



## Original Article

# Long-Term Changes in Spatial Distribution of Birds Responding to a Group-Selection Timber Harvest

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**ABSTRACT** We investigated the spatial response of 20 bird species to a group-selection timber harvest within a 40-ha forest stand over a 20-year period (5 yr preharvest and 15 yr postharvest). To characterize the spatial response of each species, we examined trends in 3 metrics: proportion of harvest-created canopy-gap area that occurred within the area used by a species in each year, average distance to the nearest gap of all observations of a species in a year, and distribution of distances between observations and gaps for each species in each year. Eight species (eastern wood-pewee [*Contopus virens*], winter wren [*Troglodytes troglodytes*], hermit thrush [*Catharus guttatus*], Nashville warbler [*Vermivora ruficapilla*], black-and-white warbler [*Mniotilta varia*], pine warbler [*Dendroica pinus*], common yellowthroat [*Geothlypis trichas*], and white-throated sparrow [*Zonotrichia albicollis*]) responded positively to the timber harvest (i.e., the proportion of gaps in their area of use increased, the distance from gaps decreased, and their use of gaps and edges [0–25 m from gaps] increased). In contrast, veeries (*Catharus fuscescens*), black-throated green warblers (*Dendroica virens*), and ovenbirds (*Seiurus aurocapillus*) avoided gaps and edges. Changes in spatial distributions were generally short-lived; by 15 years postharvest the use of the harvested areas by nearly all species had approached preharvest levels. The spatial response of birds to group-selection timber harvesting indicates that there are unlikely to be serious long-term effects of the harvest on forest bird populations. However, there may be more subtle, short-term effects, such as crowding of mature-forest bird species into surrounding forest, which merit further study. © 2012 The Wildlife Society.

**KEY WORDS** birds, group-selection timber harvest, long-term study, manipulative experiment, spatial distribution.

When bird abundance and habitat quality are positively related, abundance is an appropriate basis for making land-management decisions. However, abundance can become decoupled from habitat quality when disturbance alters habitat conditions (Bock and Jones 2004). In these cases, abundance may be insensitive to changes in habitat quality, which can lead to conclusions that bird populations are unaffected when in reality there may have been negative effects on survival and reproduction mediated through changes in habitat use and species interactions (Van Horne 1983, Hobbs and Hanley 1990, Garshelis 2000, Nielsen et al. 2005).

Studies that examine the effects of timber harvesting on bird communities typically rely on changes in abundance to reflect changes in habitat quality (Sallabanks et al. 2000).

Timber harvesting, however, causes relatively abrupt changes in vegetation followed by slower changes as the forest vegetation regenerates; these types of alterations in habitat conditions may lead to effects on bird populations that are not always manifested as changes in abundance. Therefore, to understand the effects of timber harvesting on bird populations, it is prudent to examine other aspects of their response (e.g., demographic, physiological, and spatial).

Examining changes in spatial distribution can provide important insights into the effects of timber harvesting on birds. First, shifts in spatial distribution immediately following a timber harvest can provide a measure of the degree of repulsion, attraction, or neutrality of different bird species to the harvested areas and the resulting edges. Later, as the harvested areas regenerate, shifts in spatial distribution can indicate when harvested areas become suitable for mature-forest birds and unsuitable for birds that prefer early successional vegetation. Secondly, tracking shifts in distribution can show how the distributions of different species overlap in space and time and thus lead to a better understanding of how community structure changes in response to timber harvesting. Finally, if changes in spatial distribution are considered in conjunction with abundance, they can help to elucidate the interaction between abundance and

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demographic processes. For example, if birds avoid harvested areas without a decrease in abundance it could lead to crowding in the remaining forest (Hagan et al. 1996). The resulting increase in densities of conspecific neighbors can affect territory size, reproductive success, time budgets, and foraging behaviors (Both 1998, Sillett et al. 2004, Dobbs et al. 2007), all of which can have important effects on fitness. Despite its potential importance in these regards, the explicit consideration of the spatial distribution of birds is usually neglected in studies of the effects of timber harvesting (but see Wallendorf et al. 2007).

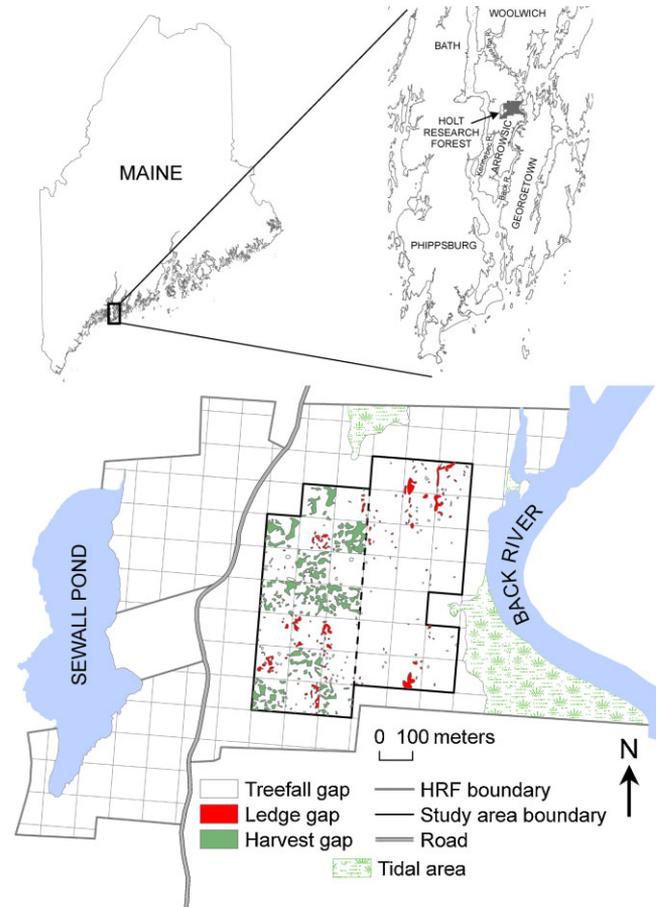
Group-selection timber harvesting is a form of uneven-aged forest management that removes small groups of trees at relatively short intervals (Smith et al. 1997), and, thus, creates small patches of early successional vegetation embedded in a matrix of mature forest. Studies of the effects of group-selection timber harvesting on birds have generally found that the small canopy gaps created by this type of timber harvest result in nominal losses of forest bird species or individuals and that the resulting patches of early successional vegetation can temporarily enhance bird species richness by providing habitat for early successional birds (e.g., Robinson and Robinson 1999, Gram et al. 2003, Campbell et al. 2007, Forsman et al. 2010, Tozer et al. 2010). The loss of forest without a change in abundance of forest bird species seems counterintuitive, however, and suggests that further investigation is necessary. In particular, it raises fundamental questions about the spatial distribution of birds in relation to gaps, their edges, and the forest matrix. For example, do forest birds use these small gaps or their edges or do they avoid them? If birds avoid these areas, does that lead to crowding in the remaining forest? Similar questions exist for early successional bird species that occupy gaps after harvesting.

We have been documenting the effects of a group-selection timber harvest on forest birds for 29 years (preharvest: 1983–1987 and postharvest: 1988–2011) as part of a broader ecosystem study of a pine–oak (*Pinus* spp.–*Quercus* spp.) forest at the Holt Research Forest in Arrowsic, Maine, USA (Witham et al. 1993). We have previously reported on the numerical response of birds to the harvest-created canopy gaps over the first 20 years of the study (Campbell et al. 2007). In this study, we examine the spatial response of birds over the same period by characterizing the strength, direction, and duration of changes in local distributions following gap creation and subsequent regeneration. We consider the spatial responses in conjunction with our previous findings on abundance because together these findings more fully elucidate the dynamics of bird response to timber harvesting.

## STUDY AREA

### Site Description

The Holt Research Forest was a 120-ha tract of forest located near the center of Arrowsic Island in the Kennebec River of Maine (43°52'N, 69°46'W; Fig. 1; Supplemental Appendix A available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). It



**Figure 1.** Map of the Holt Research Forest and the 40-ha study area in the year following the harvest (1988). Each square represents a 1-ha (100 m × 100 m) block. Ten blocks were chosen for harvest from the managed half of the forest by randomly selecting 1 block from each of 10 pairs of adjacent blocks.

occurred within the transition zone between northern red oak (*Quercus rubra*) and eastern white pine (*Pinus strobus*) forest to the west and south and red spruce (*Picea rubens*)–balsam fir (*Abies balsamea*) forest to the east and north (McMahon 1990). The principal tree species in decreasing order of trees per hectare and basal area were eastern white pine, red maple (*Acer rubrum*), northern red oak, and red spruce (Kimball et al. 1995). The forest was a result of secondary succession following the abandonment of agricultural land 70–110 years ago (Moore and Witham 1996).

The study area comprised 40 ha and was buffered by an average of 90 m (range = 17–185 m) of forest from adjacent forests, a public road, and an estuarine river (Fig. 1). The study area was divided into 40 1-ha (100 m × 100 m) blocks, which were subdivided into 4 50 m × 50 m quadrats and 16 25 m × 25 m subquadrats. The grid was demarcated on the ground with metal stakes. The western 20 ha were the managed half of the study area and the eastern 20 ha were the control half (i.e., no silvicultural treatments).

### Canopy-Gap Creation and Mapping

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 cut during the winter of 1987–1988. These harvested blocks were chosen by randomly selecting 1 block from each of 10 pairs of adjacent blocks. The harvest removed an average of 44% (13.6 m<sup>2</sup>/ha, SD = 6.7%) of the basal area, and 26% (SD = 7.5%) of the forest cover from harvested blocks. There was no effort by the forester to control the size, shape, or orientation of the resulting canopy gaps, which created a network of interconnected gaps of various shapes and sizes (Fig. 1).

In the 2 years following the harvest, all gaps in the forest were delineated on the ground and mapped in a Geographic Information System (Fig. 1; Kimball et al. 1995). Gaps were defined as an opening in the canopy that reached to within 2 m of the forest floor and exceeded 10 m<sup>2</sup> as determined by the vertical projection of the drip edge of the surrounding canopy trees (Kimball et al. 1995). Gaps were classified into 3 types: harvest gaps were canopy openings created by tree removal during the winter of 1987–1988; 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. Tree-fall gaps and ledge gaps were not mapped in harvested blocks because their boundaries were largely obscured or encompassed by those of the harvest gaps (Kimball et al. 1995).

Harvest gaps averaged 210.2 m<sup>2</sup> (SE = 32.0,  $n = 126$ ) in size and ranged from single-tree gaps <25 m<sup>2</sup> to 1 gap that exceeded 3,000 m<sup>2</sup> (Kimball et al. 1995; Supplemental Appendix B available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). The gaps were distributed proportionally to the area of soil-drainage classes and forest-cover types found in the 10 harvested blocks (Kimball et al. 1995). Tree-fall gaps averaged 24.1 m<sup>2</sup> (SE = 2.1,  $n = 80$ ) and were predominantly 10–50 m<sup>2</sup> in size. Ledge gaps, which averaged 76.1 m<sup>2</sup> (SE = 13.1,  $n = 127$ ), were also common in the 10- to 50-m<sup>2</sup> size range but some of these gaps were as large as 850 m<sup>2</sup> (Supplemental Appendix B available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Preliminary analysis of the tree-fall gaps indicated that they caused little to no change in the distributions of birds, so their results are not included in this study. Most species also showed relatively weak changes in their distribution around ledge gaps, so we focus on the harvest gaps and explicitly discuss the ledge gaps only in instances where species showed notable changes; thus, we use the term “gaps” to refer to harvest gaps unless specified otherwise. As another note of clarification, throughout this study there are measurements relating to harvest gaps prior to the harvest. Although the harvest gaps did not yet exist, we retain the terminology to indicate that we are referring to the same areas of the forest before and after the harvest.

## METHODS

### Data Collection

The locations at which birds were seen or heard were collected as part of the territory mapping methodology (IBBC 1969, Witham et al. 1993) used to estimate the number of

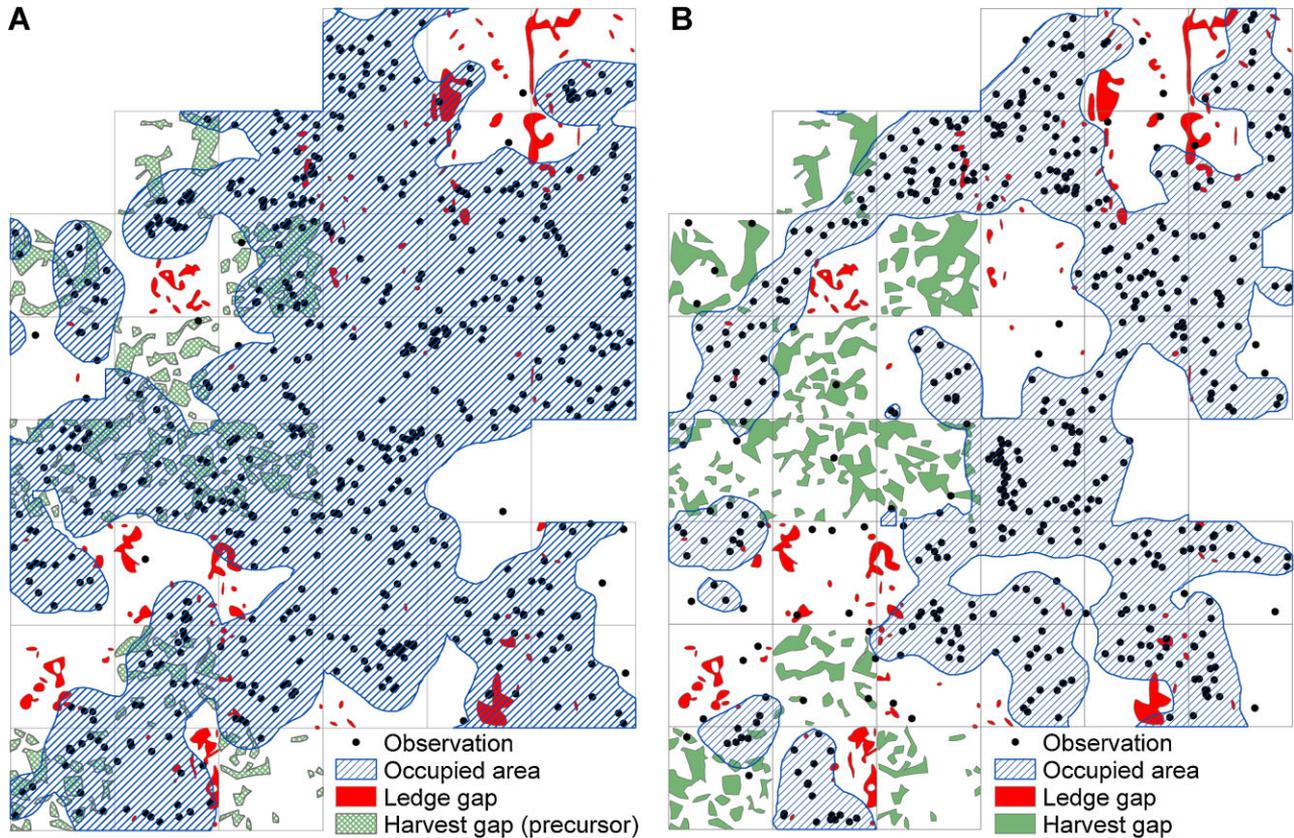
territories of all species in the study area. The data were collected in 16 visits during the breeding season (mid-May through mid-July) each year by 1 observer (J. W. W.) for all 20 years. In each visit, the entire length of all north–south transects through block centers or along the block edges were sampled between 0430 hours and 1030 hours (Fig. 1). Bird observations were plotted on paper maps of the study area using the stakes at the study grid intersections as reference points. All observations on each map were digitized into a Geographic Information System (Witham and Kimball 1996) and then compiled to generate composite maps for each species in each year.

### Data Analysis

We measured changes in the spatial distribution of birds using 3 metrics. First, we used all observations of a species in a year to delineate the portion of the study area that the species used (Fig. 2; Supplemental Appendix C available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). We termed the area encompassing this aggregation of observations the occupied area (OA) for a species and measured changes in spatial distribution relative to the gaps using the proportion of gap area that occurred within a species' OA. Second, we examined changes in average distance of all observations of a species in a year to the nearest gap of each type. Finally, because the change in average distance from gaps is only a scalar representation of the underlying distribution of distances, we also examined changes in the distribution of distances for each species in each year. The distribution of distances is important to consider because it indicates whether species are predominantly using gaps and areas surrounding gaps (i.e., edges) or whether they are using areas farther into the forest. We considered a species to have responded positively to gaps if the proportion of gap area in its OA increased, its average distance from gaps decreased, and it exhibited a greater use of gaps or edges. The converse holds for species that responded negatively. Although these metrics are not mutually exclusive, we present them all because together they provide a more complete representation of the spatial response to the timber harvest.

The use of individual observations, rather than territories, as sampling units poses potential problems with pseudoreplication (Hurlburt 1984). However, we feel that the problems associated with pseudoreplication are less severe than those associated with the assignment of points to individuals and the arbitrary drawing of territory boundaries to determine habitat use. Nevertheless, we have minimized the effects of pseudoreplication in the analyses by examining shifts in OAs and average distances as opposed to the shifts of individual observations, thus ameliorating pseudoreplication but sacrificing replication (i.e., we have only 1 measurement/species/yr). Consequently, our analysis is based on a single time-series design with intervention, in which the effects of the harvest are indicated by a discontinuity in the measurements at the time of harvesting (Campbell and Stanley 1966).

*Delineation of occupied areas.*—We delineated the boundaries of species' OAs in each year with the 90% contour of



**Figure 2.** The observations and occupied areas of the ovenbird in 1986 (A) and 1989 (B) in relation to the gaps. Note that in 1986 the harvest gaps did not yet exist; they are included to show how these areas of the forest were used prior to the harvest. Because birds did not respond strongly to treefall gaps, they have been omitted for clarity. Each square is 1-ha (100 m × 100 m).

fixed-kernel home-range estimators using the Animal Movement Extension in ArcView (Hooge and Eichenlaub 2000). The choice of bandwidth (smoothing parameter,  $h$ ) is critical with this method because it greatly affects the area of use identified by the kernel estimator (Silverman 1986, Worton 1995). Our main criterion for bandwidth selection was based on a trade-off between the exclusion of areas without observations and the inclusion of clusters of observations (i.e., isolated territories) that were separated from larger groups of observations (i.e., groups of territories). Through trial and error, we found  $h = 20$  to be the correct balance for most bird species. Although this choice of bandwidth is relatively stringent, with 16 sampling periods we were confident that areas without significant concentrations of observations should be excluded from the OA. The OAs of species with widely dispersed observations (e.g., great-crested flycatcher [*Myiarchus crinitus*], brown-headed cowbird [*Molothrus ater*], and pileated woodpecker [*Dryocopus pileatus*]) were not accurately represented by this choice of bandwidth because the density function decomposed into its constituent kernels (Kernohan et al. 2001); these species were excluded from the analyses.

*Measuring changes in spatial distribution.*—We characterized temporal changes in the proportion of gap area in an OA and the average distance to gaps as 1 of 3 types of responses: no response to gap creation (i.e., no change in the trajectories of the preharvest trends); a positive or negative response to

the gaps (i.e., a single change in the trajectories of the preharvest trends); and a positive or negative response followed by a return to preharvest levels (i.e., 2 subsequent changes in the preharvest trends). The first type of response can be modeled with a simple linear regression and the latter 2 types can be modeled with 1- and 2-breakpoint piecewise regression models, respectively (Seber and Wild 1989).

We fit all 3 models to the 20-year time series of each species using nonlinear regression (PROC NLIN; SAS Institute 2003). To meet model assumptions, proportions of gap areas were square-root transformed; transformation was not necessary for average distance. We used the Marquardt iterative method to search the parameter space for the least-squares estimates that minimized the residual sums-of-squares of each model. We used this method because it deals with ill-conditioned and singular matrices better than other methods (Seber and Wild 1989). Initial parameter estimates for the breakpoints were found by searching all possible combinations of  $x_0 = 1986\text{--}1989$  (1- and 2-breakpoint model) and  $x_1 = 1990\text{--}2000$  (2-breakpoint model) for the combination that minimized the sums-of-squares; these starting values corresponded to the years immediately before and after the harvest and 3–12 years after the harvest. 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. Convergence occurred when the relative offset convergence

measure of Bates and Watts was  $<10^{-5}$  (SAS Institute 2003). In some cases, the convergence criterion was not met, but in these cases the parameter estimates had stabilized to a precision of  $10^{-4}$  in  $<20$  iterations and the use of other iterative methods (e.g., Gauss–Newton) yielded nearly identical parameter estimates.

We used Akaike's Information Criteria (AIC) to select which of the 3 models best fit the data for each species (Burnham and Anderson 2002). We used the 2-breakpoint piecewise regression model as our global model because the other models were nested subsets of it. 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. 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<sub>s</sub>; Burnham and Anderson 2002).

For species for which a 1- or 2-breakpoint model provided a better fit to the data, the slopes of the line segments can be significantly different from zero without a net change in the metric (i.e., the metric returned to preharvest levels). To test for this outcome, we compared the proportion of gap area in an OA and the average distance to gaps in the preharvest years (1983–1987) to those in the last 5 years of the post-harvest period (1998–2002) using Mann–Whitney  $U$ -test (Zar 1999).

To examine changes in distribution of distances over time, for each year we compared the cumulative distribution curve of observed distances from gaps with the cumulative distribution curve based on all possible points spaced 5 m apart within the study area (observed and expected curves, respectively). We determined the distributions to be different if  $\geq 10\%$  of the points on the observed curve had corresponding points on the expected curve that fell outside the 95%

confidence band around the observed curve (Supplemental Appendix D available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). We did not use a standard test such as the Kolomogorov–Smirnov test (Zar 1999) because the critical values are sensitive to sample sizes, which in this case were large because of the multiple nonindependent observations for each species. We graphically represented the changes in distributions of distances from each type of gap over time by plotting the differences between the percentage of observations in each of 6 distance classes (0 m [within a gap], 0–25 m, 25–50 m, 50–75 m, 75–100 m, and  $>100$  m; i.e., percentage used) and the percentage of the study area occurring in each of these distance classes (6.6%, 29.7%, 12.8%, 7.4%, 5.4%, and 37.9% for harvest gaps, respectively, and 2.4%, 37.9%, 29.3%, 18.5%, 8.4%, and 3.5% for ledge gaps; i.e., percentage available). Positive differences indicate selection for a distance class and negative differences indicate avoidance.

## RESULTS

There were 20 species that were abundant enough for analyses ( $>1$  territory/yr, on average). The ovenbird (*Seiurus aurocapillus*) and black-throated green warbler (*Dendroica virens*) were the most abundant birds and had the first- and third-largest average OA, which covered 56% and 42% of the study area, respectively (Table 1). The black-capped chickadee (*Poecile atricapillus*) had about a third as many individuals but the second-largest average OA, which covered about 51% of the study area. Not surprisingly, the number of territories and size of an OA were highly correlated within most (15 of 20) species (Table 1) as well as across all species ( $r = 0.72$ ,  $P < 0.001$ ).

The temporal trends in the proportion of gap area in an OA, average distance to the nearest gap, and distribution of

**Table 1.** Mean, standard deviation (SD), and range of territory numbers and sizes of the occupied area (OA) of 20 bird species that bred in the 40-ha study area at the Holt Research Forest, Maine, USA, from 1983 to 2002 and Pearson's correlation ( $r$ ) between OA size and territory numbers.

Bird species	$N^a$	No. of territories			OA size (ha)			$r$	$P$ -value
		$\bar{x}^b$	SD	Range	$\bar{x}^b$	SD	Range <sup>b</sup>		
Eastern wood-pewee ( <i>Contopus virens</i> )	20	6.6	2.44	3–10	7.4	2.30	3.0–10.7	0.69	$<0.001$
Blue-headed vireo ( <i>Vireo solitarius</i> )	18	4.0	2.49	0–9	7.9	2.78	2.8–12.7	0.41	0.088
Black-capped chickadee ( <i>Poecile atricapillus</i> )	20	9.2	2.12	6–13	20.2	4.49	12.4–29.8	0.44	0.054
Brown creeper ( <i>Certhia americana</i> )	20	5.9	1.48	4–9	14.6	2.48	10.0–19.0	0.38	0.099
Red-breasted nuthatch ( <i>Sitta canadensis</i> )	20	4.7	1.53	2–8	12.2	4.98	3.7–23.2	0.71	$<0.001$
Winter wren ( <i>Troglodytes troglodytes</i> )	8	1.1	1.67	0–5	4.5	2.92	1.9–10.5	0.89	0.003
Golden-crowned kinglet ( <i>Regulus satrapa</i> )	19	2.8	1.74	0–6	4.4	2.07	0.9–7.0	0.76	$<0.001$
Veery ( <i>Catharus fuscescens</i> )	20	3.6	1.98	1–7	6.6	2.00	3.5–10.1	0.82	$<0.001$
Hermit thrush ( <i>C. guttatus</i> )	20	10.2	2.96	6–15	15.5	4.42	6.6–25.8	0.62	0.004
Nashville warbler ( <i>Vermivora ruficapilla</i> )	10	1.8	2.55	0–8	4.9	3.52	1.6–11.7	0.93	$<0.001$
Yellow-rumped warbler ( <i>Dendroica coronata</i> )	20	12.2	2.67	6–16	15.2	3.41	10.5–23.1	0.50	0.023
Black-and-white warbler ( <i>Mniotilta varia</i> )	20	4.6	1.43	2–8	9.1	3.04	4.5–18.1	0.78	$<0.001$
Blackburnian warbler ( <i>D. fusca</i> )	20	11.8	2.31	8–17	9.3	2.89	3.5–15.1	0.27	0.243
Black-throated green warbler ( <i>D. virens</i> )	20	27.7	4.78	23–40	16.8	4.04	10.7–25.9	0.63	0.003
Pine warbler ( <i>D. pinus</i> )	20	2.7	1.59	1–6	5.4	2.62	1.5–9.5	0.81	$<0.001$
Ovenbird ( <i>Seiurus aurocapillus</i> )	20	27.2	4.12	21–39	22.5	5.50	15.0–33.5	0.60	0.005
Common yellowthroat ( <i>Geothlypis trichas</i> )	20	4.8	2.55	1–9	3.5	1.90	1.1–7.9	0.72	$<0.001$
Scarlet tanager ( <i>Piranga olivacea</i> )	20	3.1	1.10	1–5	7.5	2.69	3.6–14.4	0.22	0.356
White-throated sparrow ( <i>Zonotrichia albicollis</i> )	18	4.8	3.29	0–10	5.8	2.88	1.6–10.6	0.83	$<0.001$
Purple finch ( <i>Carpodacus purpureus</i> )	20	3.8	2.05	1–9	9.8	3.52	4.8–15.7	0.78	$<0.001$

<sup>a</sup> No. of years in which  $\geq 1$  territories were established at the Holt Research Forest.

<sup>b</sup> Metric excludes years in which there were no territories for that species.

**Table 2.** Summary of 1- and 2-breakpoint regression models that describe temporal trends in the square root of the proportions of total area of harvest gaps and ledge gaps occurring in the occupied areas of bird species breeding at the Holt Research Forest, Maine, USA, 1983–2002.

Bird species	Regression summary <sup>a</sup>									Difference <sup>b</sup>	
	R <sup>2</sup>	Slope <sub>1</sub>	P <sub>1</sub>	Breakpoint <sub>1</sub>	Slope <sub>2</sub>	P <sub>2</sub>	Breakpoint <sub>2</sub>	Slope <sub>3</sub>	P <sub>3</sub>	$\bar{x}$	P-value
Harvest gaps											
Eastern wood-pewee	0.57	0.04 (0.011)	0.001	1994 (1.6)	-0.03 (0.021)	0.123				0.13	0.095
Veery	0.76	-0.04 (0.010)	0.001	1991 (0.9)	0.04 (0.007)	0.000				0.10	0.222
Black-and-white warbler	0.60	-0.05 (0.038)	0.234	1987 (1.6)	0.02 (0.005)	0.000				0.26	0.008
Black-throated green warbler	0.76	-0.06 (0.011)	0.000	1990 (0.9)	0.01 (0.006)	0.112				-0.25	0.008
Pine warbler	0.89	-0.02 (0.039)	0.641	1987 (0.6)	0.19 (0.039)	0.000	1990 (0.4)	-0.03 (0.007)	0.001	0.15	0.008
Ovenbird	0.90	-0.03 (0.025)	0.339	1987 (0.5)	-0.32 (0.111)	0.012	1989 (0.3)	0.04 (0.006)	0.000	-0.28	0.008
White-throated sparrow	0.78	-0.02 (0.044)	0.735	1987 (0.4)	0.35 (0.141)	0.026	1988 (0.4)	-0.04 (0.007)	0.000	0.04	0.905
Scarlet tanager	0.43	-0.04 (0.026)	0.157	1988 (1.7)	0.02 (0.005)	0.007				0.07	0.421
Ledge gaps											
Hermit thrush	0.74	-0.04 (0.027)	0.137	1987 (1.1)	0.14 (0.120)	0.266	1989 (0.9)	0.00 (0.006)	0.828	0.35	0.008
Ovenbird	0.59	-0.03 (0.009)	0.004	1993 (1.2)	0.04 (0.012)	0.005				0.07	0.548

<sup>a</sup> Summary includes proportion of variance explained ( $R^2$ ), estimated slope of segment  $i$  (slope <sub>$i$</sub>  [SE]), estimated breakpoint between segment  $i$  and  $i + 1$  (breakpoint <sub>$i$</sub>  [SE]), and  $P$ -value <sub>$i$</sub>  from test of  $H_0$ : Slope <sub>$i$</sub>  = 0.

<sup>b</sup> Difference between the averages of the untransformed proportions from the first 5 years (1983–1987) and last 5 years (1998–2002) of the time series. Statistical significance is based on exact  $P$ -values from Mann–Whitney  $U$ -tests of differences between the first 5 years and last 5 years of data.

distances varied among species. Trends in the proportion of harvest gap area within OAs of 12 species were best described by straight lines (4 significantly increasing and 2 significantly decreasing; Supplemental Appendix E available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)), while 8 species showed more complicated trends and were modeled with 1- or 2-breakpoint models (Table 2). Similarly, 13 species had trends in average distance to harvest gaps that were best represented by a straight line (1 significantly increasing and 3 significantly decreasing; Supplemental Appendix E available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). The trends in average distance for the remaining 7 species were best fit by higher-order breakpoint models (Table 3). Changes in the distributions of distances were generally congruent with the trends in average distance (e.g., an increase in average distance was associated with a decrease in the use of gaps and the edges and an increase in use of areas farther from the gaps).

Based on the patterns in the trends of these 3 metrics, 11 species exhibited notable and consistent responses to the harvest: 8 responded positively and 3 negatively. In contrast,

9 species showed a response that was weak (blue-headed vireo [*Vireo solitarius*], golden-crowned kinglet [*Regulus satrapa*], and yellow-rumped warbler [*Dendroica coronata*]) or a response that was inconsistent across the metrics (black-capped chickadee, brown creeper [*Certhia americana*], red-breasted nuthatch [*Sitta canadensis*], blackburnian warbler [*D. fusca*], scarlet tanager [*Piranga olivacea*], and purple finch [*Carpodacus purpureus*]).

### Species That Responded Positively to the Timber Harvest

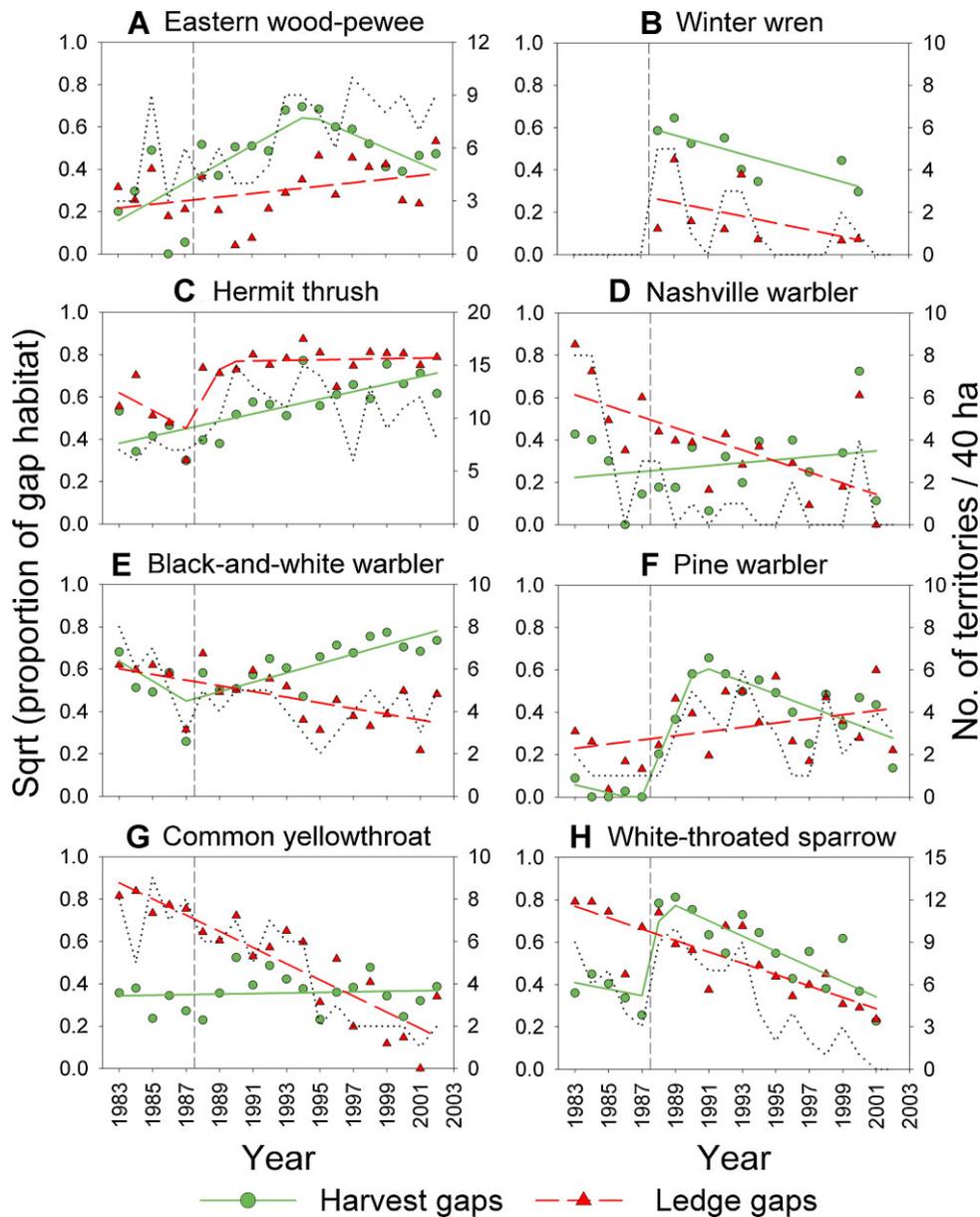
In general, the 8 species that responded positively to the harvest exhibited an increase in the amount of gap area in their OA (Fig. 3) and a decrease in their average distance to gaps (Fig. 4), and they selected gaps and edge habitats (Fig. 5). The change in these metrics was strong and immediate for winter wrens (*Troglodytes troglodytes*) and white-throated sparrows (*Zonotrichia albicollis*). Winter wrens, which were previously absent from the forest, used gaps (0 m) and forest edges (0–25 m from gaps) more than expected (Fig. 5B). White-throated sparrows increased in

**Table 3.** Summary of 1- and 2-breakpoint regression models that describe temporal trends in the average distance to the nearest harvest and ledge gaps of observations of bird species breeding at the Holt Research Forest, Maine, USA, 1983–2002.

Bird species	Regression summary <sup>a</sup>									Difference <sup>b</sup>	
	R <sup>2</sup>	Slope <sub>1</sub>	P <sub>1</sub>	Breakpoint <sub>1</sub>	Slope <sub>2</sub>	P <sub>2</sub>	Breakpoint <sub>2</sub>	Slope <sub>3</sub>	P <sub>3</sub>	$\bar{x}$	P-value
Harvest gaps											
Eastern wood-pewee	0.63	24.9 (11.59)	0.050	1986 (0.8)	-24.0 (11.59)	0.057	1991 (1.1)	5.0 (2.17)	0.037	-31.74	0.222
Veery	0.56	7.9 (3.25)	0.027	1991 (1.4)	-6.6 (1.76)	0.002				-7.13	0.690
Black-and-white warbler	0.76	2.4 (4.30)	0.581	1989 (2.0)	-6.7 (1.19)	0.000				-67.23	0.008
Black-throated green warbler	0.73	6.8 (1.41)	0.000	1989 (0.8)	-2.0 (0.56)	0.002				7.56	0.222
Pine warbler	0.83	23.4 (11.13)	0.054	1987 (0.5)	-48.6 (11.13)	0.001	1990 (0.5)	8.3 (2.08)	0.001	-61.85	0.032
Ovenbird	0.52	4.0 (1.22)	0.005	1989 (1.2)	-0.8 (0.48)	0.109				8.77	0.151
White-throated sparrow	0.83	-16.4 (3.61)	0.000	1990 (1.2)	-1.4 (1.60)	0.388				-90.85	0.016
Ledge gaps											
Blackburnian warbler	0.70	-0.5 (0.13)	0.001	1997 (0.8)	2.4 (0.67)	0.002				0.46	0.841

<sup>a</sup> Summary includes proportion of variance explained ( $R^2$ ), estimated slope of segment  $i$  (slope <sub>$i$</sub>  [SE]), estimated breakpoint between segment  $i$  and  $i + 1$  (breakpoint <sub>$i$</sub>  [SE]), and  $P$ -value <sub>$i$</sub>  from test of  $H_0$ : Slope <sub>$i$</sub>  = 0.

<sup>b</sup> Difference between the averages of the mean distances from the first 5 years (1983–1987) and last 5 years (1998–2002) of the time series. Statistical significance is based on exact  $P$ -values from Mann–Whitney  $U$ -tests of differences between the first 5 years and last 5 years of data.



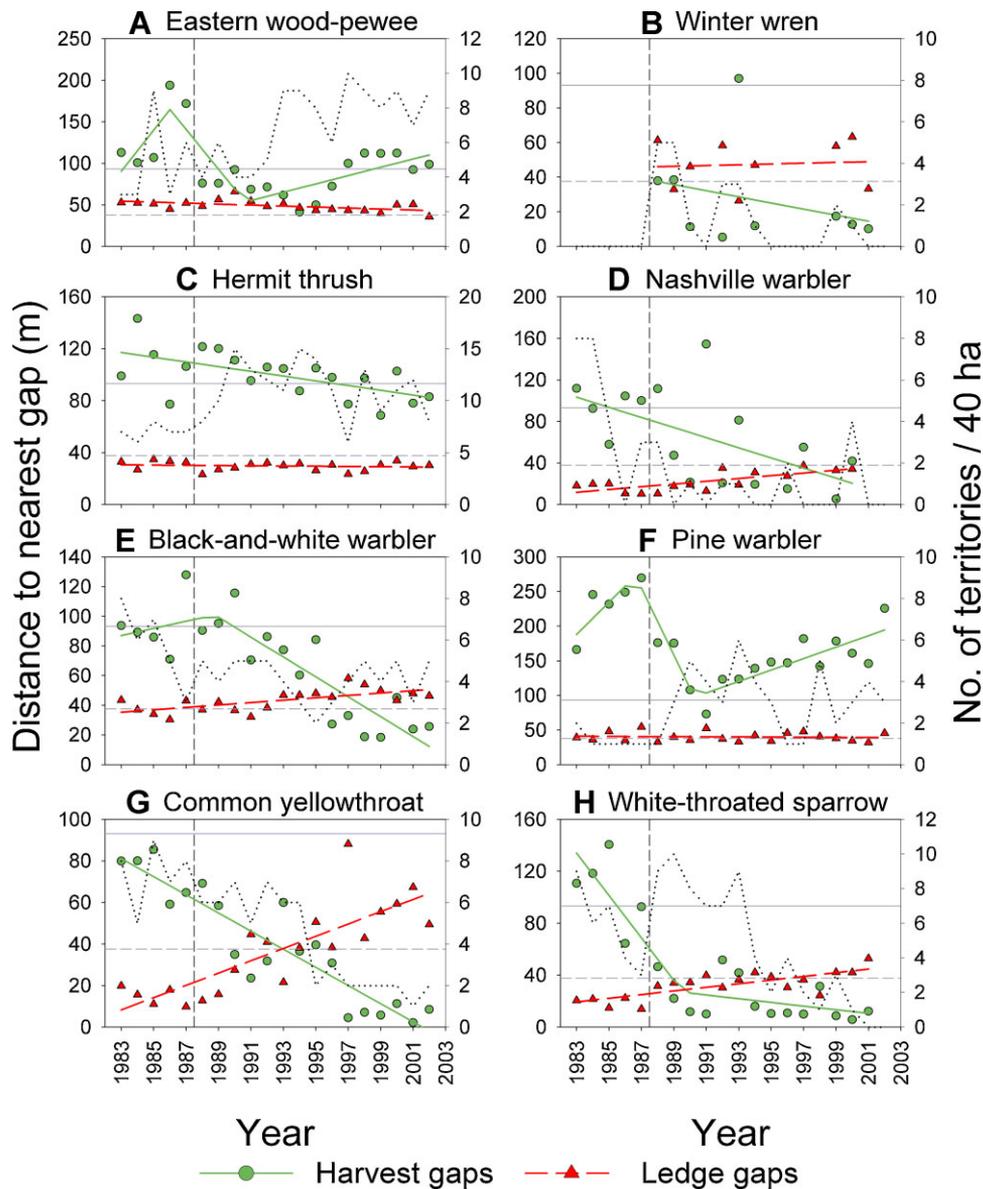
**Figure 3.** Square root of the proportion of harvest gap and ledge gap area that occur within the occupied areas of species (A–H) that responded positively to the timber harvest in the 40 ha study area of the Holt Research Forest, 1983–2002. The fluctuating dotted line represents the number of territories, which are shown to provide context for changes in the proportion of gap area. The vertical dashed line denotes the time of harvest.

abundance, occurred an average of >100 m closer to gaps (Fig. 4H), had >60% of the gap area within their OA (Fig. 3H), and selected gaps and surrounding forest edges (0–25 m; Fig. 5H; see Supplemental Appendix C available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Pine warblers (*D. pinus*) were associated with ledge gaps and salt marsh and river edges in the control half of the study area prior to the harvest. After the harvest, the species occurred on average >100 m closer to the gaps (Fig. 4F) and the proportion of gap area within its OA increased from nearly zero to almost 40% (Fig. 3F). Nevertheless, pine warblers still occurred farther from gaps than was expected under a scenario of random habitat use and showed only limited spatial and temporal use of the gap and edge habitat (Fig. 5F).

The eastern wood-pewee (*Contopus virens*) and the black-and-white warbler (*Mniotilta varia*) showed a delay in their peak use of the harvested areas. Immediately following the harvest, eastern wood-pewees selected for gap and edge habitats (Fig. 5A), but they occurred closest to gaps (Fig. 4A) and their OAs contained the highest amount of gap area (approx. 40%) during 6–8 years after the harvest (Fig. 3A). Black-and-white warblers' use of the gap and edge habitats increased gradually following the harvest until 10 years after the harvest when the metrics stabilized (Figs. 3E, 4E, and 5E).

Common yellowthroats (*Geothlypis trichas*) exhibited a steady decrease in distance to harvest gaps and an increase in use of these gaps and their edges, while their use



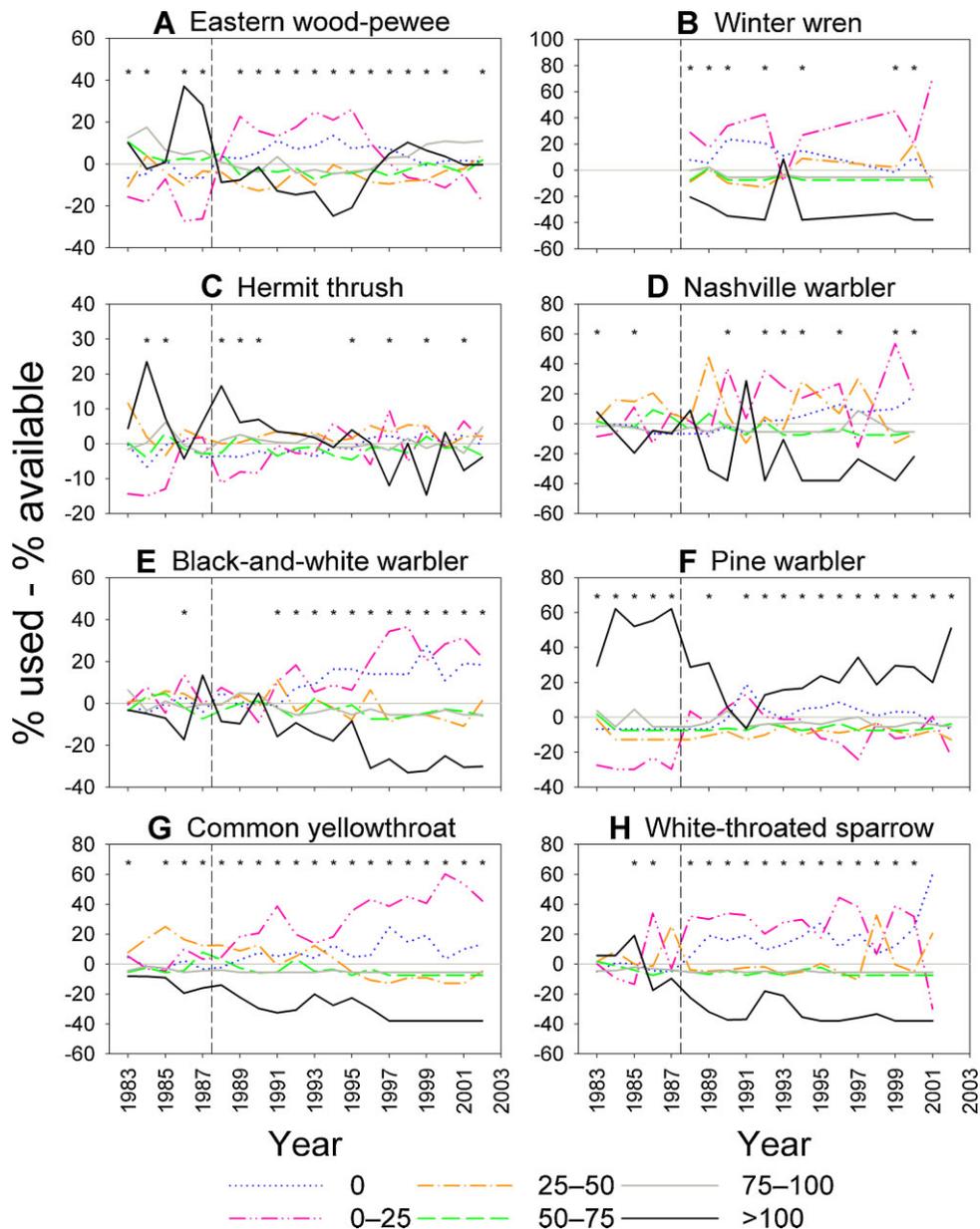
**Figure 4.** Average distance of all observations of a species to the nearest harvest gap and nearest ledge gap for species (A–H) that responded positively to gaps in the 40 ha study area of the Holt Research Forest, 1983–2002. Horizontal lines represent average distance of random points to the nearest gap of each type (solid = harvest gaps and dashed = ledge gaps). The fluctuating dotted line represents the number of territories, which are shown to provide context for changes in the average distance. The vertical dashed line denotes the time of harvest. Note different scales of y-axes.

of ledge gaps decreased and their distance to ledge gaps increased (Figs. 3G, 4G, and 5G; Supplemental Appendix F available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). This same pattern held, but to a lesser degree, for black-and-white warblers and Nashville warblers (*Vermivora ruficapilla*; Figs. 3–5; Supplemental Appendix F available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)).

Although the hermit thrush (*Catharus guttatus*) appeared to respond positively to the harvest gaps (Figs. 3C and 4C), it did not exhibit as strong a selection for gaps or the associated edge habitat as did the other species that responded positively (Fig. 5C). However, the species did show a marked increase in the amount of ledge gaps in its OA that was coincident with the creation of the harvest gaps (Fig. 3C).

### Species That Responded Negatively to the Timber Harvest

Three species showed strong negative responses to the timber harvest. Both the black-throated green warbler and ovenbird exhibited a retraction of their OAs away from harvested areas and an avoidance of gap and adjacent edge habitat (Figs. 2, 6–8). These changes resulted in smaller OAs but were not accompanied by comparable decreases in abundance (Fig. 9). Prior to the timber harvest, the veery occurred closer to the areas that were to be harvested than was expected by random use (Fig. 8A). Following the harvest, the proportion of gap area that occurred within their OA decreased, the average distance to gaps increased, and use of forest >100 m away from the gaps increased (Figs. 6A, 7A, and 8A).



**Figure 5.** Differences between the percentage of study area (% available) and the percentage of observations (% used) occurring in each distance class from harvest gaps for species (A–H) that responded positively to gaps at the Holt Research Forest, 1983–2002. Asterisks indicate years in which there was a difference between the distribution of distances of observations from gaps and the distribution based on all points in the study area occurring on a 5 m grid. The vertical dashed line denotes the time of harvest. Note different scales of y-axes.

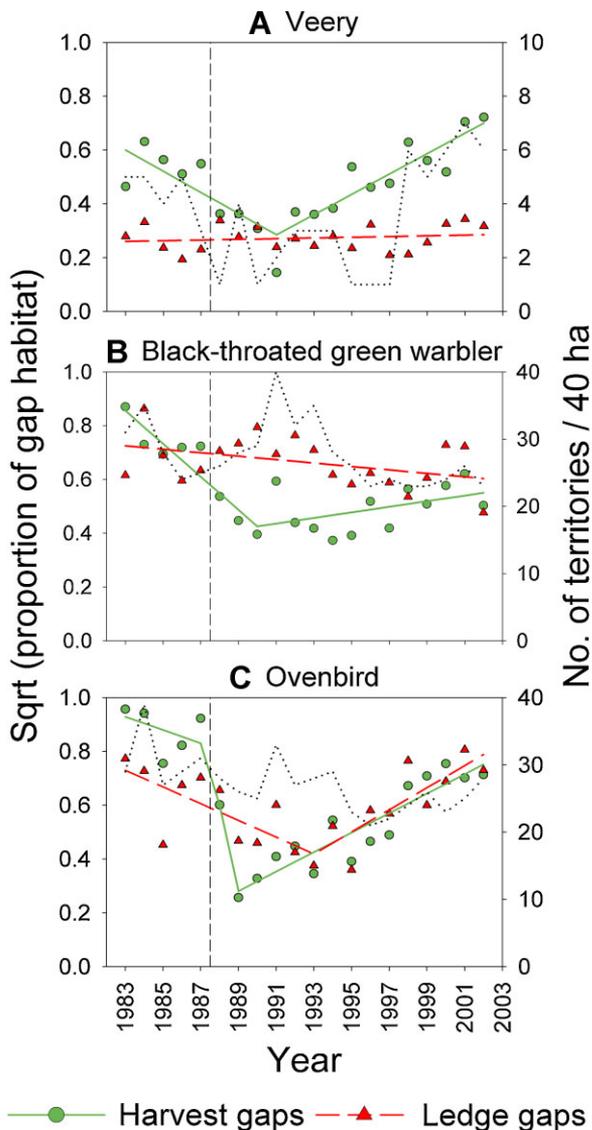
### Duration of Species' Responses

Only 1 of the 11 species that responded positively or negatively to the harvest did not show a return to preharvest levels by the end of the study in either the proportion of gap area in its OA or average distance to gaps (Tables 2 and 3). The black-and-white warbler had a higher proportion of gaps in its OA (Fig. 3E) and occurred closer to gaps (Fig. 4E) than it did during the preharvest period (Tables 2 and 3). The remaining 10 species had returned to preharvest levels in one or both measures. For example, for the black-throated green warbler and ovenbird, average distances from gaps 10–15 years after the harvest were the same as during the preharvest period (Table 3; Fig. 7) and the proportions of gap area in their OAs were approaching preharvest levels but

were still significantly different (Table 2; Fig. 6). The white-throated sparrow returned to its preharvest levels of gap area in its OA before its population declined to zero (Table 2; Fig. 3H). Similarly, the winter wren attained preharvest levels of habitat use because it was absent from the forest before the harvest and again 13 years after the harvest (Fig. 3B).

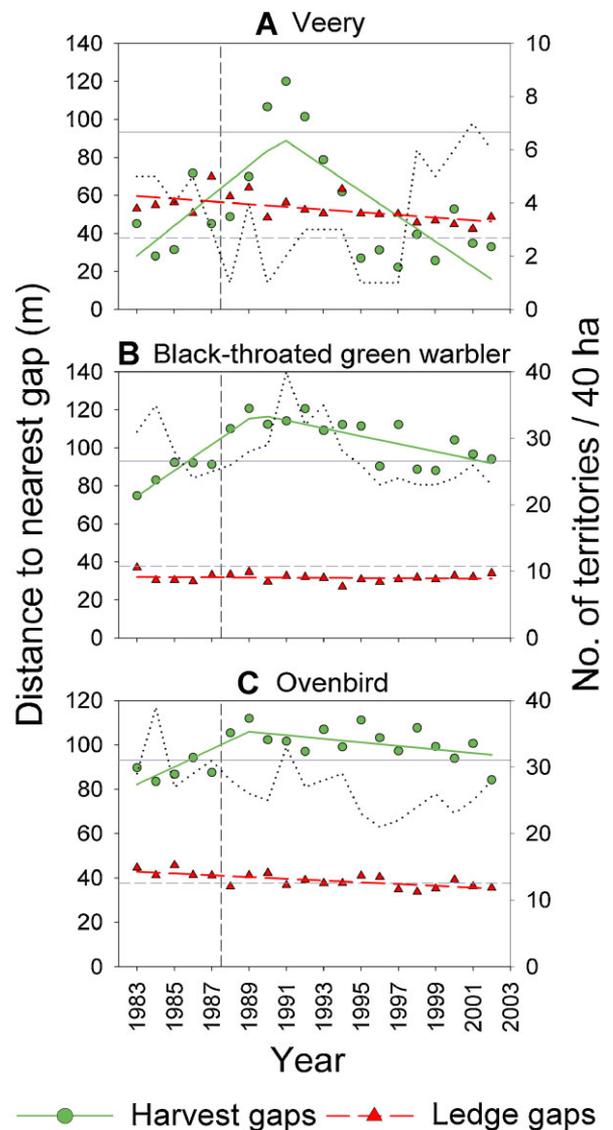
### DISCUSSION

Our examination of changes in spatial distribution of birds responding to group-selection timber harvesting showed that the distributions of species that are typically associated with early successional vegetation shifted to the recently created gaps and their edges (Figs. 3–5; Supplemental Appendix C



**Figure 6.** Square root of the proportion of harvest gap and ledge gap area that occur within the occupied areas of species (A–C) that responded negatively to the timber harvest in the 40 ha study area of the Holt Research Forest, 1983–2002. The fluctuating dotted line represents the number of territories, which are shown to provide context for changes in the proportion of gap area. The vertical dashed line denotes the time of harvest.

available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)), while mature-forest species avoided these areas (Figs. 2, 6–8). The duration of the changes in spatial distribution was generally short-lived; by 15 years after the harvest the use of the harvested areas by all but one of the affected species had reached or was approaching preharvest levels. Thus, based on changes in spatial distributions, group-selection timber harvesting is unlikely to have serious long-term consequences on forest bird populations and appears to be a relatively effective approach for maintaining bird species diversity while generating a supply of timber. These findings are consistent with those from our study on abundance, which showed an increase in abundance of early successional bird species following the timber harvest, negligible decreases in the abundance

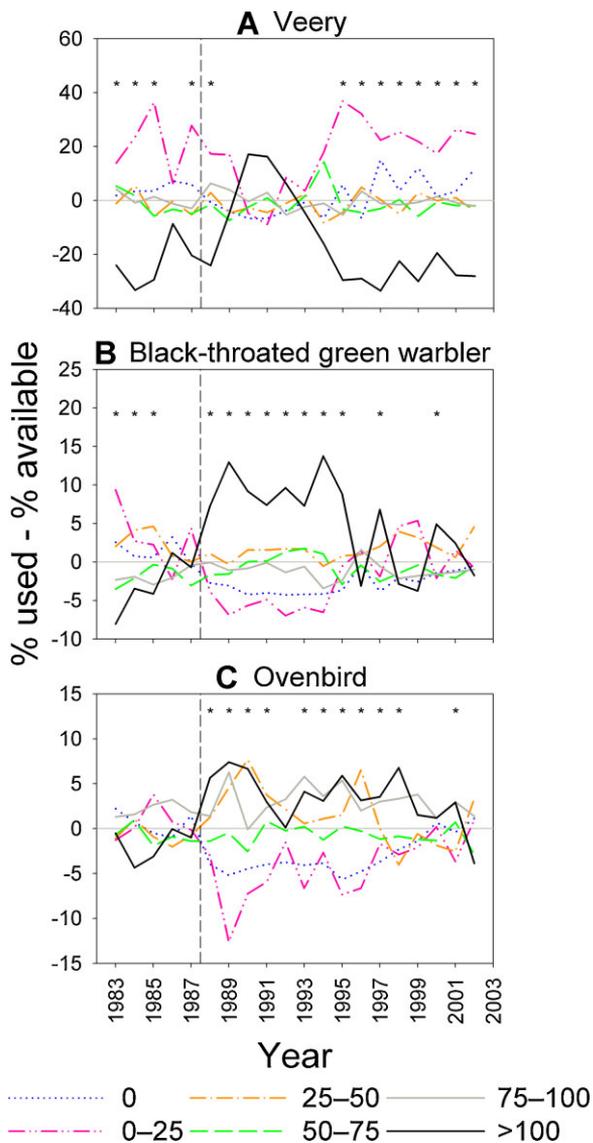


**Figure 7.** Average distance of all observations of a species to the nearest harvest gap and nearest ledge gap for species (A–C) that responded negatively to gaps in the 40 ha study area of the Holt Research Forest, 1983–2002. Horizontal lines represent average distance of random points to the nearest gap of each type (solid = harvest gaps and dashed = ledge gaps). The fluctuating dotted line represents the number of territories, which are shown to provide context for changes in the average distance. The vertical dashed line denotes the time of harvest. Note different scales of y-axes.

of mature-forest bird species, and a return to preharvest abundance levels for most species by 15 years postharvest (Campbell et al. 2007). Despite the apparent lack of long-term consequences, the changes in spatial distributions (especially when considered in conjunction with abundance) suggest more subtle, short-term effects of timber harvesting on bird populations.

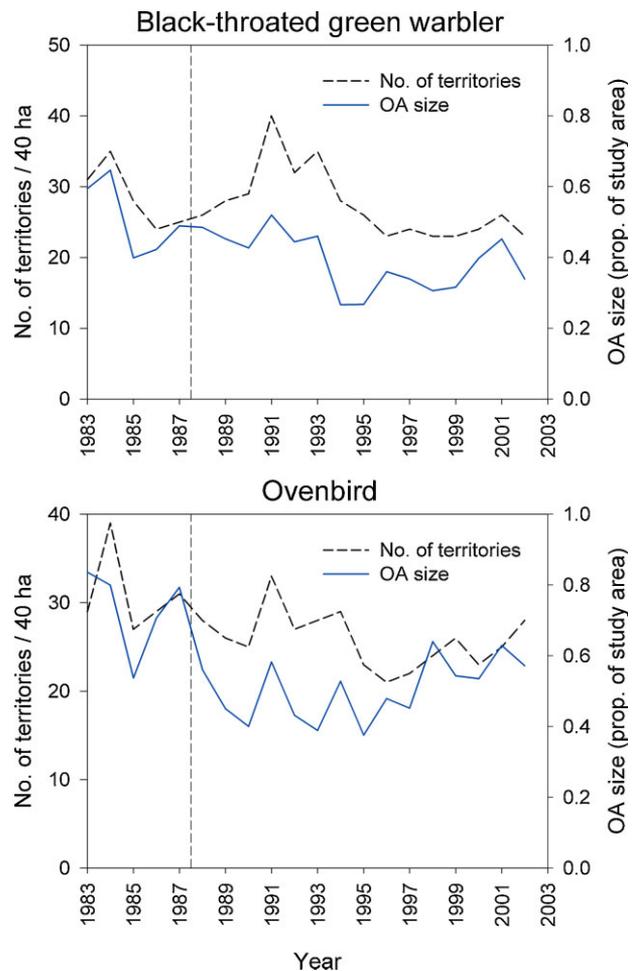
### Species That Responded Positively to the Timber Harvest

Early successional species such as the common yellowthroat, white-throated sparrow, and Nashville warbler were rare or decreasing in abundance within the study area prior to the timber harvest, probably due to the loss of early successional vegetation since postagricultural land abandonment (see also



**Figure 8.** Differences between the percentage of study area (% available) and the percentage of observations (% used) occurring in each distance class from harvest gaps for species (A–C) that responded negatively to gaps at the Holt Research Forest, 1983–2002. Asterisks indicate years in which there was a difference between the distribution of distances of observations from gaps and the distribution based on all points in the study area occurring on a 5 m grid. The vertical dashed line denotes the time of harvest. Note different scales of y-axes.

Holmes and Sherry 2001). Those that were still persisting in the study area at the start of our study largely occurred in and around the ledge gaps. Nevertheless, over the 20 years of this study, these gaps have continued to close and these species have decreased their use of these areas (Figs. 3 and 4). By creating new patches of early successional vegetation, the timber harvest temporarily bolstered populations of some of these bird species (Campbell et al. 2007). These changes in abundance were typically accompanied by an increase in the size of the OAs, the proportion of harvest gaps within their OAs, and the use of gaps (0 m) and their edges (0–25 m), as well as a decrease in average distance to the gap areas



**Figure 9.** Size of occupied area (OA; proportion of study area) and number of territories of the black-throated green warbler and ovenbird in the 40-ha study area of the Holt Research Forest, 1983–2002. The vertical dashed line denotes the time of harvest. Note different scales of y-axes.

(Figs. 3–5). Although the common yellowthroat did not increase in abundance in response to the timber harvest, individuals still seemed to prefer harvest gaps over ledge gaps. Even as their populations were declining, their distribution shifted from the ledge gaps to the harvest gaps. Although this process was apparent in the average distance from harvest gaps (Fig. 4G) and the selection of gaps and edges (Fig. 5G), movement into harvest gaps did not increase the overall proportion of harvest gaps that occurred in its OA (Fig. 3G) because the increase was likely offset by decreases in abundance and the size of its OA.

When increases in abundance were associated with an increase in size of the OAs and a spatial shift toward the harvest gaps, the gaps were being colonized by new individuals and not just occupied through the spatial expansion or movements of prior occupants. These dynamics support the idea that early successional bird species remain present in extensively forested landscapes in small numbers, primarily as “fugitive species” (sensu Hutchinson 1951). Although these species are prone to local extinction when disturbed patches regenerate, they can persist at larger spatial scales as long as disturbance generates new habitat within their dispersal

range (Sousa 1984). These types of dynamics were most prominently displayed by the winter wren and the white-throated sparrow. The former was absent from our study area prior to the harvest, and the latter was declining sharply until new individuals colonized the recently created harvest gaps (Fig. 3). By 15 years after the harvest both species stopped using the harvest gaps and became locally extinct.

Not all species that responded positively did so immediately, which suggested that the gaps became suitable for some species only after a period of regeneration. These differences led to a temporal succession of species using the harvest gaps as they grew back into mature forest: the white-throated sparrow and winter wren used the areas immediately following the harvest, the eastern wood-pewee about 7 years after the harvest, and the black-and-white warbler up to 15 years postharvest (Fig. 3).

### Species That Responded Negatively to the Timber Harvest

Three mature-forest bird species—the veery, black-throated green warbler, and ovenbird—exhibited a strong avoidance of the harvest gaps and their edges, a reduction in the size of their OAs, and minimal decreases in abundance following the harvest (Figs. 6–9; Campbell et al. 2007). The combination of these effects suggests that these species are crowding in the adjacent residual forest. Other studies have detected similar patterns. For example, Schmiegelow et al. (1997) found that abundance of Neotropical migrants increased in recently created forest fragments due to the displacement of individuals from adjacent harvested areas. Similarly, Darveau et al. (1995) showed an increase in densities of several forest bird species in riparian forest strips adjacent to new clearcuts.

In general, crowding appears to be a short-lived (<3 yr) phenomenon (Bierregaard and Lovejoy 1988, Darveau et al. 1995, Hagan et al. 1996, Schmiegelow et al. 1997), but it can last longer. For example, Warkentin et al. (2003) found that northern waterthrush (*Seiurus noveboracensis*) had elevated densities in riparian buffer strips adjacent to clearcuts for 5–10 years postharvest. In our study, the sustained decrease in the size of the OAs of the black-throated green warbler and ovenbird relative to the number of territories indicated that the crowding effects lasted up to 10 years after the timber harvest (Fig. 9).

Crowding can have important demographic effects, especially over the long-term, through density-dependent reductions in territory size. Smaller territories can lead to decreases in demographic rates by intensifying resource limitations and increasing time spent in agonistic interactions, which can, in turn, increase brood parasitism and predation on both adults and young. Sillett et al. (2004) found that territory size, the time males spent foraging (as opposed to activities associated with territorial defense), and the number of young fledged per territory were significantly greater for black-throated blue warblers in areas where densities had been experimentally reduced. Our data strongly suggest that average territory sizes of ovenbirds and black-throated green warblers decreased due to crowding (Fig. 9). However, because we could

not measure territory size directly, we do not know whether the reduction in territory size was diffused equally across most individuals, whether the effects were most acute nearest the gaps, or whether the effects were shaped by the interaction between habitat quality and dominance of males (Fretwell and Lucas 1969, Hagan et al. 1996, Rodenhouse et al. 1997). Distinguishing among these outcomes is important, especially when crowding persists for many years, because they can lead to different population-level effects.

Loss of mature forest from harvesting was accompanied by an increase in the amount of edge habitat within the forest. The effects of edges within a forest-dominated matrix on breeding birds are equivocal—some studies have found higher nest predation and brood parasitism near these types of edges (Brittingham and Temple 1983, King et al. 1996, Flaspohler et al. 2001, Manolis et al. 2002), while others have not (e.g., Rudnicky and Hunter 1993, Hanski et al. 1996, Driscoll and Donovan 2004). In our study, mature-forest bird species avoided the gaps and edges after the harvest, but they started to recolonize these areas 4 years later (Fig. 8) and had reached or were approaching preharvest levels of use by 15 years postharvest (Tables 2 and 3). Similarly, Wallendorf et al. (2007) found a decrease in the density of ovenbirds in a 100-m buffer around clearcuts for 4 years postharvest. Thus, if there were an increase in the occurrence of nest predators and parasites in edges in the years following the timber harvest, the tendency for mature-forest bird species to avoid these areas would help to mitigate the negative effects.

### Harvest Gaps Versus Natural Gaps

In general birds responded much more strongly to harvest gaps than the natural (ledge and tree-fall) gaps; at least 4 factors may have been responsible. First, individual harvest gaps were significantly larger on average and collectively covered a greater area than the natural gaps (Fig. 1; Supplemental Appendix B available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com)). Second, the harvest gaps were grouped in 1-ha blocks such that together they may have acted functionally as a single large opening (Hunter 1993). Third, harvest gaps were distributed proportionally to the area of soil drainage classes and forest cover types, whereas the tree-fall gaps were relatively more abundant on the mesic sites that had either mixed or conifer stands, and the ledge gaps were concentrated on areas with shallow, excessively drained soils (Kimball et al. 1995). The variation in forest cover type (Holmes and Robinson 1981, Rice et al. 1984) and underlying moisture gradient (Smith 1977, Karr and Freemark 1983) may have contributed to the differences in bird response among the gap types. Fourth, the vegetation dynamics were very different in the harvest and natural gaps during our study. The transition from mature forest to harvest gaps was abrupt followed by relatively fast regeneration. In contrast, the ledge gaps were present at the start of the study and were regenerating slowly throughout the study period because of poor site conditions, and tree-fall gaps were constantly appearing and quickly closing from the growth of adjacent trees.

## Study Limitations

Our study has 4 limitations that require exposition. First, although the study area is fairly large for a single territory mapping area, its small size limits the extrapolation of our results to larger spatial scales (James and McCulloch 1995). However, the vegetation of the study site is generally representative of the region (i.e., it is mature forest in a predominantly forested landscape; Supplemental Appendix A available online at [www.onlinelibrary.wiley.com](http://www.onlinelibrary.wiley.com); McWilliams et al. 2005), so it is unlikely that our results are atypical. Second, because we examined the spatial distribution of each bird species across the entire study area, there is no spatial replication in the experiment. Although spatial replication is certainly important, temporal replication can be just as important as spatial replication and perhaps more so in a temporally variable system, such as regenerating forest. We have sampled bird populations intensively over 20 consecutive years (5 yr preharvest, 15 yr postharvest), a long enough period to discriminate responses from year-to-year variability as well as capture the full temporal response (i.e., a return to preharvest distributions) of most species. This type of long-term, intensive research at a single location can detect important patterns that can be missed in spatially replicated short-term studies (Sallabanks et al. 2000, Collins 2001). Third, group-selection cuts were limited to individual blocks to provide controls for both the harvested blocks and the managed half of the study area. In a typical commercial operation, cutting would have occurred throughout most of the forest and would have converted a greater portion of the forest into early successional vegetation. Finally, we dichotomized the vegetation as forest or gap. Although this is a crude depiction of forest structure (see Lieberman et al. 1989), birds were clearly distributed non-randomly with respect to these 2 vegetation types and bird community structure varied temporally as birds tracked post-harvest changes in vegetation. Thus, this coarse description of the vegetation is apparently adequate for determining the distributions of many species in a forest managed for timber. Despite these limitations, our study represents the longest running experiment investigating a group-selection timber harvest and the only one to explicitly examine the changes in spatial distribution resulting from the harvest. As such, our findings contribute important insights into long-term responses of birds to forest management.

## MANAGEMENT IMPLICATIONS

The explicit examination of spatial distribution can provide managers who seek to extract timber while maintaining bird diversity with guidance in 3 key areas: length of interval between harvest reentries, minimum spacing of harvest gaps, and sensitivities and response thresholds of different species. Our findings suggest that 15 years may be an appropriate length for the inter-cut interval; by this time, the use and avoidance of the harvested areas by nearly all early- and late-successional species, respectively, had approached their preharvest levels. However, further study is needed to determine whether these areas can adequately sustain late-successional bird species following the additional removal of surrounding

mature forest (see Tozer et al. 2010). With regard to the spacing among gaps, the most sensitive late-successional species (ovenbird and black-throated green warbler) avoided areas within 25 m of the gaps, which suggests that to maintain these species in the landscape the areas between gaps should be at least large enough to hold a territory surrounded by a 25-m buffer. However, it is unclear whether birds will actually use these minimum-size areas or whether they require larger areas of undisturbed forest before deciding to settle near a gap. In contrast, early-successional bird species may have used relatively small gaps only because they occurred as part of a cluster of gaps. Further research on the spatial configuration of gaps is necessary to distinguish among these possibilities. Finally, knowing the strength and duration of changes in spatial distributions can also be used to quantify the sensitivities of different bird species to changes in stand structure and identify potential spatial and temporal thresholds in their responses (Gu enette and Villard 2005, Vanderwel et al. 2007). For example, both the winter wren and white-throated sparrow exhibited high use of the gaps immediately after the harvest, but the decrease in gap use and the near absence of the winter wren in the forest only 7 years after the harvest compared to the use of the gaps by the white-throated sparrow for 14 years suggests that the winter wren is more sensitive to temporal change. Similarly, the temporal succession of birds that use the regenerating gaps indicates differing tolerance thresholds to the suitability of gaps in the postharvest period.

Our findings also highlight the importance of considering other aspects of species responses in conjunction with abundance to understand the effects of timber harvesting on bird populations. By combining our findings on spatial distribution and abundance, we found that mature-forest bird species, such as the black-throated green warbler and the ovenbird, avoided harvested areas without changes in abundance, which led to crowding into the surrounding forest and potentially negative demographic consequences. In this case, management recommendations based solely on abundance would be misleading about the degree to which the timber harvest affected the populations of these species. Nevertheless, we expect that abundance will continue to be used by managers to make land-use decisions because of its relative ease of measurement, familiarity, historical precedence, and biological relevance. Indeed, in most cases, abundance will be a suitable basis for decisions (Bock and Jones 2004). However, when dealing with timber harvesting and other human disturbances, abundance metrics should be treated cautiously because they may be insensitive to more subtle effects on bird populations.

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