39
Common Yellowthroat (*Geothlypis trichas*)	20	4.8	2.55	53.05	5.5	1–9
Scarlet Tanager (*Piranga olivacea*)	20	3.1	1.10	36.03	3.0	1–5
White-throated Sparrow (*Zonotrichia albicollis*)	18	4.8	3.29	68.47	4.0	0–10
Purple Finch (*Carpodacus purpureus*)	20	3.8	2.05	54.63	3.5	1–9
American Goldfinch (*Carduelis tristis*)	17	2.0	1.32	67.53	2.0	0–4

Number of years in which one or more territories were established at the Holt Research Forest.

found by searching all possible combinations of $x_0 = $ 1986–1989 and $x_1 = $ 1990–2000 for the combination that minimized the sums of squares. We bounded the final breakpoint estimates by the range of years of the study (1983–2002) and further constrained x_1 to be greater than x_0. All other parameters were initially estimated as zero. There were a few cases in which the convergence criterion was not met. In these cases the parameter estimates stabilized to a precision of 10^{-4} in <20 iterations and the use of other iterative methods (Marquardt and Newton) yielded nearly the same parameter estimates.

We used Akaike's information criteria (AIC) to select the model that best fit the data for each species (Burnham & Anderson 2002). We used the two-breakpoint piecewise regression model as our global model because the other models were nested subsets of this model. Examination of the global model of each species indicated a good fit to the data and normal or nearly normal residuals for most species; therefore, we used the least-squares case of AIC, which calculates AIC based on the residual sum of squares. Because the sample size (n) was small relative to the number of parameters (K) (i.e., $n/K < 40$), we used the small sample AIC (AIC$_c$) (Burnham & Anderson 2002). None of the data on species' trends was best fit by a two-breakpoint model; therefore, for the remain-

der of the paper we restrict our discussion to trends that were modeled by zero- (simple linear) and one-breakpoint models.

We calculated population trends (not log transformed) by taking the antilog of the slope estimate(s) of the best model for each species: trend = $e^{(\ln[\beta_i] - [\text{variance}])}$, where $\ln[\beta_i] = $ the slope of the ith line segment ($i = 1, 2$) and variance$_i$ is the square of the standard error of the corresponding slope estimate from the regression model (Holmes & Sherry 1988). We used t tests to determine whether trends were significantly different from zero and converted trends to average percent annual changes: %AC = (trend-1)(100). Trends that were significantly different from zero ($\alpha = 0.05$) were considered increasing or decreasing. Trends that were not significant were considered stable.

For species for which a one-breakpoint model provided a better fit to the data, the slopes of the different line segments can significantly differ from zero without a net change in abundance (i.e., there was a return in abundance to preharvest levels). To test for differences between initial and final abundances, we compared the abundances in the preharvest years (1983–1987) to the abundances in the last 5 years of the postharvest period (1998–2002) with Mann–Whitney tests (Zar 1999).

Results

Over the 20-year period, 47 species were observed. Forty-three species were present in the preharvest period and an additional 4 species were present in the postharvest period. The Eastern Phoebe (*Sayornis phoebe*), Ruby-throated Hummingbird (*Archilochus colubris*), Tufted Titmouse, and Winter Wren appeared after the harvest, but only the latter two appeared regularly. (Scientific names not provided in text are provided in Table 1.)

Twenty-eight species could be reliably counted by territory mapping. Fifteen occurred as breeders at the Holt Research Forest in all 20 years, with the remainder absent in 1 to as many as 17 years (Table 1). The Ovenbird and Black-throated Green Warbler were the most abundant bird species in the forest; they represented 14–24% and 13–23%, respectively, of all territories in each year.

Response of the Bird Community

The total numbers of species in the managed and control halves of the study area were not significantly different prior to the harvest. In the 15 years following the harvest, the managed half of the study area supported an average of four more species than the control half (Fig. 2; Wilcoxon paired-sample test, $p < 0.001$). Combined abundances of the 28 species showed no change over the 20-year period in either half of the study area (control, %AC = −0.279, $p = 0.532$; managed, %AC = −0.252, $p = 0.533$) and did not differ significantly between the control and managed portions of the study area (Fig. 2).

Response of Individual Bird Species

There were 22 species abundant enough for individual analyses. Eight of these species were apparently unaffected by the timber harvest (Table 2): populations of
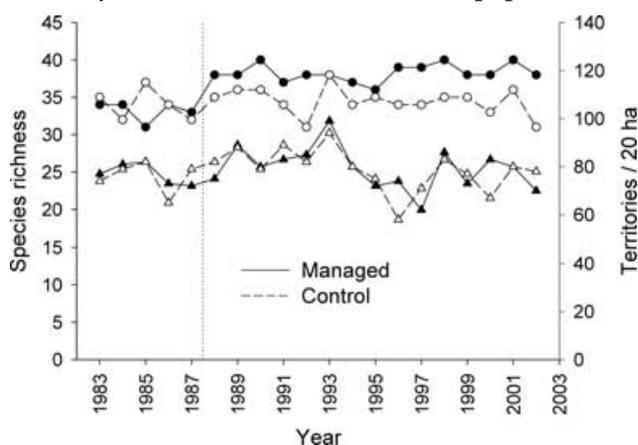

Figure 2. Total species richness (circles) and combined abundances (number of territories) of 28 species (triangles) of forest birds in the 20-ha control and managed halves of the study area at the Holt Research Forest, 1983–2002. Dotted vertical line denotes the time of the harvest treatment.

the Hairy Woodpecker, Red-breasted Nuthatch, Golden-crowned Kinglet, Blackburnian Warbler, and Scarlet Tanager were stable in both halves of the study area. Similarly, the Blue-headed Vireo, Purple Finch, and American Goldfinch had significantly increasing trends of similar magnitude in both halves.

Among the 14 species with population trends that were different in harvested and control areas (Tables 2 & 3), 7 had relatively strong positive responses to the harvest. The Eastern Wood-Pewee showed a highly significant increase in the managed half until 1994 when the population began to decline (Fig. 3a). The converse was true in the control half, in which population size decreased and then later increased. Similarly, the White-throated Sparrow increased in abundance in the managed half following the harvest until 1992, after which it decreased (Fig. 3i). In the control half, this species declined sharply. The Winter Wren did not occur in the study area prior to the harvest (Fig. 3b), but following the harvest it appeared almost exclusively in the managed half for 7 years until it largely disappeared (i.e., it was absent in 6 of the 8 subsequent years). Likewise, the Pine Warbler was absent in the managed half until after the harvest (Fig. 3g). In the control half, this species maintained a relatively stable population over the 20-year period. Populations of the Nashville Warbler, Black-and-white Warbler, and Common Yellowthroat showed relatively steep declines in the control half of the study area and more protracted declines or stable populations in the managed half (Figs. 3d, f, h).

The Yellow-rumped Warbler (Fig. 3e) and Hermit Thrush (Fig. 3c) also had trends that were indicative of a positive response to the harvest. Populations of both species increased linearly in the managed half of the study area over the 20 years of the study and were stable or decreased in the control half during the postharvest period.

Only the Veery showed a strong negative response to the timber harvest; its numbers declined sharply in the managed half following the harvest (Fig. 4c). Nevertheless, about 5 years after the timber harvest the numbers in the managed half started to increase. The population in the control half remained relatively stable. The Black-capped Chickadee, Brown Creeper, and Ovenbird also had significantly decreasing trends in the managed half of the study area and stable populations in the control half, but their declines were relatively weak (Figs. 4a, b, e). Although the population of the Black-throated Green Warbler remained stable in the managed half of the study area following the harvest, the pattern of increase and decrease in the control half suggests a negative response to the harvest (Fig. 4d).

There was a temporary increase in the average number of detections of the American Crow following the harvest, and it tended to use the managed half of the study area (S.P.C., unpublished data). The number of detections of the Brown-headed Cowbird and Blue Jay fluctuated considerably from year to year but showed no obvious

Table 2. Population trends of 19 bird species for which a zero-breakpoint (simple linear) regression model best describes the trends in the control and/or managed half of the Holt Research Forest, 1983–2002.

Bird species	Location	R^2	Slope (SE)[a]	Annual change (%)[b]
Hairy Woodpecker	control	0.03	−0.02 (0.024)	−1.66
	managed	0.03	0.02 (0.024)	1.78
Blue-headed Vireo	control	0.22	0.06 (0.025)	5.81*
	managed	0.31	0.08 (0.027)	7.86*
Black-capped Chickadee	control	0.04	0.01 (0.012)	1.06
	managed	—[c]	—	—
Brown Creeper	control	0.17	0.02 (0.009)	1.77
	managed	0.25	−0.05 (0.019)	−4.61*
Red-breasted Nuthatch	control	0.00	0.00 (0.015)	0.07
	managed	0.01	−0.01 (0.020)	−0.88
Winter Wren	control	0.05	−0.02 (0.019)	−1.77
	managed	—	—	—
Golden-crowned Kinglet	control	—	—	—
	managed	0.14	−0.04 (0.022)	−3.78
Veery	control	0.08	−0.03 (0.026)	−3.22
	managed	—	—	—
Hermit Thrush	control	—	—	—
	managed	0.41	0.05 (0.013)	4.66**
Nashville Warbler	control	—	—	—
	managed	0.24	−0.08 (0.032)	−7.33*
Yellow-rumped Warbler	control	—	—	—
	managed	0.60	0.04 (0.007)	3.90***
Black-and-white Warbler	control	0.64	−0.09 (0.017)	−9.01***
	managed	0.05	0.01 (0.013)	1.23
Blackburnian Warbler	control	0.01	0.00 (0.010)	−0.44
	managed	0.01	0.00 (0.012)	−0.39
Pine Warbler	control	0.13	0.02 (0.013)	2.13
	managed	—	—	—
Ovenbird	control	0.18	−0.01 (0.005)	−1.09
	managed	0.30	−0.02 (0.007)	−1.89*
Common Yellowthroat	control	0.65	−0.10 (0.018)	−9.80***
	managed	—	—	—
Scarlet Tanager	control	0.04	−0.01 (0.015)	−1.30
	managed	0.02	0.02 (0.027)	1.67
Purple Finch	control	0.50	0.08 (0.019)	8.55***
	managed	0.27	0.05 (0.018)	4.83*
American Goldfinch	control	0.39	0.06 (0.018)	6.35**
	managed	0.50	0.09 (0.021)	9.09**

[a]*Least-squares regression slope of bird abundance against time.*
[b]*Percent annual change in bird abundance:* *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.*
[c]*Dashes indicate that a one-breakpoint regression model provides a better fit to the data of these locations.*

increasing or decreasing trend or tendency to concentrate in the managed areas.

Discussion

The first cutting cycle of a group-selection harvest did not result in overwhelmingly positive or negative effects on the bird community of the Holt Research Forest. There was a slight increase in the number of species in the managed half of the study area, but no change in the combined abundance of 28 bird species in either half of the study area (Fig. 2). Among the individual species, the responses were quite varied, but in general the group-selection harvest temporarily benefited some early successional bird species, while retaining the mature-forest bird community. These findings are consistent with those of other studies on the effects of group-selection harvesting on birds (Annand & Thompson 1997; Germaine et al. 1997; Robinson & Robinson 1999; Costello et al. 2000).

Response of Early Successional Bird Species to Timber Harvest

Early successional bird species were present in the forest prior to the harvest, probably due to the presence of ledge gaps (Fig. 1). Ledge gaps occurred in areas of shallow soils or exposed bedrock that have been slow to reach closed-canopy conditions since agricultural activities ceased. Nonetheless, these gaps have been filling

Table 3. Population trends of 12 bird species for which a one-breakpoint regression model best describes the trends in the control and/or managed half of the Holt Research Forest, 1983–2002.

Bird species	Location	R²	Slope 1 (SE)[a]	Breakpoint (SE)[b]	Slope 2 (SE)[a]	Annual change 1 (%)[c]	Annual change 2 (%)[c]	Abundance difference[d]
Eastern Wood-Pewee	control	0.49	−0.09 (0.047)	1993 (1.6)	0.15 (0.047)	−8.84	15.78**	1.8
	managed	0.66	0.19 (0.040)	1994 (1.4)	−0.14 (0.074)	20.90***	−12.92	1.6
Black-capped Chickadee	control	—[e]	—	—	—	—	—	—
	managed	0.44	0.16 (0.092)	1987 (1.4)	−0.03 (0.011)	16.35	−3.33**	−0.8
Winter Wren	control	—	—	—	—	—	—	—
	managed	0.30	0.31 (0.182)	1989 (1.9)	−0.09 (0.051)	34.62	−8.23	0.6
Golden-crowned Kinglet	control	0.32	0.55 (0.284)	1986 (1.0)	−0.06 (0.034)	66.57	−6.02	0.2
	managed	—	—	—	—	—	—	—
Veery	control	—	—	—	—	—	—	—
	managed	0.64	−0.29 (0.084)	1990 (1.0)	0.18 (0.046)	−25.51**	19.93**	1.6
Hermit Thrush	control	0.40	0.09 (0.042)	1991 (1.7)	−0.07 (0.031)	9.61*	−7.21*	0.2
	managed	—	—	—	—	—	—	—
Nashville Warbler	control	0.74	−0.61 (0.184)	1986 (0.7)	−0.04 (0.022)	−46.46**	−4.30	−1.8*
	managed	—	—	—	—	—	—	—
Yellow-rumped Warbler	control	0.42	0.18 (0.095)	1986 (1.3)	0.00 (0.012)	19.38	0.09	2.8
	managed	—	—	—	—	—	—	—
Black-throated Green Warbler	control	0.52	0.06 (0.023)	1992 (1.4)	−0.06 (0.017)	5.94*	−5.55**	−0.8
	managed	0.54	−0.08 (0.034)	1988 (1.8)	0.00 (0.010)	−7.76*	−0.35	−3.8**
Pine Warbler	control	—	—	—	—	—	—	—
	managed	0.44	0.21 (0.077)	1991 (2.0)	−0.06 (0.057)	23.18*	−5.47	1.2*
Common Yellowthroat	control	—	—	—	—	—	—	—
	managed	0.76	0.02 (0.033)	1992 (1.7)	−0.12 (0.024)	1.48	−11.49***	−3.6**
White-throated Sparrow	control	0.73	−0.32 (0.096)	1989 (1.7)	−0.05 (0.038)	−27.61**	−4.89	−3.0**
	managed	0.78	0.14 (0.056)	1992 (1.0)	−0.25 (0.041)	14.73*	−22.10***	−1.8

[a]*Least-squares regression slope of bird abundance against time for the time periods before (Slope 1) and after (Slope 2) the breakpoint (i.e., 1983 breakpoint and breakpoint 2002, respectively).*
[b]*Estimated year at which the regression slope changes.*
[c]*Percent annual changes in bird abundance at the Holt Research Forest:* *p < 0.05, **p < 0.01, ***p < 0.001.*
[d]*Abundance difference is the difference between the average of the first 5 years (1983–1987) and last 5 years (1998–2002) of the time series. Statistical significance is based on exact p values for Mann–Whitney test of difference in abundances between the first 5 and last 5 years of data.*
[e]*Dashes indicate that a simple linear regression model provides a better fit to the data for these locations.*

in over the 20 years of our study and there has been a decrease in the use of these gaps by early successional species, as evidenced by the decline of species such as the Common Yellowthroat and White-throated Sparrow in the control half of the study area (Figs. 3h and 3i). In contrast, the creation of early successional habitat by the group-selection harvest delayed the decline of early successional bird species in the managed half of the study area (Figs. 3d, f, h, i). Nevertheless, except for the Black-and-white Warbler, the duration of the effects were relatively short (5–8 years).

Early successional species are sensitive to the sizes of disturbed patches (Rudnicky & Hunter 1993a), so the group-selection cuts in this study (mean size = 0.02 ha) were clearly not big enough for species that select extensive areas of second-growth habitat. Similarly, Robinson and Robinson (1999) noted that group-selection cuts did not attract birds that typically appeared in large clearcuts, and Moorman and Guynn (2001) found that the largest group-selection openings (0.5 ha) supported the most species and the greatest abundance of early successional bird species. Nevertheless, the clustering of small gaps in our study (Fig. 1) may have approximated the conditions of larger gaps (Hunter 1993) and thus provided habitat

for more early successional species than if the gaps had been more evenly distributed.

Response of Late Successional Bird Species to Timber Harvest

The Veery was the only species that showed a strong negative response to the loss of mature forest (Fig. 4c). Interestingly, the Winter Wren responded positively to the harvest (Figs. 3b, g), even though it usually is associated with older forests that have abundant dead woody material (Hejl et al. 2002). Nevertheless, the species also uses slash piles following logging operations (Tobalske et al. 1991), which was the case in our study. Given its affiliation with closed-canopy, pine-dominated stands, it is unclear why the Pine Warbler increased in abundance in the managed half of the study area immediately following the harvest. One possibility is that regional populations of Pine Warblers were increasing (S.P.C., unpublished data) and the remaining intact canopy and pines in the harvested area provided sufficient habitat.

Although most of the late successional species showed little to no change in relative abundance, we could not definitively conclude that their habitat quality was unaffected without knowledge of population parameters
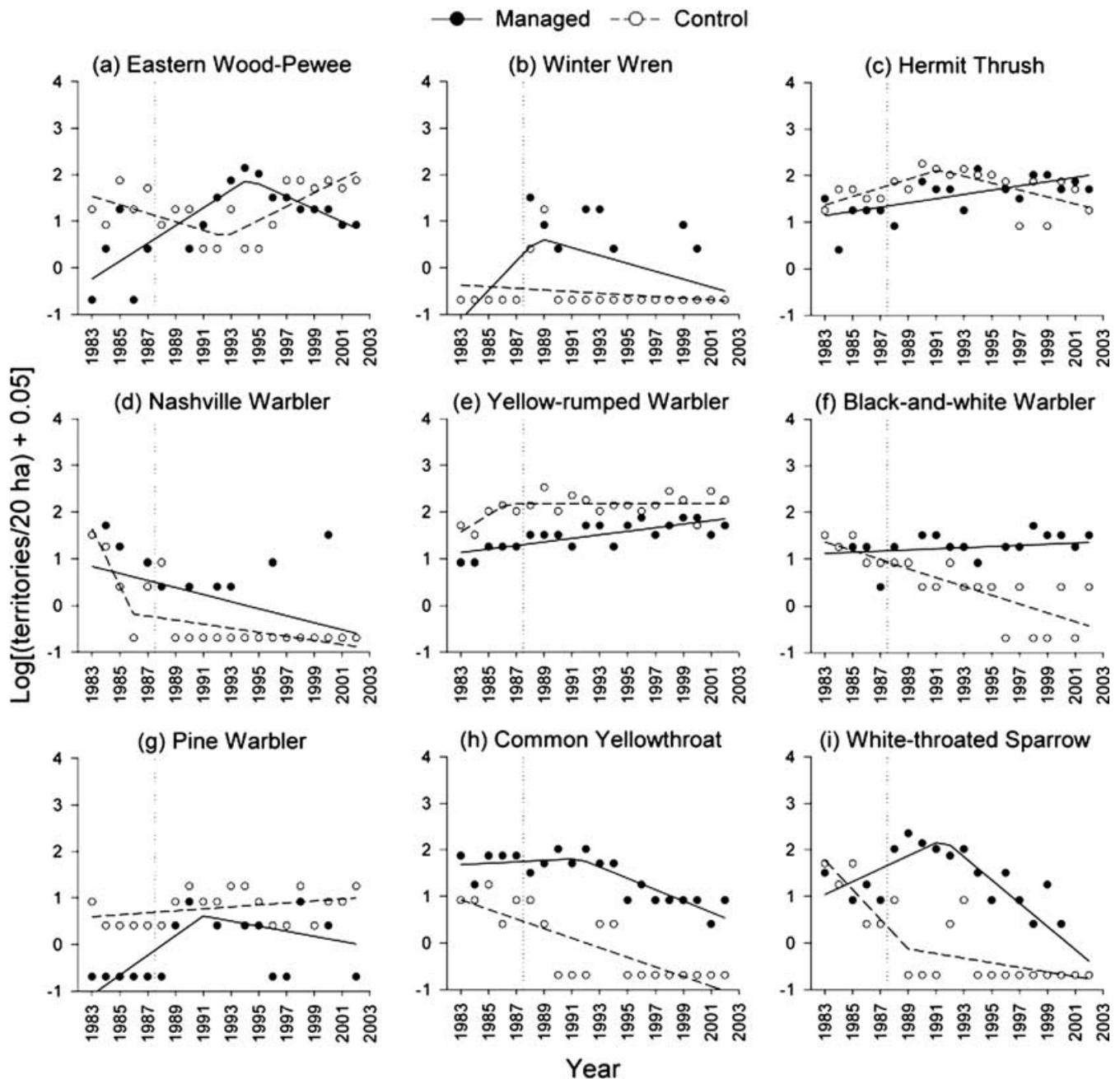
Figure 3. Abundance (number of territories) trends of (a–i) bird species that responded positively to a selection timber harvest at the Holt Research Forest, 1983–2002. The study area is divided into a 20-ha managed area, where the harvest occurred, and a 20-ha control area. Dotted vertical line denotes the time of the harvest treatment.

such as pairing success, nesting success, productivity, and survival. Results were equivocal from studies that measured these variables in a setting similar to ours. For example, King et al. (1996) found no reduction in pairing success of Ovenbirds near small clearcut edges, but Ziehmer (1993, cited in Faaborg et al. 1995) documented lower pairing success of Red-eyed Vireos and Wood Thrushes (*Hylocichla mustelina*) around openings in a formerly continuous forest. Similarly, results of some studies showed higher nest predation near edges in forest-

dominated landscapes (King et al. 1996; Manolis et al. 2002), whereas others found no relationship (Rudnicky & Hunter 1993*b*; Hanski et al. 1996; Driscoll & Donovan 2004). Finally, the creation of small openings in extensive and unfragmented forests did not lead to an increase in abundance of avian nest predators and brood parasites in some studies (Annand & Thompson 1997; Germaine et al. 1997), whereas Robinson and Robinson (1999) found more Brown-headed Cowbirds and Blue Jays in selection-cut openings. We witnessed an increase in the average
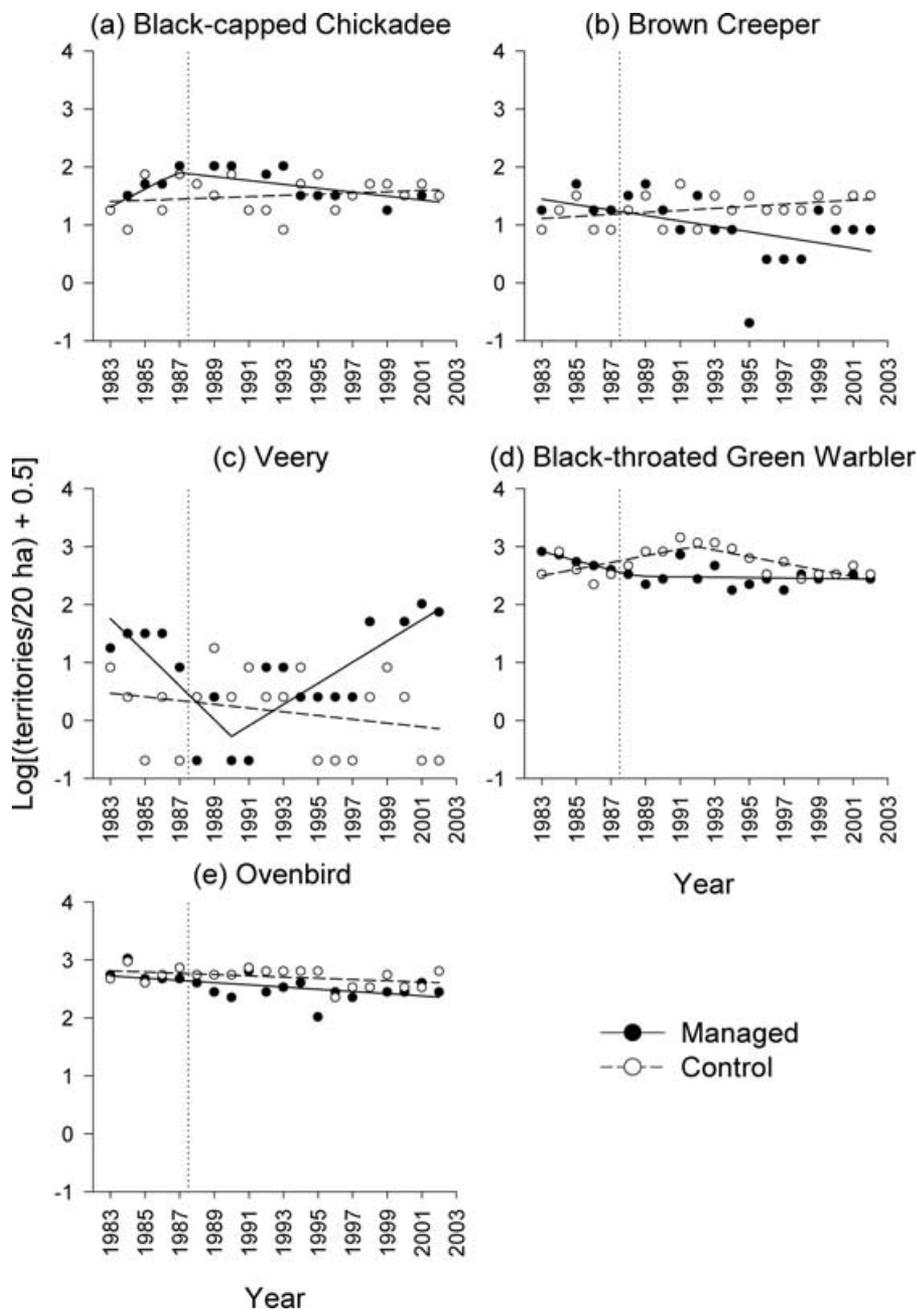
Figure 4. Abundance (number of territories) trends of (a–e) bird species that responded negatively to a selection timber harvest at the Holt Research Forest, 1983–2002. The study area is divided into a 20-ha managed area, where the harvest occurred, and a 20-ha control area. Dotted vertical line denotes the time of the harvest treatment.

number of detections of American Crows in the managed half of the study area but not of Blue Jays and Brown-headed cowbirds.

Response to Factors Other than Timber Harvest

Some bird species were probably unaffected by the harvest and their population trends reflected a response to other influences, such as factors operating at regional scales (e.g., migration and wintering grounds mortality). For example, the Tufted Titmouse, which was not abundant enough to analyze individually, appeared in our study area in 1997 as a result of the northward expansion of its range. Similarly, regional increases in the American

Goldfinch and Blue-headed Vireo likely contributed to their increase in the Holt Research Forest. Nevertheless, most species were probably not overwhelmingly influenced by regional population trends. Only 18% of the species had changes in their local populations that correlated positively with statewide populations (Sauer et al. 2004), and only 27% of the species had local trends that were qualitatively the same (i.e., significant in the same direction but not necessarily the same magnitude) as the statewide trends (S.P.C., unpublished data). These results suggest that most bird species were primarily responding to local habitat conditions.

In some cases birds may be responding to changes in local habitat conditions that are unrelated to the harvest.

For example, Holmes and Sherry (2001) attributed the changes in bird populations in an undisturbed forest over a 30-year period (1969–1998) to successional changes in vegetation. In our study changes in populations of the Nashville Warbler, Black-and-white Warbler, Common Yellowthroat, and White-throated Sparrow in the control half of the study area and of the Purple Finch in both halves of the study area are most likely tied to forest succession.

Study Limitations

Three limitations of our study require exposition. First, the small size of the study area limits the extrapolation of our results to larger spatial scales (James & McCulloch 1995). Nevertheless, our local habitat conditions (i.e., relatively mature forest in a predominately forested landscape) are generally representative of habitat conditions in the region (McWilliams et al. 2005), so there is no reason to believe that our results are atypical. Second, by examining bird response in the managed and control halves of the study area, there is no spatial replication in the experiment. Although spatial replication is obviously important, temporal replication can be just as important as spatial replication and maybe more so in a temporally variable system, such as regenerating forest. We have sampled bird populations intensively over 20 consecutive years. This type of long-term, intensive data from a single location can detect important patterns that can be missed in well-replicated short-term studies. Third, to provide for proper controls for both the harvested blocks and the managed half of the study area, group-selection cuts were limited to individual blocks. In commercial operations group-selection cuts would have been made throughout the forest and overall a greater area of the forest would be in early successional habitat. Despite these limitations our study represents the longest-running experiment investigating this phenomenon and thus contributes important insights into long-term responses of birds to forest disturbance.

Management Implications

Natural disturbance regimes offer a benchmark to forest managers seeking to provide a range of habitat conditions at the scales and frequencies to which various organisms are adapted (Attiwill 1994; Seymour & Hunter 1999; Seymour et al. 2002). In the northeastern United States the natural disturbance regime of forests is dominated by the death or windthrow of individual or small groups of trees (Seymour et al. 2002). Large-scale, stand-replacing disturbances brought on by fire, catastrophic winds, or ice storms also occur, but they are relatively infrequent (Lorimer & White 2003).

The first-cutting cycle of a group-selection timber harvest creates patches of early successional habitat that are similar to the small openings created most frequently by natural disturbance. These patches provide ephemeral habitat for early successional species and have little effect on the abundances of mature closed-canopy bird species. Nevertheless, this outcome would likely change with repeated harvests depending on the duration of intercut intervals. If intervals are short (e.g., 10–15 years), the frequent removal of canopy trees would ensure a constant source of habitat for early successional species, but it may have a negative effect on the mature-forest species. Longer intervals would be less likely to affect the mature-forest bird species, but would provide less habitat for early successional bird species. To mimic large natural disturbances, silvicultural practices such as clearcutting would be needed. Nevertheless, given the infrequency of large-scale natural disturbances in this region, large clearcuts would be rare and so too would species dependent on large tracts of early successional forest.

Our findings are especially relevant because the number of land ownerships comparable in size to the Holt Research Forest is increasing. In the United States the number of small privately owned forests is on the rise; currently they comprise 42% of the nation's forestland and nearly 47% of this land is in tracts of <40 ha (Butler & Leatherberry 2004). In general, we expect that the fine-scale heterogeneity created by the independent and asynchronous harvesting of these areas will provide large-scale habitat conditions that are suitable for many bird species. Nevertheless, the independent management of these forests is not likely to produce large tracts of a given habitat type on which some species depend (e.g., area-sensitive, mature-forest species). Management of these species will require more coordinated efforts among landowners where site-specific and landscape goals are nested hierarchically within regional goals (Thompson et al. 1995; Thompson & DeGraaf 2001).

Acknowledgments

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