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Stephen P. Campbell

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**THE LONG-TERM EFFECTS OF A GROUP-SELECTION TIMBER HARVEST
ON THE BIRD COMMUNITY OF AN OAK-PINE FOREST IN MAINE**

By

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A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

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(in Wildlife Ecology)

The Graduate School

The University of Maine

August, 2007

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Thesis Advisor: Dr. Malcolm L. Hunter, Jr.

An Abstract of the Thesis Presented
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Bird populations have been monitored at the Holt Research Forest in Arrowsic, Maine since 1983 as part of a long-term forest ecosystem study. In the winter of 1987-1988, 10 ha of the 40-ha study area were subjected to a group-selection timber harvest (i.e., a harvest that creates canopy gaps by removing small groups of trees). I analyzed the first 20 years of these data (5 years of pre-harvest data and 15 years of post-harvest data) for changes in abundance and spatial distribution of birds in response to the harvest. Although species' responses to the group-selection harvest were idiosyncratic, two general patterns emerged. Bird species dependent on early successional habitat exhibited temporary (≤ 8 years) increases in abundance and a positive spatial response to the gaps (i.e., use of gaps increased, distance from gaps decreased, and use of edges [0-25 m from gaps] increased). In contrast, mature-forest bird species showed little change in abundance but relatively strong distributional shifts away from disturbed areas and the surrounding forest. The duration of the responses was generally short-lived; by 15 years

after the harvest, abundance levels of nearly all species and their use of the disturbed areas had approached pre-harvest levels.

Using the five years of pre-harvest data, I also assessed the roles of stochastic and deterministic processes in year-to-year changes in habitat use by comparing observed patterns in habitat use with patterns generated from null models. Although some species exhibited near random habitat use, observed patterns of variability for most species were matched by those generated from null models when random variability was constrained, which suggests that the variability in most species has both deterministic and stochastic components. In particular, null models that incorporated habitat preference or site fidelity each reproduced the observed patterns of variability for nearly half of the species examined. Support for these two models suggest that any factor that causes birds to return to the same site repeatedly and limits the spatial extent of the variability can generate spatial distribution patterns similar to those that were observed.

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Chapter 1

LONG-TERM EFFECTS OF GROUP-SELECTION TIMBER HARVESTING ON THE ABUNDANCE OF FOREST BIRDS

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). However, 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 post-treatment 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 I 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) forest ecosystem study of an oak-pine forest at the Holt Research Forest in Arrowsic, Maine (Witham et al. 1993). Specifically, I examined the first 20 years of data on bird abundance (5 years of pretreatment data and 15 years of post-treatment 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. 1.1). It occurs within the transition zone between oak-pine forest to the west and south and coastal 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).

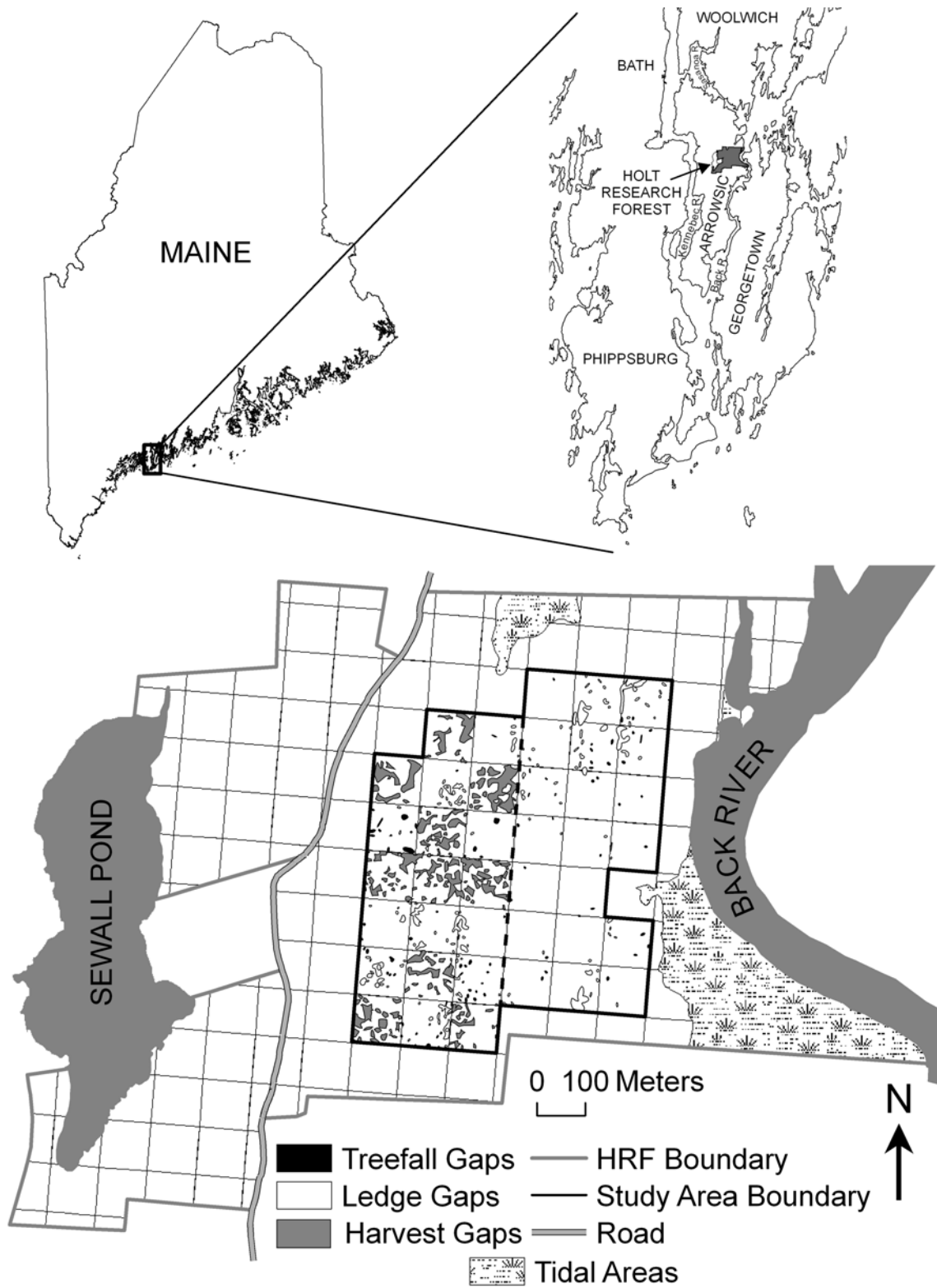


Figure 1.1. Map of the Holt Research Forest and the 40-ha study area in 1988, the year following the experimental treatment.

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. 1.1). The study area is divided into a grid of 40 1-ha (100 x 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. 1.1). 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 m²/ha, SD = 6.7%) of the basal area, and 26% (SD = 7.5%) of the forest cover from harvested blocks. The gaps averaged 210 m² (SE = 32.0, *n* = 126) and ranged from single tree gaps < 25m² to one gap that exceeded 3000 m² (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).

This design, although adequate for the 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, I counted territories at the scale of the managed and control halves of the study area. However, aggregating control and

managed blocks in the managed half diminished the effect of the harvest in my comparisons and therefore my findings are conservative. Also, 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. Witham) conducted territory mapping (IBBC 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 to 10:30 (Fig 1.1.). 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. Witham. A minimum of five records of occurrence was required to denote a territory, and an emphasis was placed on observations of counter-singing males. Territories that straddled the inner boundary between the control and managed halves of the study area or the outer boundary of the study area were counted where a majority of their points fell.

Data Analysis

I characterized the response of birds to the harvest by describing changes in the community and 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 I 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 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, I examined species that averaged more than one territory per year and three species that can have negative effects on the productivity of bird populations: 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 I used average number of detections per visit as an abundance index.

I 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).

I 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 ($\ln[\text{territories}/20 \text{ ha} + 0.5]$). I 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 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. I 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.

I used Akaike's information criteria (AIC) to select the model that best fit the data for each species (Burnham & Anderson 2002). I used the two-breakpoint piecewise regression model as my 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, I 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., $n/K < 40$), I 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 remainder of the paper I restrict my discussion to trends that were modeled by zero- (simple linear) and one-breakpoint models.

I calculated population trends (not log transformed) by taking the antilog of the slope estimate(s) of the best model for each species: $\text{trend} = e^{(\ln[\beta_i] - 0.5[\text{variance}_i])}$, where $\ln[\beta_i]$ = the slope of the i^{th} 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). I used t tests to determine whether trends were significantly different from zero and converted trends to average percent annual changes: $\%AC = (\text{trend} - 1)(100)$. 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, I 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 1.1.)

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 1.1). 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 (Appendices A.1).

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. 1.2; Wilcoxon paired-sample test, $p < 0.001$). Combined abundances of 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. 1.2).

Table 1.1. 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 from 1983-2002.

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

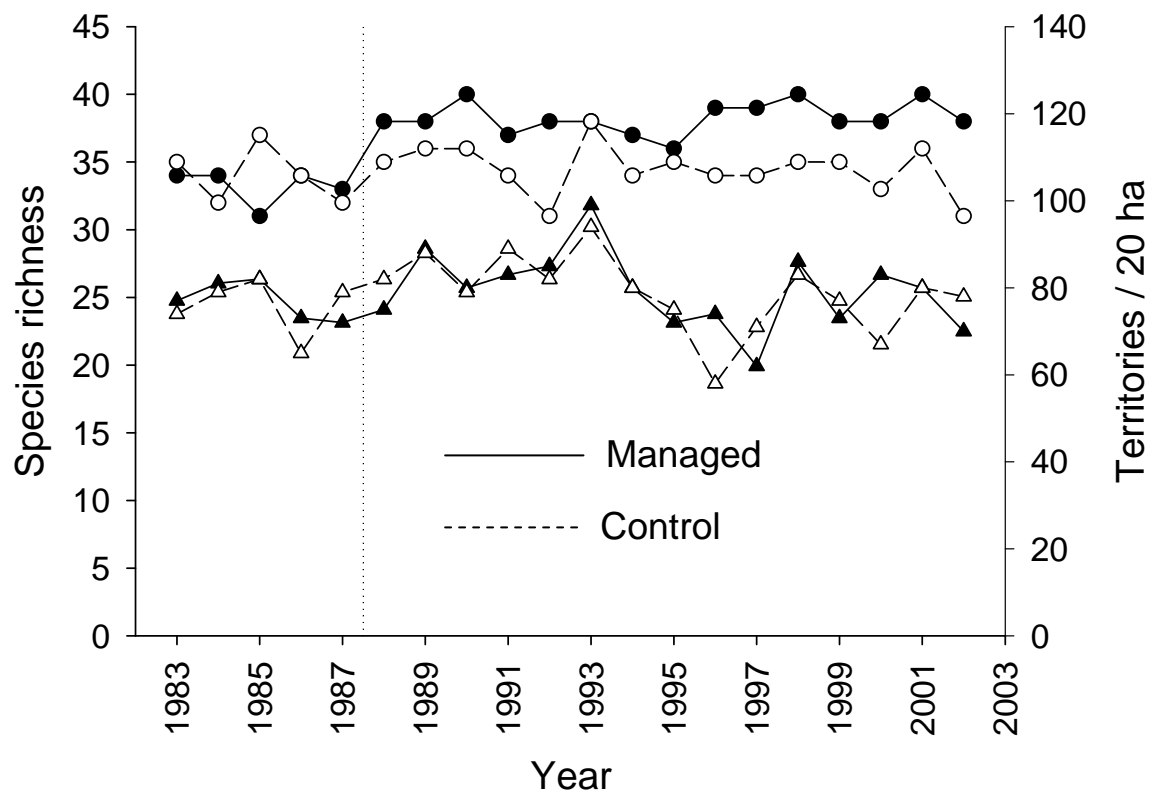


Figure 1.2. Total species richness (circles) and combined abundances (number of territories) of 28 species (triangles) of forest birds in the 20-ha control and managed halves of the study area at the Holt Research Forest, 1983-2002. Dotted vertical line denotes the time of the harvest treatment.

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 1.2): populations of 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 1.2, 1.3), 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. 1.3A). 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. 1.3I). In the control half, this species declined sharply. The Winter Wren did not occur in the study area prior to the harvest (Fig. 1.3B), 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 out of the 8 subsequent years). Likewise, the Pine Warbler was absent in the managed half until after the harvest (Fig. 1.3G). 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

Table 1.2. 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	—	—	—

Table 1.2 (Continued).

Bird Species	Location	R^2	Slope (SE) ^a	Annual change (%) ^b
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.

Table 1.3. 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	R^2	Slope1 (SE) ^a	Breakpoint (SE) ^b	Slope2 (SE) ^a	Annual change1 (%) ^c	Annual change2 (%) ^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 **

Table 1.3 (Continued).

Bird Species	Location	R^2	Slope1 (SE) ^a	Breakpoint (SE) ^b	Slope2 (SE) ^a	Annual change1 (%) ^c	Annual change2 (%) ^c	Abundance difference ^d
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 (Slope1) and after (Slope2) 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 of these locations..

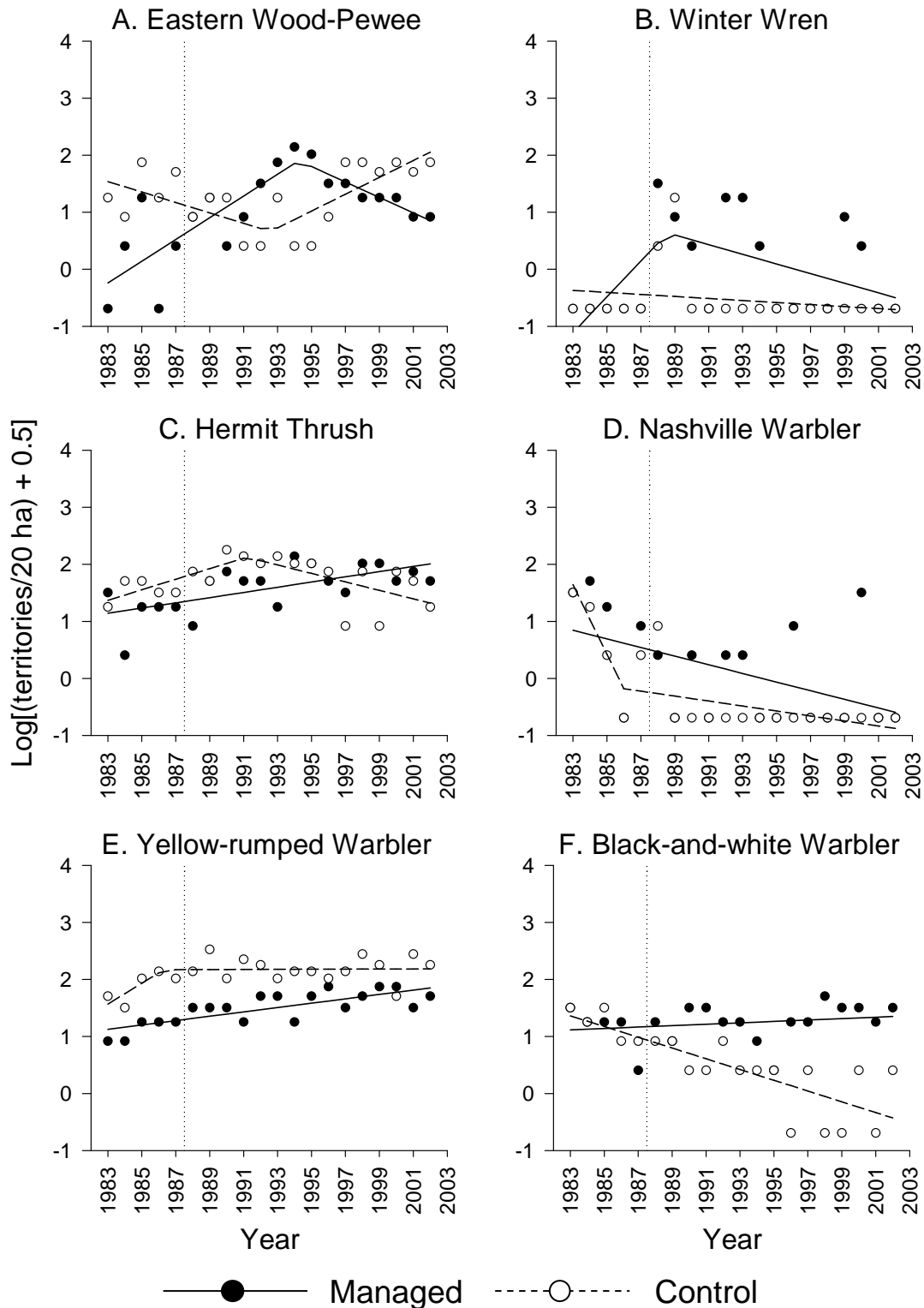
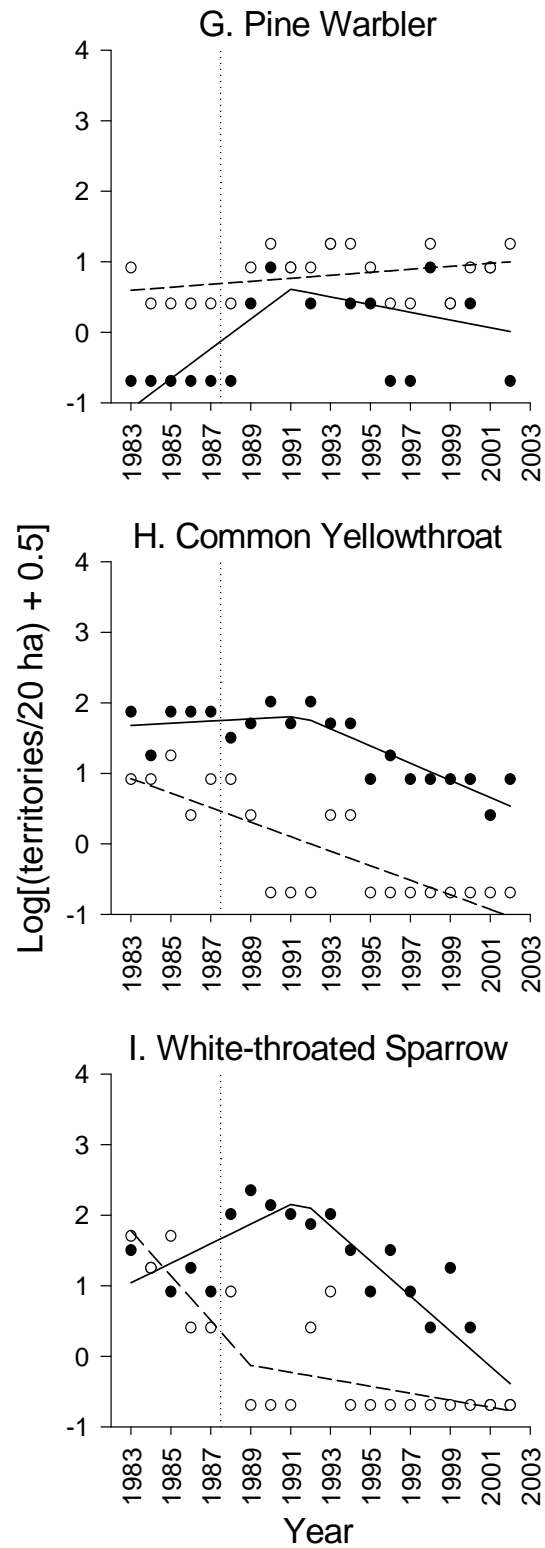


Figure 1.3. Abundance trends (number of territories) trends of (A-I) bird species that responded positively to a selection timber harvest at the Holt Research Forest, 1983-2002. The study area is divided into a 20-ha managed area where the harvest occurred and a 20-ha control area. Dotted vertical line denotes the time of the harvest treatment.



—●— Managed - - - ○ - - - Control

Figure 1.3 (Continued).

area and more protracted declines or stable populations in the managed half (Figs. 1.3D, F, H).

The Yellow-rumped Warbler (Fig. 1.3E) and Hermit Thrush (Fig. 1.3C) 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. 1.4C). However, 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. 1.4A, 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 relative to population in the control half suggests a negative response to the harvest (Fig. 1.4D).

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 (Fig. 1.5A). The number of detections of the Brown-headed Cowbird and Blue Jay fluctuated considerably from year to year but showed no obvious increasing or decreasing trend or tendency to concentrate in the managed areas (Figs. 1.5B, C).

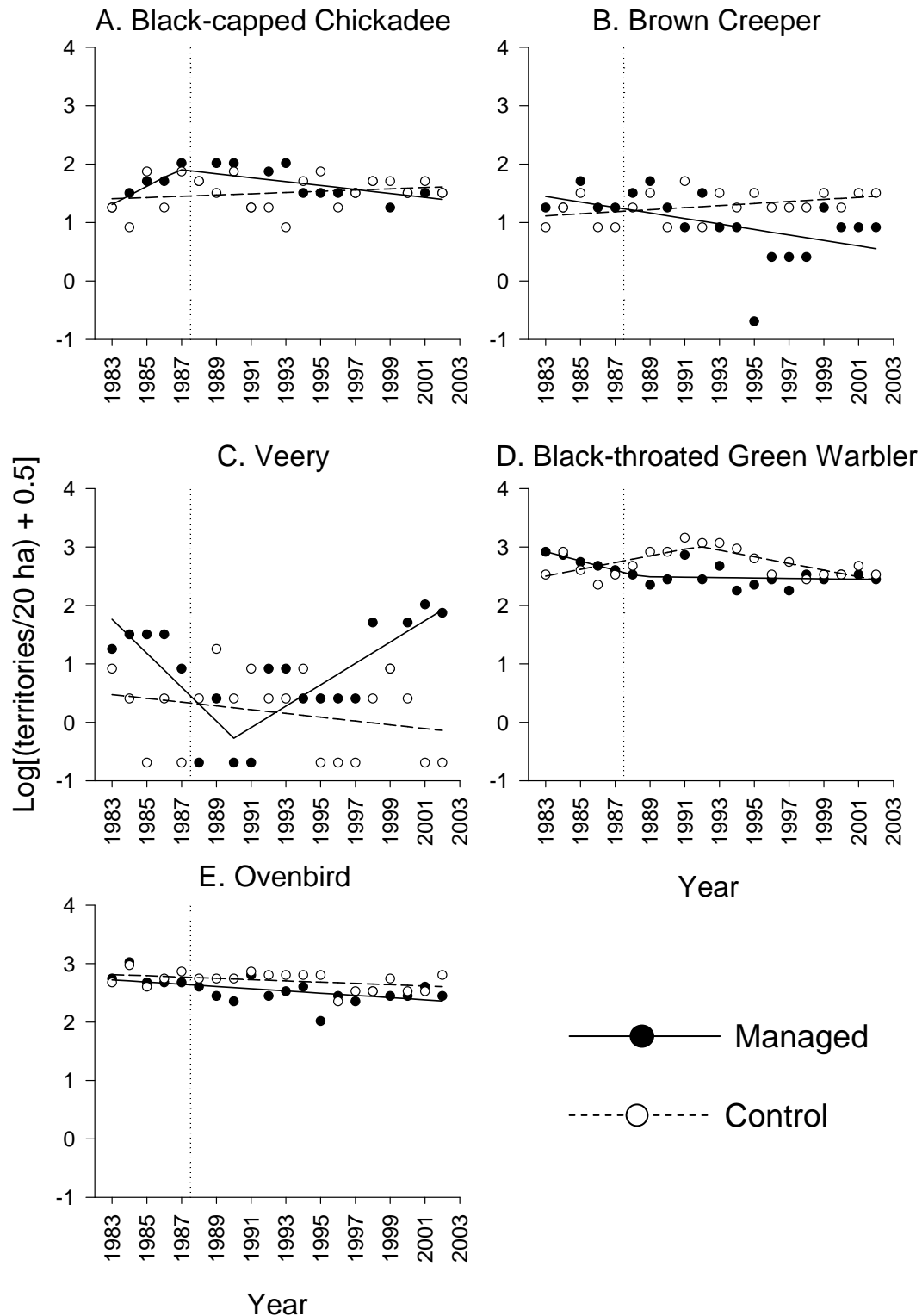


Figure 1.4. Abundance (number of territories) trends of (A-E) bird species that responded negatively to a selection timber harvest at the Holt Research Forest, 1983-2002. The study area is divided into a 20-ha managed area where the harvest occurred and a 20-ha control area. Dotted vertical line denotes the time of the harvest treatment.

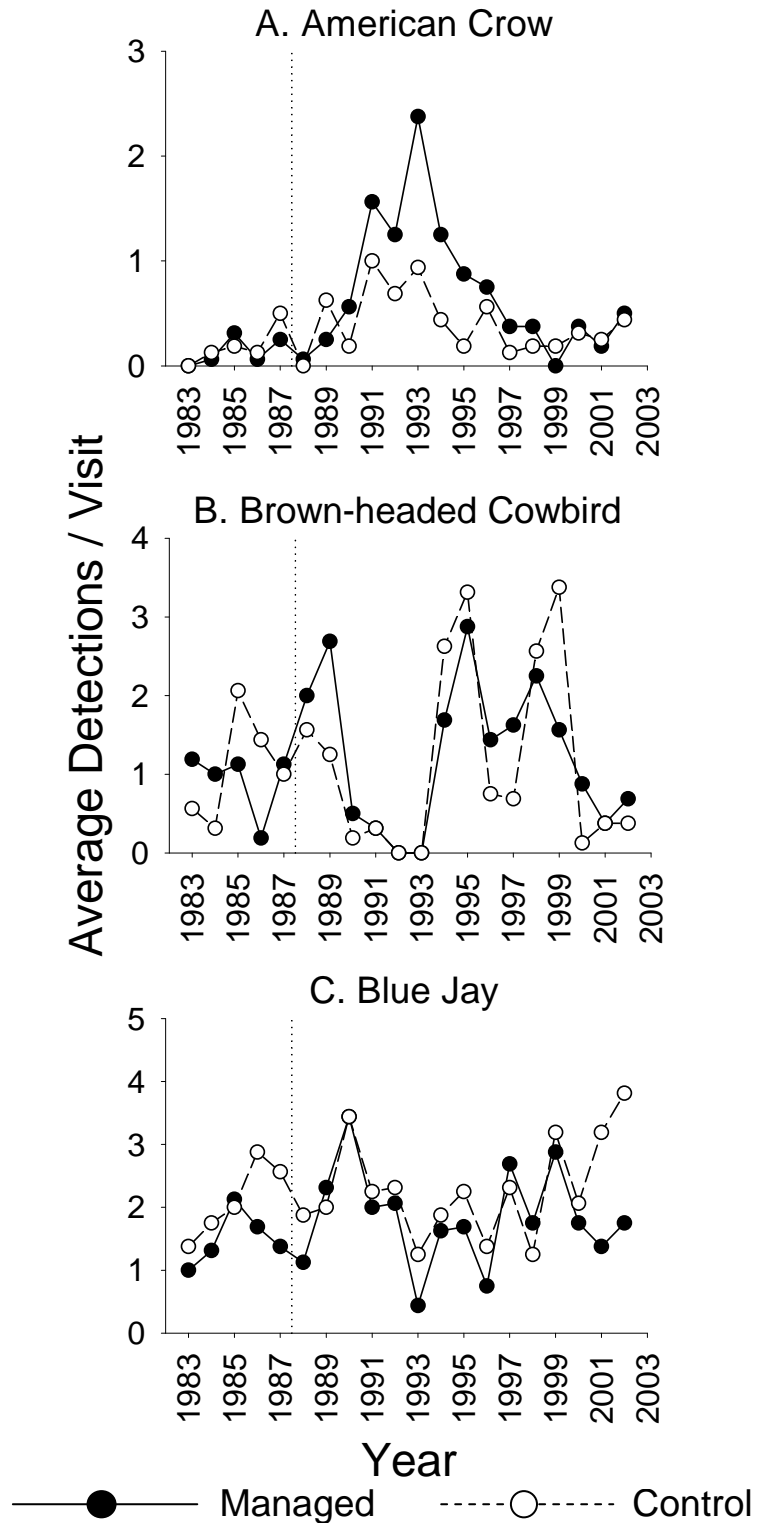


Figure 1.5. Average number of detections of potential nest predators (A and C) and a brood parasite (B) in the 20-ha managed and control halves of the study area at the Holt Research Forest, 1983-2002. Dotted vertical line denotes the time of the harvest treatment.

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. 1.2). 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. 1.1). 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 in over the 20 years of the 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. 1.3H, I). 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. 1.3D, F, H, I). However, 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 (Rudnický & 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 my study (Fig. 1.1) 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. 1.4C). Interestingly, the Winter Wren responded positively to the harvest (Figs. 1.3B, G), even though it usually is associated with older forests that have abundant dead woody material (Hejl et al. 2002). However, the species also uses slash piles following logging operations (Tobalske et al. 1991), which was the case in my 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, I could not definitively conclude that their habitat quality was unaffected without knowledge of population parameters 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 Ziehm (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 (Rudnicki & Hunter 1993b; 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. I witnessed an increase in the average number of detections of American Crows in the managed half of the study area (Fig. 1.5A) but not of Blue Jays nor of 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 my 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. However, 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 (Table A.2; 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 (Tables A.3, A.4). 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 my 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 my study require exposition. First, the small size of the study area limits the extrapolation of my results to larger spatial scales (James & McCulloch 1995). However, the 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 my 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. In this study, bird populations have been intensively sampled 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, my 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 U.S, 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. However, 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. However, 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.

My 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, I 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. However, 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).

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Chapter 2

LONG-TERM CHANGES IN SPATIAL DISTRIBUTION OF BIRDS RESPONDING TO SMALL-SCALE DISTURBANCES

INTRODUCTION

Disturbance is a key component in many models of species diversity and community structure (see Connell 1978, Petraitis et al. 1989, Roberts and Gilliam 1995 for reviews). While these models are useful tools for explaining the relationship between disturbance and overall patterns of species diversity, they do not predict the distribution and abundance of individual species. To construct predictive models of diversity as it relates to disturbance, we need to know how the life-history characteristics of the affected species interact with the effects of different types of disturbances (Pickett 1976, Halpern 1989, Roberts and Gilliam 1995). Specifically, we need to understand how different types of disturbance affect vegetation structure, distributions of competitors and predators, and resource availability, and in turn how different species respond to these altered conditions in terms of their abundance, distribution, survival, and reproduction.

In the forests of the northeastern U.S., the natural disturbance regime is dominated by the death or windthrow of individual or small groups of trees, which create a mosaic that is characterized by small-scale gap-phase dynamics (Lorimer 1977, Bormann and Likens 1979, Runkle 1982, Seymour et al. 2002, Lorimer and White 2003). Gaps range from $<25 \text{ m}^2$ to $\sim 0.1 \text{ ha}$ and form at an average rate of 0.5% to 2.0% of total land area per year, yielding natural return intervals (average time between disturbances for a given site) of 50-200 years (Runkle 1982, 1985). Large-scale, stand-replacing

disturbances brought on by fire or extensive windthrow also occur; their return interval is 500-1000 years, but their effects are more long term (Lorimer 1977, Bormann and Likens 1979, Seymour et al. 2002, Lorimer and White 2003).

The effect of these small-scale disturbances (i.e., gaps) on forest plant communities has been extensively studied (see reviews by Bormann and Likens 1981, Runkle 1985, Platt and Strong 1989, Mooney and Godron 1983, Attiwill 1994, Oliver and Larson 1996); however, the effects of small-scale disturbances on animal communities are less well understood, even for well-studied taxa such as birds. Most of the studies on gaps and birds have been of limited duration and have only compared bird assemblages in pre-existing gaps to undisturbed forest, thus precluding any direct comparisons between pre- and post-disturbance conditions (e.g., Schemske and Brokaw 1981, Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986, Levey 1988, Greenberg and Lanham 2001, Wunderle et al. 2005). Even studies of small disturbances caused by forest management (e.g., group-selection cuts), which lend themselves better to experimental work, have generally lacked pre- and post-treatment data and have been relatively short term (< 4years) (Sallabanks et al. 2000, but see Gram et al. 2003).

Short-term studies contribute little to our understanding of dynamic responses of birds to changes in vegetation structure, which is typically a long-term phenomenon. Furthermore, interannual variability in bird populations and distributions (e.g., Karr and Freemark 1983, Holmes and Sherry 2001) may cause short-term studies to generate information on population change that is unrelated to the habitat changes under investigation (Sallabanks et al. 2000, Collins 2001). Studies that have looked at the longer-term effects of disturbance have done so retrospectively across sites with varying

durations since disturbance (e.g., Robinson and Robinson 1999). Such studies rely on the assumption that the pre-disturbance vegetation and environment and post-disturbance influences were uniform among sites (Halpern 1989). If this assumption is violated, observed patterns could become confounded with historical or stochastic phenomena.

A long-term study (24 years to date) involving repeated observations of birds during pre- and post-disturbance periods is being conducted at the Holt Research Forest in Arrowsic, ME. This work is being conducted as part of a more comprehensive oak-pine forest ecosystem study that was established with the broad goals of monitoring long-term changes in the forest's plant and animal communities and documenting the effects of forest management practices on these communities (Witham et al. 1993). I have previously reported on the first 20 years (5 years of pre-treatment data and 15 years of post-treatment data) of the numerical response of birds to these disturbances (Chapter 1). In this paper, I examine their spatial response over the same period by characterizing changes in the spatial distribution of birds responding to gap creation and subsequent regeneration.

STUDY AREA

Site Description

The Holt Research Forest is 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. 2.1). It occurs within the transition zone between oak-pine (*Quercus rubra* and *Pinus strobus*) forest to the west and south and coastal spruce-fir (*Picea rubens* and *Abies balsamea*) to the east and north (McMahon 1990). The principal tree species in decreasing order of

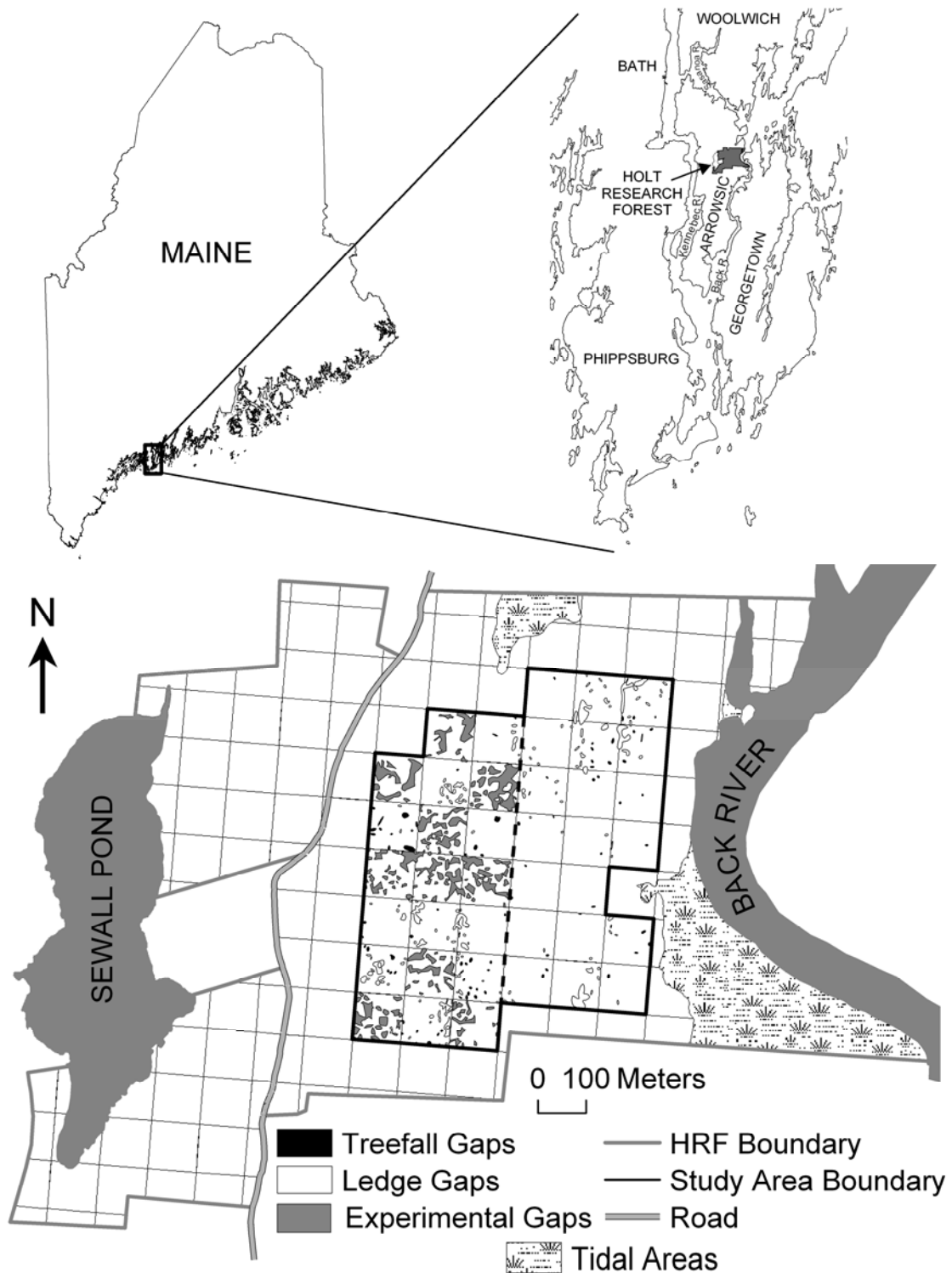


Figure 2.1. Map of the Holt Research Forest and the 40-ha study area in the year following the experimental treatment (1988). Ten 1-ha blocks were chosen for experimental treatment from the treated half of the forest by randomly selecting one block from each of ten pairs of adjacent blocks.

trees per hectare and basal area are eastern white pine, red maple (*Acer rubrum*), northern red oak, and red spruce (Kimball et al. 1995). The forest is a result of secondary succession following the abandonment of agricultural land 70-110 years ago (Moore and Witham 1996).

The study area comprises 40 ha and is buffered by an average of 90 m (range: 17-185 m) of forest from adjacent forests, a public road, and an estuarine river (Fig. 2.1). The study area is demarcated on the ground by a hierarchical grid system with 40 1-ha (100 m x 100 m) blocks, 160 50 m x 50 m quadrats, and 640 25 m x 25 m subquadrats. The western 20 ha were designated as the treated half of the study area, and the eastern 20 ha as the control half (i.e., no silvicultural treatments).

Canopy Gap Creation and Mapping

After five years (1983-1987) of baseline data collection on the entire study area, ten 1-ha blocks within the treated half of the study area were partially cut during the winter of 1987-1988 (Fig. 2.1). The treated blocks were chosen by randomly selecting one block from each of 10 pairs of adjacent blocks. The treatment removed an average of 44% (13.6 m²/ha, SD = 6.7%) of the basal area, and 26% (SD = 7.5%) of the forest cover from treated blocks. There was no effort to control the size, shape, or orientation of the resulting canopy gaps, which created a network of interconnected gaps of various shapes and sizes.

In the two years following the disturbance, all gaps in the forest were delineated and mapped in a geographic information system (Fig. 2.1; 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 m² as determined by the vertical projection of the drip edge of the surrounding canopy trees (Kimball et al. 1995). Gaps were classified into three categories: experimentally-created gaps (hereafter experimental gaps) were canopy openings created by tree removal during the winter of 1987-1988; treefall 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. Treefall gaps and ledge gaps were not mapped in treated blocks because their distribution could not be accurately determined after the creation of the experimental gaps (Kimball et al. 1995).

The experimental gaps averaged 210 m² (SE = 32.0, n= 126) in size and ranged from single tree gaps less than 25 m² to one gap that exceeded 3000 m² (Kimball et al. 1995). The gaps were distributed proportionally to the area of soil drainage classes and forest cover types found in the 10 treated blocks (Kimball et al. 1995). Treefall gaps averaged 24 m² (SE = 2.1, n = 80) and were predominantly in the smallest size class (93% were between 10 and 50 m² in size). Ledge gaps, which averaged 76 m² (SE = 13.1, n = 127), were also common in the smallest size classes but also occurred in all but the largest size class (>1000 m²).

In this paper I only focus on the response of birds to experimental gaps and ledge gaps because preliminary analysis of the treefall gaps indicated that they caused little to no change in the distributions of birds. Moreover, treefall gaps are small and ephemeral; many closed because of lateral canopy expansion of surrounding trees soon after they were mapped and following the creation of the gap map, new treefall gaps have appeared and closed. Because most species showed relatively weak changes in their distribution

around ledge gaps compared to experimental gaps, I focus on the results for the experimental gaps and explicitly discuss the ledge gaps only in instances where species showed notable changes. Given this focus, I use the term “gaps” to refer to the experimental gaps, unless specified otherwise.

Finally, throughout this paper there are measurements relating to gaps prior to the disturbance. Although the experimental gaps did not yet exist, I retain the terminology as a heuristic tool for showing the change in the use of the same areas of the forest before and after the disturbance.

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 (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 0430 to 1030 hr (Fig. 2.1). Only one observer (J. W. Witham) collected the data for all 20 years. All locations were digitized into a geographic information system (Witham and Kimball 1996). Data for all 16 visits were compiled and composite maps were made for each species in each year.

Data Analysis

Territory mapping does not reliably associate observations with individual birds, so I could not accurately delineate territory boundaries and was unable to identify the spatial extent of habitat used by individuals. Instead, I examined changes in spatial distribution at the species level. I used all the registrations of a species in a year to delineate the portion of the study area that the species used. I termed this aggregation of locations the “occupied area” (OA) for a species (Figs. B.1, B.2) and determined changes in spatial distribution of a species using the proportion of gap area that occurred within a species’ OA and the average distance of all observations within a species’ OA to the nearest gap of each type. Because the change in average distance from gaps is only a scalar representation of the underlying distribution of distances, I also examined changes in the distribution of distances for each species in each year. I considered a species to have responded positively to gaps if the area of gaps in its OA increased, its average distance from these areas decreased, and it exhibited a greater use of gaps or areas surrounding the gaps (i.e., edges). The converse holds for species that responded negatively. While these measurements are not mutually exclusive, I present them all because together they provide a more complete representation of the response to the disturbances.

Delineation of Occupied Areas

I delineated the boundaries of species’ OAs in each year with the 90% contour of 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). My main criterion for bandwidth selection was based on a tradeoff 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, I found $h = 20$ to be the right balance for most bird species. While this choice of bandwidth is relatively stringent, with 16 sampling periods I was confident that areas without significant concentrations of observations should be excluded from the OA. I did not use more objective means of choosing h , such as least-squares cross-validation, because it oversmoothed the data and included large areas where birds were not observed.

The OAs of species with widely-dispersed observations were not accurately represented by this choice of bandwidth because the density function decomposed into its constituent kernels (Kernohan et al. 2001). This included species that were not reliably sampled by territory mapping because they were not very vocal (e.g., Great-crested Flycatcher [*Myiarchus crinitus*] and Brown-headed Cowbird [*Molothrus ater*]) or had territories that were large relative to the study area (e.g., Pileated Woodpecker [*Dryocopus pileatus*]); these were excluded from the analyses.

Measuring Changes in Spatial Distribution

I characterized temporal changes in the proportion of gap area in an OA and the average distance to gaps as one of three types of responses: no response to the disturbance (i.e., no change in the trajectories of the pre-disturbance trends of gap area and distance), a positive or negative response to the disturbance (i.e., a single change in

the trajectories of the pre-disturbance trends), and a positive or negative response followed by a return to pre-disturbance levels (i.e., two subsequent changes in the pre-disturbance 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 and Wild 1989).

I fit all three models to the 20-year time series of each species using nonlinear regression (PROC NLIN; SAS Institute 2003). To help meet model assumptions, proportions of gap areas were square-root transformed; transformation was not necessary for average distance. I 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. I used this method because it better deals with ill-conditioned and singular matrices than other methods (Seber and Wild 1989). Convergence occurred when the relative offset convergence measure of Bates and Watts was less than 10^{-5} (SAS Institute 2003). Initial parameter estimates for the breakpoints were found by searching all possible combinations of $x_0 = 1986-1989$ (one- and two- breakpoint model) and $x_1 = 1990-2000$ (two-breakpoint model) for the combination that minimized the sums-of-squares; these starting values corresponded to the years immediately before and after the disturbance and 3-12 years after the disturbance. I 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 some cases in which the convergence criterion was not met, but in these cases the parameter estimates had stabilized to a precision of 10^{-4} in less than 20 iterations and the use of other iterative methods (e.g., Gauss-Newton) yielded nearly identical parameter estimates.

I used Akaike's Information Criteria (AIC) to select which of the three models best fit the data for each species (Burnham and Anderson 2002). I used the two-breakpoint piecewise regression model as my global model, since 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 I used the least squares case of AIC, which calculates AIC based on the residual sum of squares. Since the sample size (n) was small relative to the number of parameters (K) (i.e., $n/K < 40$), I used the small sample AIC (AIC_c) (Burnham and Anderson 2002).

I determined if spatial distributions returned to their pre-disturbance levels by comparing the proportion of gap area in an OA and the average distance to gaps in the pre-disturbance years (1983-1987) to those in the last five years of the post-disturbance period (1998-2002) using Mann-Whitney tests (Zar 1999).

To examine changes in distribution of distances over time, I conducted Kolmogorov-Smirnov tests (Zar 1999) that compared the cumulative distribution of observed distances with the cumulative distribution of distances based on all possible points spaced 5 m apart within the study area (observed and expected distributions, respectively). However, the critical value for the Kolmogorov-Smirnov test decreases with increasing sample size, so the likelihood of finding the observed and expected distributions to be different for very small and biologically insignificant deviations is high for abundant species. For example, the Ovenbird and Black-throated Green Warbler had a maximum of 614 and 715 observations/year, respectively, so in these years the distributions of these species will be considered different at $\alpha = 0.05$ if at any point the difference in curves exceeds 5.2 % and 4.8%, respectively. Therefore, to be conservative

I also determined the percentage of observations for which the corresponding point on the expected curve fell outside the 95% confidence band of the curve based on the observed data. If the percentage of observations exceeded 10% I determined the distributions to be substantially different. The two different methods provided the same results for 86% of the comparisons (Fig. B.3, Table B.1). Disagreement between the two methods generally occurred in years when a species was abundant and differences between the curves were small. I believe that this alternative method detected differences that were more biologically meaningful.

I graphically represented the changes in distributions of distances from each type of gap over time by plotting the differences between the percentage of observations (i.e., percentage used) and the percentage of the study area (i.e., percentage available) occurring in each of six distance classes (0 m [within a gap], 0-25 m, 25-50 m, 50-75 m, 75-100 m, and >100m). The percentage of the study area occurring in each of the distance classes was 6.6, 29.7, 12.8, 7.4, 5.4, and 37.9% for experimental gaps, respectively, and 2.4, 37.9, 29.3, 18.5, 8.4, and 3.5% for ledge gaps.

Additional Statistical Considerations

The use of individual locations rather than territories as sampling units poses potential problems with pseudoreplication (Hurlburt 1984). However, I 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. Additionally, I have taken measures to minimize the effects of pseudoreplication in the analyses. For instance, by examining shifts in OAs as opposed to the shifts of individual

locations, the problem of pseudoreplication is ameliorated but replication is sacrificed (i.e., there is only one measurement/species/year). Thus, my analysis is based on a single time series design with intervention, where the results of experimental changes are indicated by a discontinuity in the measurements (Campbell and Stanley 1966). The weakness of this design is that it does not remove the effects of competing causes (James and McCullough 1995); however, I examined the numerical response of birds in the control and treated halves of the study area and found that the disturbance-induced changes in vegetation caused differences in abundances in each half for many species (Chapter 1). Therefore, I am confident that the distributional shifts I observed were also a result of the disturbance.

I conducted numerous statistical tests, but I did not control for experimentwise error rates (e.g., Bonferoni adjusted p-values), because I was not making inferences to a larger population of birds. Rather I was only interested in measuring the strength of differences that exist within my data, so I retained $\alpha = 0.05$ for the rejection of all null hypotheses. Consequently, my results are only directly applicable to the bird populations at the Holt Research Forest. Nevertheless, my data represent a relatively long time series, and differences sustained over time probably indicate a real effect that is applicable to other systems.

RESULTS

There were 20 species that could be reliably sampled by territory mapping, that were abundant enough for analyses (>1 territory/year, on average), and that had territories that were small relative to the study area. The Ovenbird and Black-throated Green

Warbler were the most abundant birds and had the first and third largest average OA covering 56% and 42% of the study area, respectively (Tables 2.1, B.2). The Black-capped Chickadee, which averaged about a third as many individuals as either the Ovenbird or Black-throated Green Warbler, had the second largest average OA, covering 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 2.1) as well as across all species ($r = 0.72$, $p < 0.0001$). Because these two quantities are not independent, I included the number of territories on the graphs containing trends in proportion of gap area in OAs and average distance to the nearest gap so that changes in the metrics can be viewed within the context of changes in abundance.

The temporal trends in the proportion of gap area in an OA and the average distance to the nearest gap were idiosyncratic among species. Trends in the proportion of experimental gap area within OAs of 12 species were best described by straight lines (four significantly increasing and two significantly decreasing) (Table 2.2), while eight species showed more complicated responses and were modeled with one- or two-breakpoint models (Tables 2.3, 2.4). Similarly, 13 species had trends in average distance to experimental gaps that were best represented by a straight line (one significantly increasing and three significantly decreasing) (Table 2.5). The trends in average distance for the remaining seven species were best fit by higher order breakpoint models (Tables 2.6, 2.7).

Based on the patterns in these trends, eleven species exhibited notable responses to the disturbance that were consistent across the metrics: eight responded positively and

Table 2.1. 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 from 1983-2002 and Pearson's correlation (r) between OA size and territory numbers.

Bird Species	N†	Territories			OA Size (ha)			r	P-value
		Mean ‡	SD	Range	Mean ‡	SD	Range ‡		
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 atricapilla</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>Catharus 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>Dendroica 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>Dendroica virens</i>)	20	27.7	4.78	23-40	16.8	4.04	10.7-25.9	0.63	0.003
Pine Warbler (<i>Dendroica 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

Table 2.1 (Continued).

Bird Species	N†	Territories			OA Size (ha)			r	P-value
		Mean ‡	SD	Range	Mean ‡	SD	Range ‡		
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

† N, number of years in which one or more territories were established at the Holt Research Forest.

‡ Metric excludes years in which there were no territories for that species.

Table 2.2. Summary of simple linear (zero-breakpoint) regression models describing temporal trends in the square root of proportions of total areas of experimental gaps and ledge gaps occurring in the OAs of 19 bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	Experimental Gaps			Ledge Gaps		
	R ²	Slope	P-value	R ²	Slope	P-Value
Eastern Wood-Pewee	---†	---	---	0.15	0.01 (0.005)	0.088
Blue-headed Vireo	0.01	0.00 (0.005)	0.649	0.15	0.01 (0.004)	0.090
Black-capped Chickadee	0.23	0.01 (0.003)	0.032	0.46	0.01 (0.003)	0.001
Brown Creeper	0.11	-0.01 (0.004)	0.158	0.18	0.01 (0.003)	0.058
Red-breasted Nuthatch	0.45	0.01 (0.003)	0.001	0.21	0.01 (0.005)	0.045
Winter Wren	0.64	-0.02 (0.007)	0.017	0.23	-0.02 (0.012)	0.231
Golden-crowned Kinglet	0.05	-0.00 (0.004)	0.344	0.10	0.01 (0.003)	0.177
Veery	---	---	---	0.03	0.00 (0.002)	0.493
Hermit Thrush	0.60	0.02 (0.003)	0.000	---	---	---
Nashville Warbler	0.05	0.01 (0.008)	0.374	0.45	-0.03 (0.007)	0.003
Yellow-rumped Warbler	0.01	-0.00 (0.005)	0.637	0.17	0.01 (0.003)	0.068
Black-and-white Warbler	---	---	---	0.40	-0.01 (0.004)	0.003
Blackburnian Warbler	0.20	-0.01 (0.004)	0.046	0.18	-0.01 (0.004)	0.059
Black-throated Green Warbler	---	---	---	0.17	-0.01 (0.003)	0.073
Pine Warbler	---	---	---	0.14	0.01 (0.006)	0.100
Common Yellowthroat	0.01	0.00 (0.003)	0.697	0.81	-0.04 (0.004)	0.000
Scarlet Tanager	---	---	---	0.20	0.01 (0.005)	0.047
White-throated Sparrow	---	---	---	0.70	-0.03 (0.004)	0.000
Purple Finch	0.45	0.01 (0.003)	0.001	0.41	0.01 (0.004)	0.002

Note: Summary includes proportion of variance explained (R²), estimated slope (standard error), and P-value from test of H₀: Slope = 0.

† Trend is better fit by a higher-order breakpoint model.

Table 2.3. Summary of one-breakpoint regression models describing temporal trends in the square root of the proportions of total areas of experimental gaps and ledge gaps occurring in the OAs of six bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	R ²	Slope ₁	P-Value ₁	Breakpoint	Slope ₂	P-Value ₂
Experimental Gaps:						
Eastern Wood-Pewee	0.57	0.04 (0.011)	0.001	1994 (1.6)	-0.03 (0.021)	0.123
Veery	0.76	-0.04 (0.010)	0.001	1991 (0.9)	0.04 (0.007)	0.000
Black-and-white Warbler	0.60	-0.05 (0.038)	0.234	1987 (1.6)	0.02 (0.005)	0.000
Black-throated Green Warbler	0.76	-0.06 (0.011)	0.000	1990 (0.9)	0.01 (0.006)	0.112
Scarlet Tanager	0.43	-0.04 (0.026)	0.157	1988 (1.7)	0.02 (0.005)	0.007
Ledge Gaps:						
Ovenbird	0.59	-0.03 (0.009)	0.004	1993 (1.2)	0.04 (0.012)	0.005

Note: Summary includes proportion of variance explained (R²), estimated slope of segment i (slope_i [standard error]), estimated breakpoint (standard error), and P-value_i from test of H₀: Slope_i = 0.

Table 2.4. Summary of two-breakpoint regression models describing temporal trends in the square root of the proportions of total areas of experimental gaps and ledge gaps occurring in the OAs of four bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	R ²	Slope ₁	P-Value ₁	Breakpoint ₁	Slope ₂	P-Value ₂	Breakpoint ₂	Slope ₃	P-Value ₃
Experimental Gaps:									
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
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
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
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

Note: Summary includes proportion of variance explained (R²), estimated slope of segment i (slope_i [standard error]), estimated breakpoint between segment i and i + 1 (breakpoint_i [standard error]), and P-value_i from test of H₀: Slope_i = 0.

Table 2.5. Summary of simple linear (zero-breakpoint) regression models describing temporal trends in the average distance to the nearest experimental and ledge gaps of observations of 20 bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	Experimental Gaps			Ledge Gaps		
	R ²	Slope	P-value	R ²	Slope	P-value
Eastern Wood-Pewee	---†	---	---	0.29	-0.6 (0.22)	0.015
Blue-headed Vireo	0.00	0.3 (1.67)	0.868	0.24	-0.4 (0.15)	0.027
Black-capped Chickadee	0.03	0.3 (0.33)	0.447	0.04	0.1 (0.10)	0.419
Brown Creeper	0.40	1.7 (0.50)	0.003	0.04	-0.1 (0.12)	0.406
Red-breasted Nuthatch	0.02	0.5 (0.83)	0.571	0.08	0.2 (0.17)	0.242
Winter Wren	0.09	-1.8 (2.13)	0.435	0.01	0.2 (1.06)	0.841
Golden-crowned Kinglet	0.02	0.6 (1.18)	0.607	0.10	-0.4 (0.25)	0.182
Veery	---	---	---	0.36	-0.7 (0.22)	0.005
Hermit Thrush	0.36	-1.8 (0.58)	0.006	0.02	-0.1 (0.13)	0.525
Nashville Warbler	0.35	-4.9 (1.79)	0.017	0.56	1.3 (0.32)	0.001
Yellow-rumped Warbler	0.02	-0.3 (0.45)	0.566	0.33	0.3 (0.11)	0.008
Black-and-white Warbler	---	---	---	0.44	0.8 (0.22)	0.001
Blackburnian Warbler	0.01	0.1 (0.43)	0.752	---	---	---
Black-throated Green Warbler	---	---	---	0.02	-0.0 (0.09)	0.587
Pine Warbler	---	---	---	0.01	-0.1 (0.27)	0.741
Ovenbird	---	---	---	0.51	-0.4 (0.09)	0.000
Common Yellowthroat	0.84	-4.4 (0.45)	0.000	0.67	3.0 (0.49)	0.000
Scarlet Tanager	0.01	-0.4 (0.98)	0.723	0.01	0.1 (0.31)	0.687
White-throated Sparrow	---	---	---	0.58	1.4 (0.29)	0.000
Purple Finch	0.11	1.4 (0.93)	0.145	0.07	0.2 (0.14)	0.270

Note: Summary includes proportion of variance explained (R²), estimated slope (standard error), and P-value from test of H₀: Slope = 0.

† Trend is better fit by a higher-order breakpoint model.

Table 2.6. Summary of one-breakpoint regression models describing temporal trends in the average distance to the nearest experimental and ledge gaps of observations of six bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	R ²	Slope ₁	P-Value ₁	Breakpoint	Slope ₂	P-value ₂
Experimental Gaps:						
Veery	0.56	7.9 (3.25)	0.027	1991 (1.4)	-6.6 (1.76)	0.002
Black-and-white Warbler	0.76	2.4 (4.30)	0.581	1989 (2.0)	-6.7 (1.19)	0.000
Black-throated Green Warbler	0.73	6.8 (1.41)	0.000	1989 (0.8)	-2.0 (0.56)	0.002
Ovenbird	0.52	4.0 (1.22)	0.005	1989 (1.2)	-0.8 (0.48)	0.109
White-throated Sparrow	0.83	-16.4 (3.61)	0.000	1990 (1.2)	-1.4 (1.60)	0.388
Ledge Gaps:						
Blackburnian Warbler	0.70	-0.5 (0.13)	0.001	1997 (0.8)	2.4 (0.67)	0.002

Note: Summary includes proportion of variance explained (R²), estimated slope of segment i (slope_i [standard error]), estimated breakpoint (standard error), and P-value_i from test of H₀: Slope_i = 0.

Table 2.7. Summary of two-breakpoint regression models describing the temporal trends in the average distance to the nearest experimental gaps of observations of two bird species breeding at the Holt Research Forest, 1983-2002.

Bird Species	R ²	Slope ₁	P-value ₁	Breakpoint ₁	Slope ₂	P-Value ₂	Breakpoint ₂	Slope ₃	P-value ₃
Experimental 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
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

Note: Summary includes proportion of variance explained (R²), estimated slope of segment i (slope_i [standard error]), estimated breakpoint between segment i and i + 1 (breakpoint_i [standard error]), and P-value_i from test of H₀: Slope_i = 0.

three negatively. In contrast, nine species showed a weak response or a response that was inconsistent across the metrics. The Black-capped Chickadee, Brown Creeper, Red-breasted Nuthatch, Blackburnian Warbler, Scarlet Tanager, and Purple Finch showed a significant trend in only one of the metrics, which suggests that their changes in distribution were probably unrelated to the disturbance (Tables 2.2, 2.3, 2.5). The Blue-headed Vireo, Golden-crowned Kinglet, and Yellow-rumped Warbler showed no directional change in the metrics over the 20-year period of the study (Tables 2.2, 2.5), which suggests that their distributions remained relatively stable.

Species that Responded Positively to Disturbance

In general, the eight species that responded positively to the disturbance increased the amount of disturbed area in their OA (Fig. 2.2), decreased their average distance to gaps (Fig. 2.3), and selected gaps and edge habitats (Fig. 2.4). Winter Wrens and White-throated Sparrows responded strongly and immediately to the disturbance. Winter Wrens, which were previously absent from the forest, appeared at the disturbed patches following the disturbance as indicated by their greater than expected use of the within gap habitat (0m) and forest edges (0-25 m from gaps) (Fig. 2.4B). Immediately following the disturbance, White-throated Sparrows moved an average of over 100 m closer to gaps (Fig. 2.3H), included over 60% of the gap area within their OA (Fig. 2.2H) and selected for gaps and surrounding forest edges (0-25 m) (Fig. 2.4H). By 3-5 years after the disturbance these species began to decline in their use of the disturbed patches.

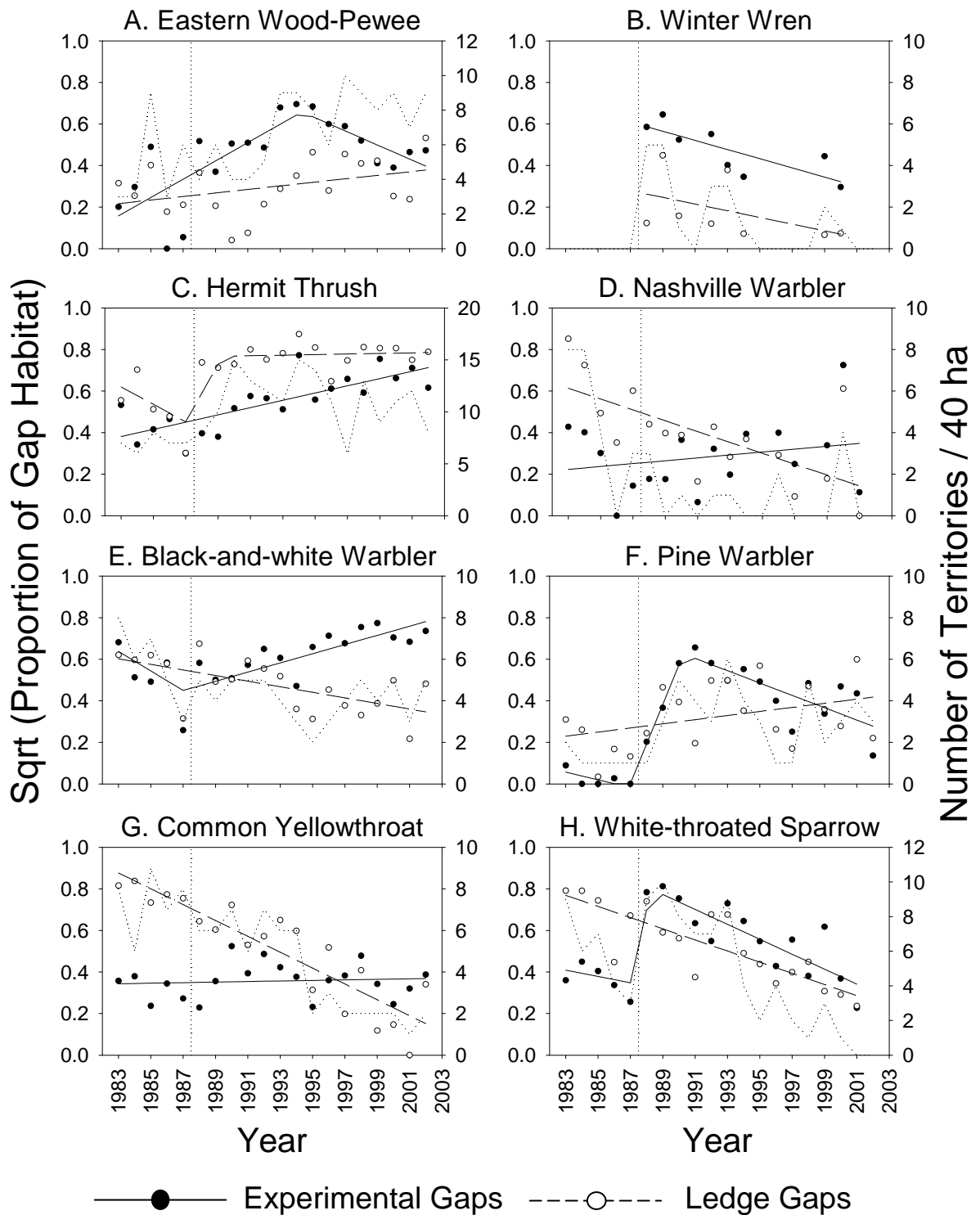


Figure 2.2. Square root of the proportion of area of experimental gaps and ledge gaps that occurs within each species OA and the number of territories for species that responded positively to the disturbance in the 40 ha study area of the Holt Research Forest, 1983-2002. Vertical dotted line denotes the time of disturbance and the fluctuating dotted line represents the number of territories.

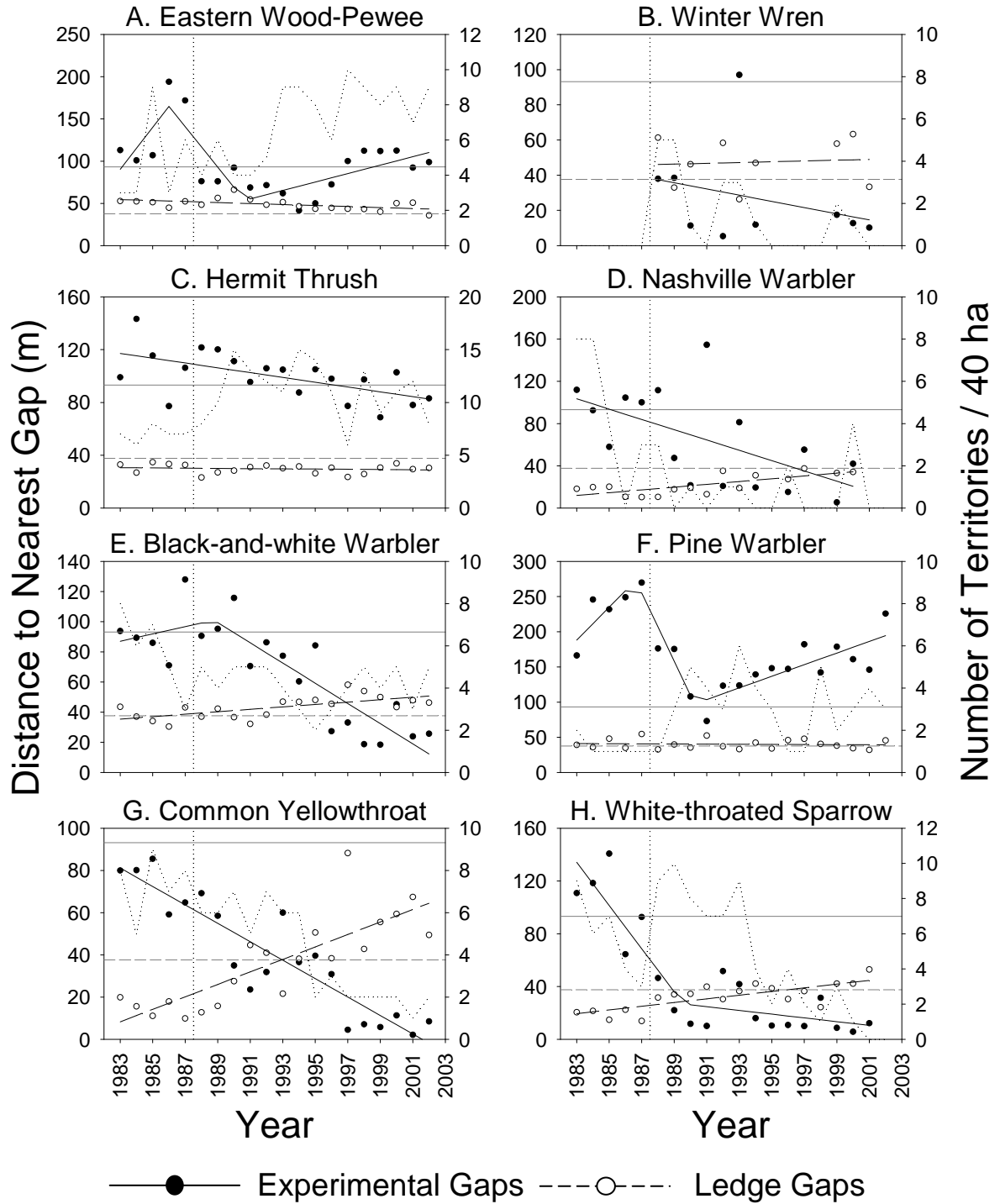


Figure 2.3. Average distance of all observations of a species to the nearest experimental gap and nearest ledge gap and the number of territories of species that responded positively to gaps in the 40 ha study area of the Holt Research Forest, 1983-2002. Horizontal lines represent average distance of random points to the nearest gap of each type (solid = experimental gaps and dashed = ledge gaps). The vertical dotted line denotes the time of disturbance and the fluctuating dotted line represents the number of territories. Note different scales of y-axes.

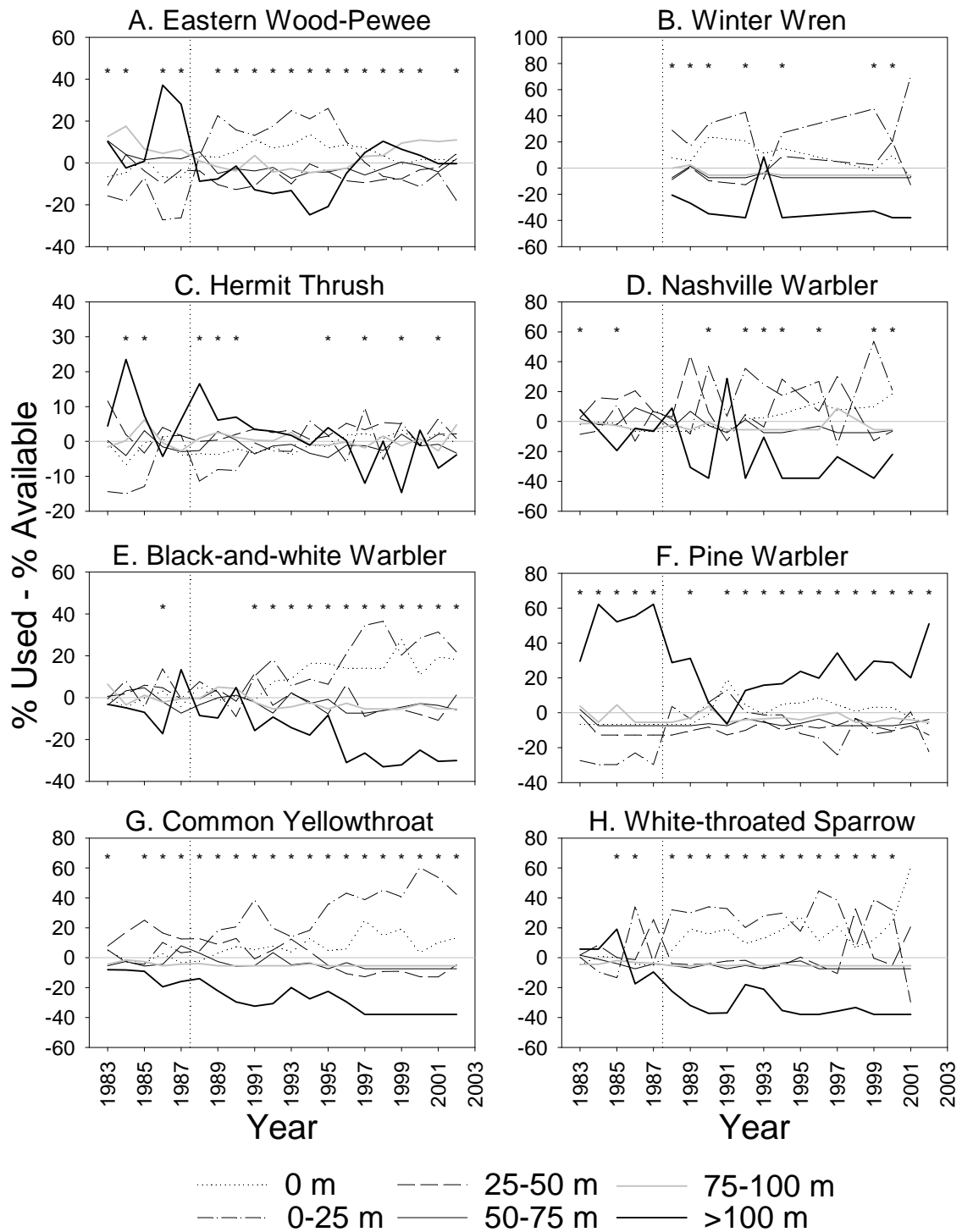


Figure 2.4. Differences between the percentage of study area (% available) and the percentage of observations (% used) occurring in each distance class from experimental gaps for species that responded positively to gaps at the Holt Research Forest, 1983-2002. Asterisks indicate years in which the “confidence band” test (see text) detected 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 dotted line denotes the time of disturbance. Note different scales of y-axes.

Pine Warblers occurred in the eastern half of the study area prior to the disturbance. After the disturbance, some individuals appeared near the disturbed areas so that the species was on average over 100 m closer to the gaps (Fig. 2.3F) and increased the amount of gap area within its OA from nearly zero to almost 40% (Fig. 2.2F). The species still occurred farther from the gaps than would be expected under a scenario of random habitat use because some individuals still occurred in the far eastern half of the study area. Despite the apparent positive response to the disturbance as indicated by the inclusion of gaps in their OA, Pine Warblers showed only limited spatial and temporal use of the gap and edge habitat (Fig. 2.4F).

The Eastern Wood-Pewee and the Black-and-white Warbler showed a delay in their peak use of the disturbed areas. Immediately following the disturbance Eastern Wood-Pewees selected for gap and edge habitats relative to areas farther into the forest (Fig. 2.4A), but they occurred closest to gaps (Fig. 2.3A) and included the highest amount of gap area (~ 40%) within their OA during 6-8 years after the disturbance (Fig. 2.2A). Black-and-white Warblers use of the gap and edge habitats increased gradually following the disturbance until 10 years after the disturbance when the metrics stabilized (Figs. 2.2E, 2.3E, 2.4E).

Common Yellowthroats appeared to demonstrate a trade-off between the experimental gaps and ledge gaps; their decrease in use of (Fig. 2.2G) and increase in distance from the ledge gaps (Figs. 2.3G, 2.5C) likely reflected their movement into experimental gaps and edge habitats (Fig. 2.4G). Because this species was also declining in abundance, its movement into the experimental gaps did not increase the overall proportion of experimental gaps that occurred in its OA (Fig. 2.2G). This same pattern

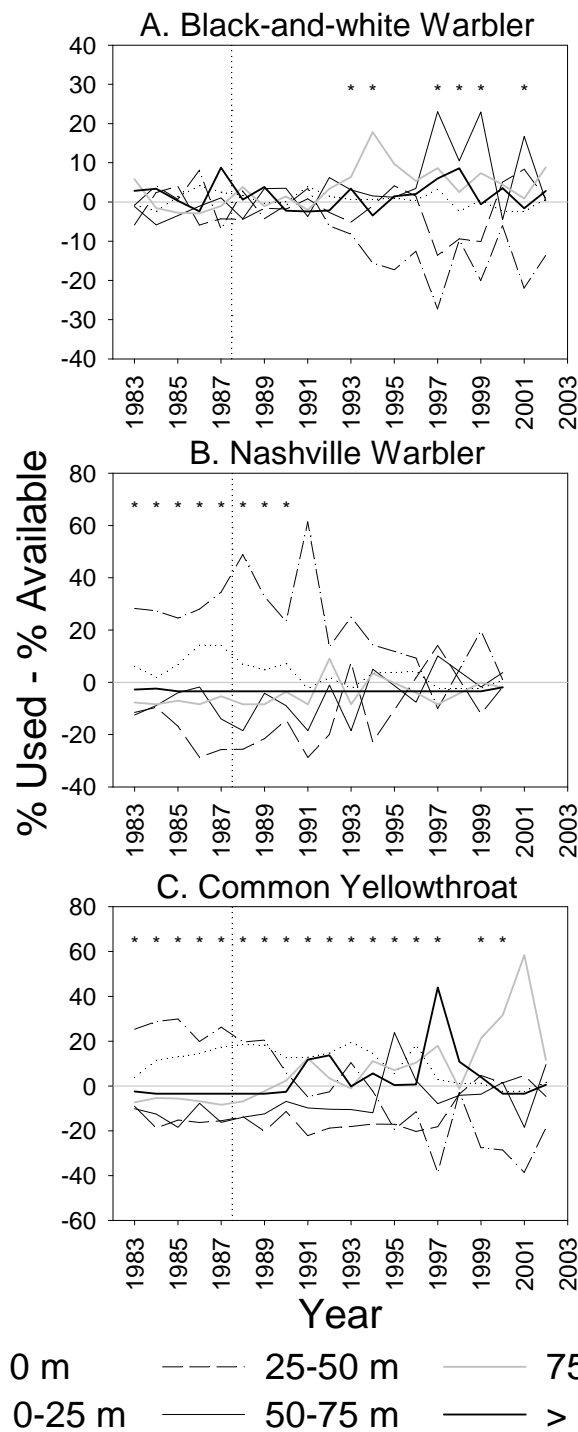


Figure 2.5. Differences between the percentage of study area (% available) and the percentage of observations (% used) occurring in each distance class from ledge gaps for a subset of species that responded positively to experimental gaps at the Holt Research Forest, 1983-2002. Asterisks indicate years in which the “confidence band” test (see text) detected 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 dotted line denotes the time of disturbance. Note different scales of y-axes.

held, but to a lesser degree, for Black-and-white Warblers and the Nashville Warblers (Figs. 2.2-2.5).

Although the Hermit Thrush showed a positive response to the experimental gaps that increased gradually over time (Figs. 2.2C, 2.3C), it did not exhibit as strong a selection for gaps or the associated edge habitat as did the other species that responded positively (Fig. 2.4C). However, the species did show a marked increase in the inclusion of ledge gaps in its OA that was coincident with the creation of the experimental gaps (Fig. 2.2C). The change in the use of ledge gaps was probably incidental to the population increase following the disturbance rather than selection for ledge gaps *per se* because the species showed no meaningful changes in its use of the different distance classes from ledge gaps.

Species that Responded Negatively to Disturbance

Three species showed strong negative responses to the disturbance. Both the Black-throated Green Warbler and Ovenbird exhibited a retraction of their OAs away from disturbed areas (Figs. 2.6, 2.7) and an avoidance of gap and adjacent edge habitat (Fig. 2.8). These changes resulted in smaller OAs but were not accompanied by comparable decreases in abundance (Fig. 2.9). Prior to disturbance, the Veery occurred closer to the areas that were to become experimental gaps than was expected by random use (Fig. 2.8A), which suggests that these areas contained habitat elements that the Veeries were selecting. Following the disturbance, individuals of this species shifted away from these areas (Figs. 2.6A, 2.7A) and showed increasing use of forest greater

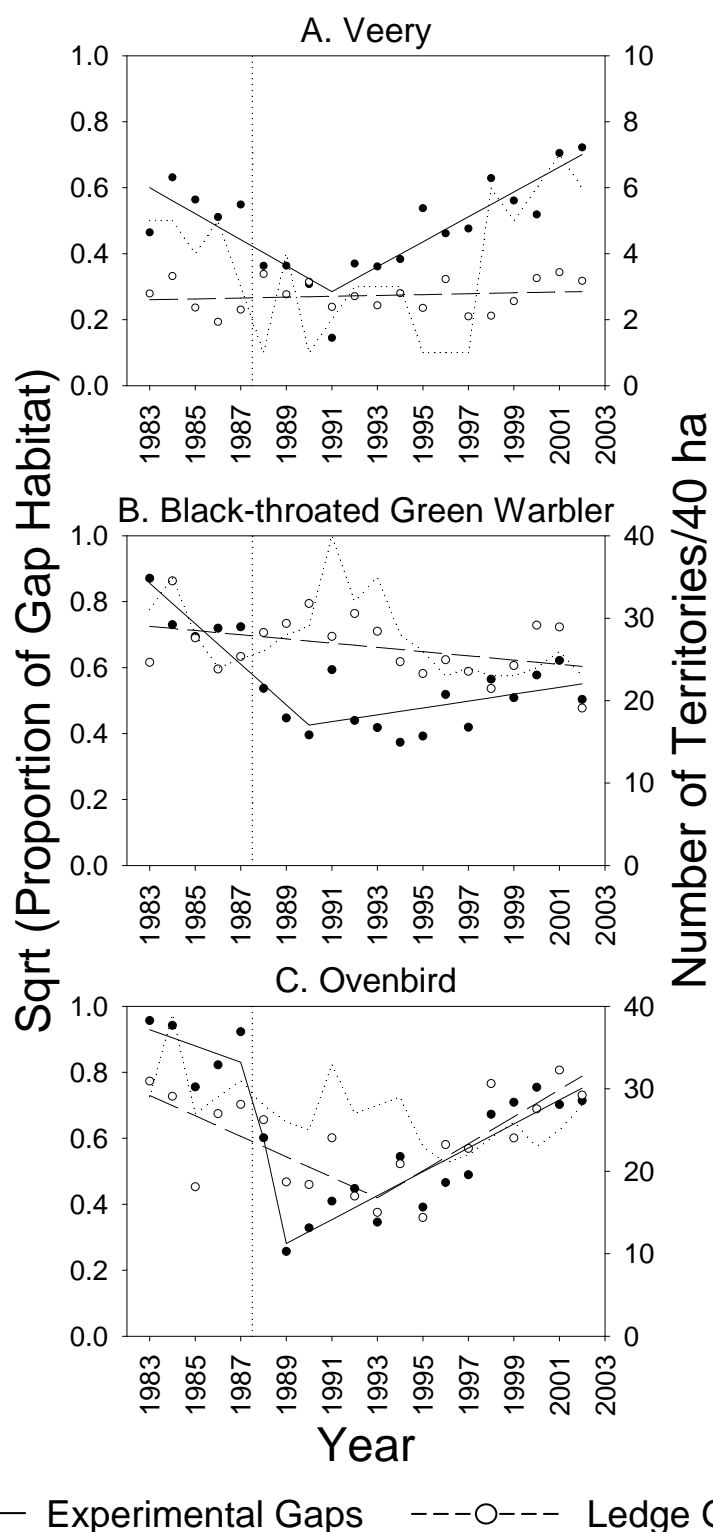


Figure 2.6. Square root of the proportion of area of experimental gaps and ledge gaps that occurs within each species OA and the number of territories for species that responded negatively to the disturbance in the 40 ha study area of the Holt Research Forest, 1983-2002. Vertical dotted line denotes the time of disturbance and the fluctuating dotted line represents the number of territories.

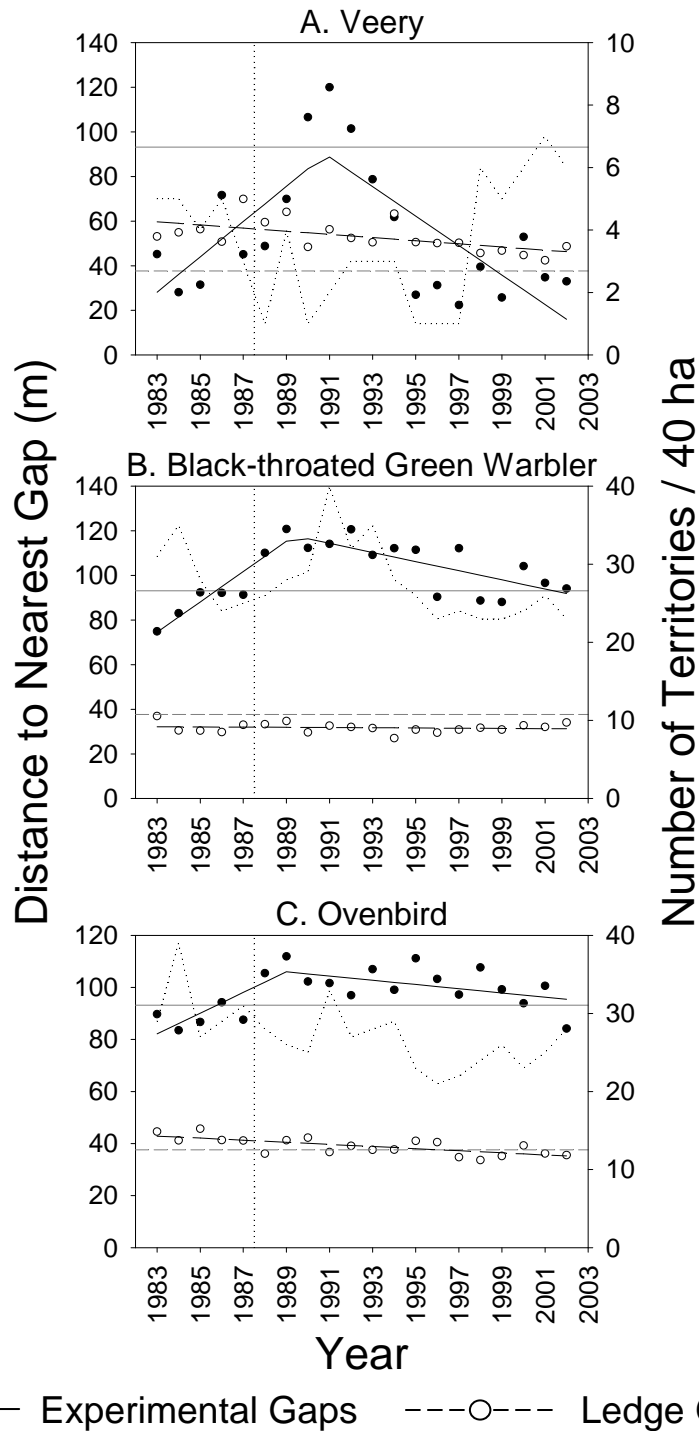


Figure 2.7. Average distance of all observations of a species to the nearest experimental gap and nearest ledge gap and the number of territories of species that responded negatively to gaps in the 40 ha study area of the Holt Research Forest, 1983-2002. Horizontal lines represent average distance of random points to the nearest gap of each type (solid = experimental gaps and dashed = ledge gaps). The vertical dotted line denotes the time of disturbance and the fluctuating dotted line represents the number of territories. Note different scales of y-axes.

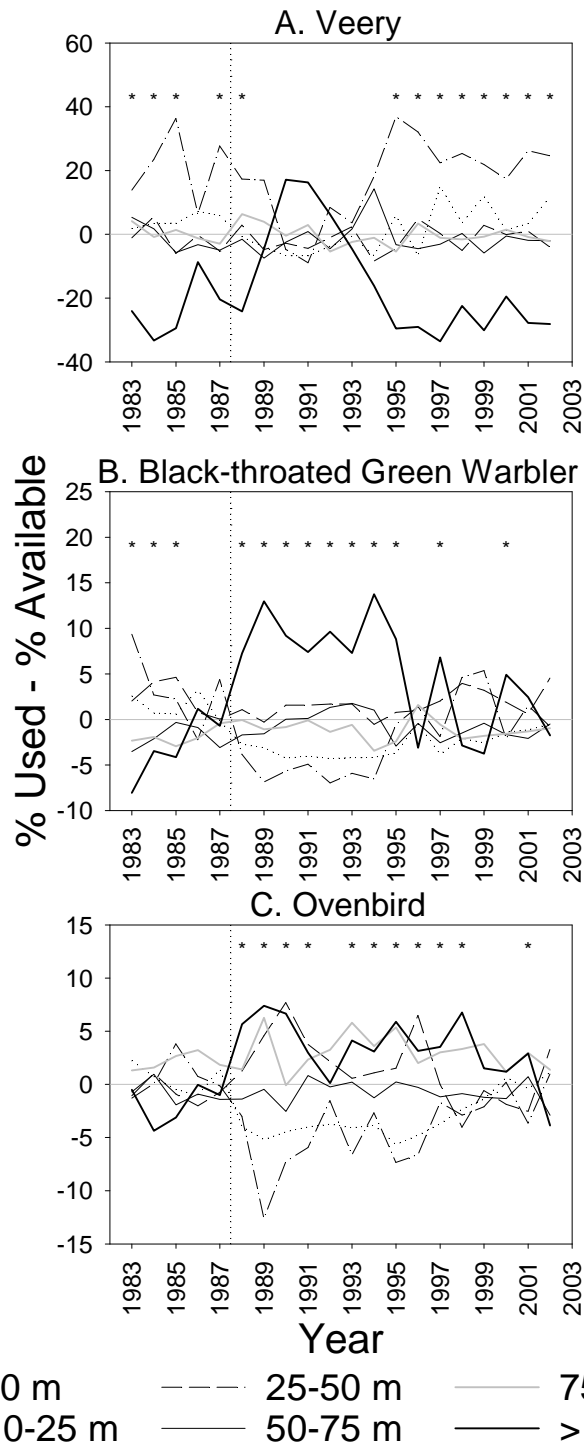


Figure 2.8. Differences between the percentage of study area (% available) and the percentage of observations (% used) occurring in each distance class from experimental gaps for species that responded negatively to gaps at the Holt Research Forest, 1983-2002. Asterisks indicate years in which the “confidence band” test (see text) detected 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 dotted line denotes the time of disturbance. Note different scales of y-axes.

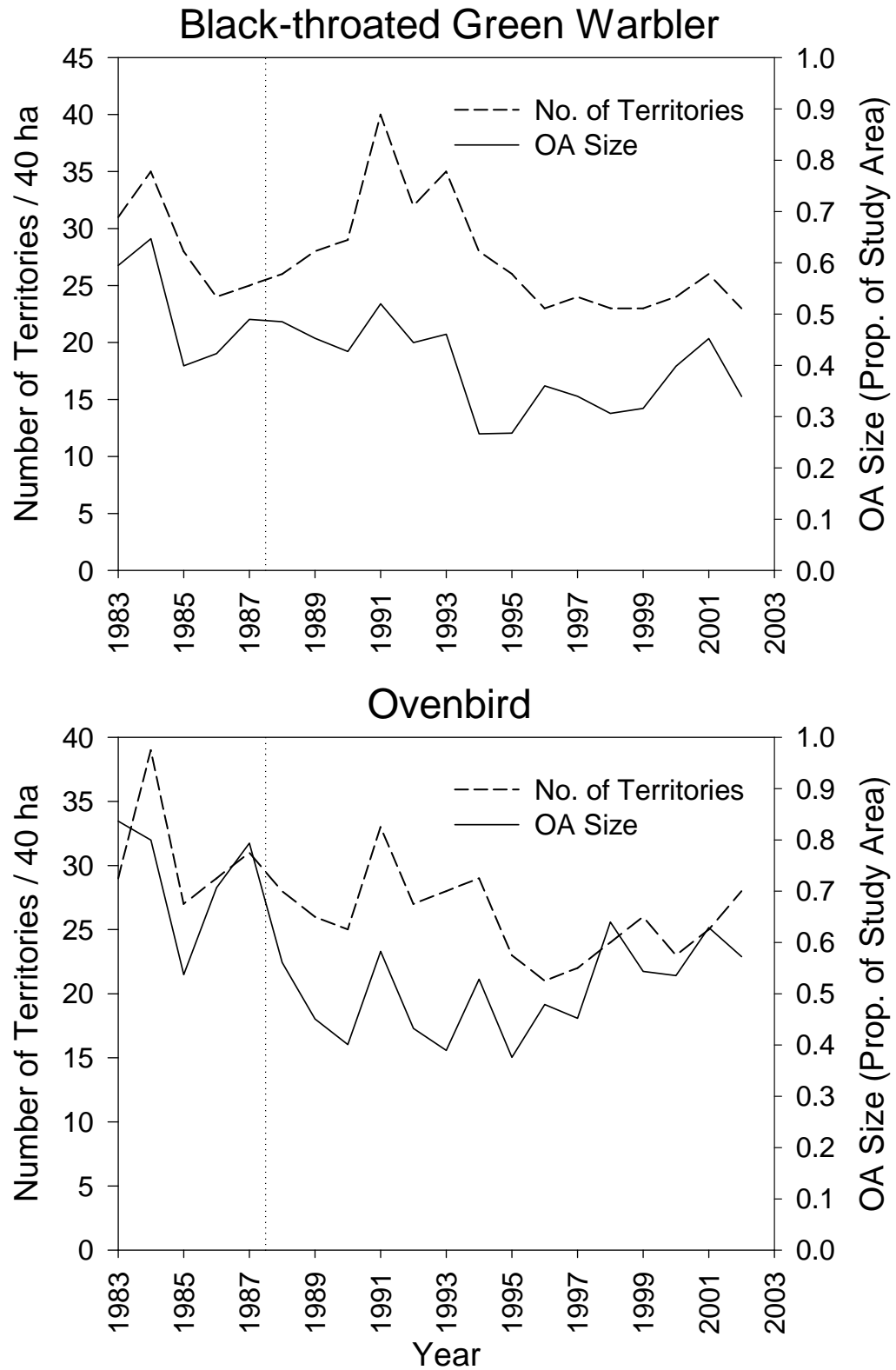


Figure 2.9. Sizes of OA (as proportions of the study area) and number of territories of the Black-throated Green Warbler and Ovenbird in the 40-ha study area of the Holt Research Forest, 1983-2002.

than 100 m away from the gaps (Fig. 2.8A). About five years after the disturbance these trends reversed and Veeries began to recolonize the areas they had previously abandoned.

Duration of Species' Responses

Only one of the 11 species that responded positively or negatively to the disturbance did not show a return to pre-disturbance levels in either the proportion of gap area in its OA and average distance to gaps. The Black-and-white Warbler retained a higher proportion of gaps in its OA (Fig. 2.2) and occurred closer to gaps (Fig. 2.3) than to the same areas during the pre-disturbance period (Table B.3). The remaining 10 species had returned to pre-disturbance levels in one or both measures. For example, for species such as the Black-throated Green Warbler and Ovenbird, average distances from gaps 10-15 years after the disturbance were the same as during the pre-disturbance period (Fig. 2.7), and the proportions of gap area in their OAs were approaching pre-disturbance levels but were still significantly different (Fig. 2.6) (Table B.3). Other species such as the White-throated Sparrow did not return to pre-disturbance levels because their populations declined to zero (Figs. 2.2, 2.3). Finally, species like the Winter Wren attained pre-disturbance levels of habitat use because it was absent from the forest before the disturbance and was absent again by 13 years after the disturbance (Figs. 2.2, 2.3).

DISCUSSION

In this study, environmental heterogeneity was experimentally created through small-scale disturbances in a forest and the resulting vegetation was categorized as either gap or forest. While this is obviously a crude depiction of the forest (see Lieberman et al.

1989), birds were clearly distributed non-randomly with respect to these two vegetation types and bird community structure varied temporally across the forest as birds tracked post-disturbance changes in vegetation. Bird species that are typically associated with early successional habitat increased in abundance and their distributions shifted to the recently disturbed areas (Figs. 2.2, 2.3, 2.4), while bird species that prefer mature forest habitat shifted their distributions away from the disturbed areas but showed negligible decreases in abundance (Figs. 2.6, 2.7, 2.8). Thus, experimental gaps helped maintain bird species diversity within the landscape by effecting a disturbance-mediated coexistence (Denslow 1985) between early- and late-successional bird species. However, the duration of the coexistence was generally short-lived; by 15 years after the disturbance the use of the disturbed areas by most species had reached or were approaching pre-disturbance levels.

Not all species exhibited a directional response to the disturbance; nearly half of the species (9 of 20) I examined showed little or no consistent change in the proportion of gaps in their OA and the average distance to gaps. While it is likely that these species were affected by the disturbance in more subtle ways, such as modification in foraging behaviors (e.g., Maurer and Whitmore 1981, Franzreb 1983), I focus my discussion on those species that showed relatively strong positive or negative distributional shifts.

Species that Responded Positively to Disturbance

Bird species that are typically associated with early successional habitat were rare or decreasing in abundance within the study area prior to the disturbance. This was most likely due to the loss of early successional habitat through successional changes since

post-agricultural land abandonment (see also Holmes and Sherry 2001). The experimental disturbance temporarily bolstered the populations of some of these bird species (Chapter 1) and the changes in abundance were typically accompanied by changes in distributions. In general, there was an increase in the proportion of gap habitat within these species' OAs, a decrease in average distance to the gap areas, and an increase in the use of the habitat in the gap (0 m) and edge habitats (0-25m).

There was a temporal succession of bird species using the post-disturbance patches as they transitioned from gap to mature phase. For example, the White-throated Sparrow and Winter Wren showed maximum use immediately following the disturbance, while the Eastern Wood-Pewee peaked in its use about 7 years after the disturbance (Fig. 2.2). The Black-and-white Warbler exhibited increased use of disturbed patches for up to 15 years post-disturbance. Correspondingly, species preferring mature forest habitat started to recolonize these areas four years after disturbance (Fig. 2.6) and had reached or were approaching pre-disturbance levels of use by 15 years post-disturbance (Table B.3).

The use of experimental gaps by the White-throated Sparrow suggested density dependent regulation of population size based on the relationship between territorial behavior and habitat heterogeneity (Fretwell and Lucas 1969, Rodenhouse et al. 1997). The population increased in response to the availability of experimental gaps, but as the suitability of the experimental and ledge gaps decreased, individuals in the lowest quality habitat dropped out of the population first and the OAs retracted (Fig 2.2H) such that the last individuals showed almost exclusive use of the remaining gap and the edge habitats (Figs. 2.3H, 2.4H). Common Yellowthroats showed similar dynamics (Figs. 2.3G, 2.4G),

except that their movement from the ledge gaps to the experimental gaps (Figs. 2.4G, 2.5C) prevented a decrease in the proportion of experimental gaps in their OA (Fig 2.2G).

Bird species that prefer early successional habitat remain present in extensively forested landscapes in small numbers, primarily as “fugitive species” (*sensu* Hutchinson 1951) that opportunistically take advantage of the favorable habitat conditions created by disturbances. Although these species are prone to local extinction when disturbed patches regenerate, these species can persist at larger spatial scales as long as disturbance generates colonizable space within the dispersal range of extant populations before populations go extinct (Sousa 1984). In this study, these types of dynamics were most prominently displayed by the Winter Wren and the White-throated Sparrow. The former was absent from the study area prior to the disturbances, and the latter was declining sharply until its numbers increased following the disturbance. By 15 years after the disturbance both species had become locally extinct. Lent and Capen (1995) also found that the Chestnut-sided Warbler (*Dendroica pensylvanica*), Mourning Warbler (*Oporornis philadelphia*), Common Yellowthroat, and White-throated Sparrow are species that may adopt fugitive strategies in northern hardwood forests.

Species that Responded Negatively to Disturbance

Mature-forest bird species exhibited minimal decreases in abundance following the disturbance (Fig. 2.6, Chapter 1). Nevertheless, the Veery, Black-throated Green Warbler and Ovenbird showed a strong avoidance of the experimental gaps and edge habitats. The avoidance of these areas without corresponding decreases in abundance reduced the per capita area available for territories so that the territory size was reduced

for at least some of the individual birds. Since I could not measure territory size directly, I do not know if the effects on territory size were diffused equally across all individuals within a given neighborhood (e.g., ideal-free distribution), if the effects were most acute nearest the gaps, or if the effects were manifested in a still more complex pattern based on the interaction between habitat quality and dominance of males (e.g., ideal- despotic distribution) (Fretwell and Lucas 1969, Rodenhouse et al. 1997).

Regardless of the pattern of the effects, I know that densities of the Black-throated Green Warbler and Ovenbird increased in the remaining forest; both showed contractions in their OAs without comparable decreases in abundance (Fig. 2.9). Crowding during the breeding season can lead to density dependent decreases in demographic rates by reducing territory size, intensifying resource limitations, increasing time spent in agonistic interactions, increasing predation rates on both adults and young and brood parasitism rates, or a combination of these factors. For example, Sillett et al. (2004) found that territory size, the time males spent foraging (as opposed to activities associated territorial defense), and the number of young fledged per territory were significantly greater for Black-throated Blue Warblers (*Dendroica caerulescens*) in areas where densities had been experimentally reduced.

Loss of mature forest from disturbance was accompanied by an increase in the amount of edge habitat within the forest. While edges have typically been a cause for concern for forest birds because of greater rates of parasitism by Brown-headed Cowbirds (e.g., Brittingham and Temple 1983, Robinson 1992) and nest predation (e.g., Wilcove 1985, Robinson 1992), much of the support for the existence of these negative effects comes from studies on relatively static, external edges of forest fragments surrounded by

agricultural or suburban areas (see reviews by Paton 1994, Hartley and Hunter 1998, Báraty and Báldi 2004). In contrast, disturbance within extensively forested areas results in patches of early successional habitat that are functionally fragments within the forest (Rudnický and Hunter 1993a). The resulting edges are internal and ephemeral because there is typically a rapid transition back to forest vegetation following the disturbance. The evidence for negative effects of these latter types of edges is equivocal. Some studies found higher nest predation near edges of openings within a forest-dominated matrix (Brittingham and Temple 1983, Yahner and Scott 1988, King et al. 1996, Manolis et al. 2002), while others found no relationship (Ratti and Reese 1988, Rudnický and Hunter 1993b, Hanski et al. 1996, Driscoll and Donovan 2004). Similarly, in some studies the creation of small openings in extensive and unfragmented forests did not result in an increase in abundance of avian nest predators and brood parasites (Annand and Thompson 1997, Germaine et al. 1997), but it did in other studies (Robinson and Robinson 1999).

My limited data on potential avian nest predators and brood parasites suggests that Blue Jays (*Cyanocitta cristata*) and Brown-headed Cowbirds showed no change in the average number of detections per sampling visit over the course of the study (Chapter 1), and neither demonstrated an increase in their use of gaps or edge areas (Campbell, unpublished data). In contrast, the American Crow (*Corvus brachyrhynchos*) exhibited a temporary increase (6 years) in average number of detections per visit following the disturbance, tended to use the half of the study area in which the disturbances were located (Chapter 1), and exhibited selection for edges (0-25 m) (Campbell, unpublished data). Nonetheless, I found that birds that are typical of mature forest habitat, and thus

most susceptible to predation and parasitism in edges, avoided gaps and forest immediately adjacent to the gaps (Fig. 2.8), which may have partially mitigated any increased susceptibility to predation and parasitism near edges.

Although mature forest bird species avoided the disturbed areas during the breeding season, these areas may play important roles during the non-breeding season. For example, post-breeding adults and juveniles of mature forest birds may move to second-growth areas in late summer because dense vegetation is better cover from predators (Anders et al. 1998, Vega Rivera et al. 1998, Pagen et al. 2000). Other studies have shown that during migration many avian species used treefall gaps because of their increased understory foliage, soft mass production, and insect abundance (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986).

Experimental Gaps vs. Natural Gaps

In general birds responded much more strongly to experimental gaps than the natural (ledge and treefall) gaps. This discrepancy may have been caused by various factors. First, experimental gaps were significantly larger and collectively had a greater spatial extent than the natural gaps (Kimball et al. 1995). The greater area of early successional habitat in experimental gaps may displace entire breeding territories of mature forest birds or accommodate those of early successional bird species. Nevertheless, the Holt Research Forest is still a relatively young forest, whereas older forests have higher rates of gap formation and larger gaps that would be less likely to be closed by lateral expansion of surrounding trees (Runkle 1982, Lorimer 1989). As the

forest matures the size distribution of the natural gaps will converge in similarity to that of the experimental gaps.

Second, the experimental gaps were grouped in 1-ha blocks such that together they may have acted functionally as a single large opening (Hunter 1993). Larger areas of disturbance (e.g., large-scale blowdown or a clearcut) have proportionally less edge habitat to negatively affect bird species that prefer mature forest and they attract birds of more open areas or birds that require extensive areas of second-growth habitat (Rudnicki and Hunter 1993a, Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000, Moorman and Guynn 2001). If the same disturbed areas were dispersed more evenly over the treated half of the study area, as were the natural gaps, I may have witnessed different results.

Third, experimental gaps were distributed proportionally to the area of soil drainage classes and forest cover types, whereas the treefall gaps tended to be proportionally 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, conditions were more suitable for tree regeneration in experimental gaps than in ledge gaps, so the experimental gaps were forested at the start of the study and the ledge gaps were not. Consequently, I was able to directly examine avian responses to experimental gaps because I examined the use of the same area of the forest before and after it became a gap. On the other hand, detecting responses to ledge gaps was less

direct because I could only examine the change in the use of the pre-existing gaps over time. Furthermore, because ledge gaps regenerated more slowly than the experimental gaps, associated changes in spatial distribution were not likely to be as apparent.

CONCLUSIONS

This study represents the longest continuous experimental investigation of the effects of small-scale disturbances on forest birds and thus provides important insight into understanding bird response to disturbance over time. I found notable alterations in the spatial distributions of 11 of the 20 bird species I examined: eight species responded positively to the disturbances (i.e., the proportion of gaps in their OAs increased, and average distance of observations from gaps decreased) and three species responded negatively by avoiding disturbed areas and the forest immediately surrounding these areas. These differences in response allowed early- and late-successional bird species to coexist. However, the coexistence was temporary; by 15 years after the disturbance, most of the bird species that responded favorably to the disturbance were no longer using the disturbed areas and those that responded negatively had started to recolonize these areas. Importantly, the five years of pre-disturbance data and 15 years of post-disturbance data were long enough periods to discriminate responses from the year-to-year variability that can obscure studies of shorter duration and to capture the full temporal response (i.e., a return to pre-disturbance distributions) of most species.

In addition to an improved understanding of bird response to small-scale disturbances, my findings also emphasize the importance of explicitly considering the spatial component of the response. First, knowing the magnitude of displacement or

attraction to disturbed areas and the timing and pattern with which species return to or abandon these areas is fundamental to understanding habitat use of individual species and community structure over space and time. For example, even though the direction of the response was similar within the groups of early- and late-successional bird species, the magnitude, timing, and pattern of the post-disturbance shifts varied considerably by species. These individualistic shifts in distributions over time likely created complex changes in bird community structure, especially in and around the disturbed areas. The use of gap edges during the post-disturbance period is particularly relevant given the possibility of increased nest predation and brood parasitism in these areas. Secondly, when spatial data are combined with abundance data they can elucidate more complex dynamics than can either type of data on their own. For example, the OAs of the Black-throated Green Warbler and Ovenbird decreased in size following the disturbance without concomitant decreases in abundance, which led to more individuals in less area and possibly an increase in intraspecific competition. Finally, we typically lack a quantitative understanding of how species respond to different types of disturbance. Simple spatial metrics from experimental studies can be used to quantify the sensitivities of different bird species to disturbances and to parameterize models that predict how individual species and communities will respond to different types of disturbance. These types of information are of interest from both theoretical and applied standpoints, because they address fundamental questions of abundance and distribution and because they are important for effective land planning and resource management for different types of natural and anthropogenic changes in vegetation.

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Chapter 3

ARE YEAR-TO-YEAR CHANGES IN AVIAN HABITAT USE STOCHASTIC OR DETERMINISTIC?

INTRODUCTION

The physical and biological environments that organisms require to survive and reproduce vary in time and space. Temporal variation results from natural changes such as vegetation succession, seasonality, and climatic fluctuations; spatial variation results from factors acting differentially across the landscape such as disturbances, soils, and moisture gradients. These two sources of variation interact to create unique arrangements of resources and thus different habitats in time and space (Block and Brennan 1993).

The ability of organisms to distinguish and select among habitats has important ecological consequences for individuals and the communities they constitute (Holt 1987, Jaenike and Holt 1991). Consequently, considerable attention has been given to the theory of habitat selection (Cody 1985, Jones 2001). The core assumption of habitat selection research is that many organisms choose to settle in environments that enhance the probability of survival and reproduction and therefore increase fitness (Levins 1968, Orians 1980, Klopfer and Ganzhorn 1985). A necessary corollary of this assumption is that there are environmental cues to which individuals respond in a deterministic fashion when deciding to settle. Accordingly, deterministic models should be able to describe the spatial and temporal variation in distribution patterns.

Well-known examples of deterministic models include the model of habitat selection in birds by Fretwell and Lucas (1969) and Brown (1969). The Fretwell-Lucas

model assumes that birds fill different habitats in a manner determined by the interaction between density of conspecifics and intrinsic quality of the habitat. The ideal-free variation of this model states that birds choose to settle in the best habitat first, until crowding decreases the suitability of the best habitat to a level equal to the next best habitat. At this point, birds would be equally well-off by settling in the uncrowded, lower-quality habitat as they would be settling in the preferred habitat. The ideal-dominance variation assumes that dominant individuals monopolize the best habitat and thus maintain higher fitness levels than those individuals forced into lower quality habitats. The “buffer” effect is a related idea that extends the spatial dynamics of ideal-dominance habitat occupancy over multiple years (Svårdson 1949, Kluyver and Tinbergen 1953, Brown 1969). It posits that densities in high-quality habitat will be consistent across years, because intrinsic properties of the habitat (e.g., availability of food, cover, and nesting sites) and the territorial exclusion of surplus individuals act together to buffer against year-to-year fluctuations. In contrast, densities will be more variable in marginal habitats as populations fluctuate.

These models have played an important role in shaping our thinking on intraspecific population dynamics and community organization (O'Connor 1987, Rosenzweig 1987), however they have only received limited empirical support (e.g., Kluyver and Tinbergen 1953, O'Connor 1986, 1987, Petit and Petit 1996). For example, tests of the Fretwell-Lucas model have examined only a few specific predictions at a time (e.g., O'Connor 1982, Clark and Weatherhead 1987, Eckert and Weatherhead 1987a, b, Morris 1989; but see Petit and Petit 1996) rather than simultaneously addressing all aspects of the model (e.g., settling patterns, population density, habitat suitability and

fitness) (Petit and Petit 1996). Additionally, it does not necessarily follow that the proposed processes are in fact creating the observed patterns. In other words, if the theory does not generate unique predictions, it is possible to obtain the “right” pattern for the “wrong” reasons (Dayton 1973). Finally, the emphasis of these tests is on verification of a particular theory rather than testing among alternative hypotheses (Wiens 1984). An alternative that is rarely tested is the absence of the hypothesized mechanism (i.e., a null model; Gotelli and Graves 1996). If a pattern can be produced by a null model, parsimony dictates that there would be no need to invoke the mechanism because it adds unnecessary complexity (Gotelli and Graves 1996).

In this chapter I examine the need to explicitly invoke deterministic processes (i.e., birds tracking variations in habitat) to explain patterns of habitat occupancy in birds. Specifically, I ask if habitat use is predictable among years or if the variation in habitat use is great enough that there may be a stochastic component to the decision of birds to settle in a particular area (Haila et al. 1996). Thus, I investigate stochasticity as an alternative to the deterministic explanation of variation in the patterns of spatial distribution. I address this issue using a 5-year data set of bird locations collected at the Holt Research Forest in Arrowsic, Maine (Witham et al. 1993).

METHODS

Study Area

The Holt Research Forest is 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). It occurs within the transition zone between oak-pine forest to the west and south and coastal spruce-fir to

the east and north (McMahon 1990). The principal tree species in decreasing order of trees per hectare and 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, Table C.1). The forest is a result of secondary succession following the abandonment of agricultural land 70-110 years ago (Moore and Witham 1996).

The study area comprises 40 ha and is buffered by an average of 90 m (range: 17-185 m) of forest from adjacent forests, a public road, and an estuarine river. The study area is demarcated on the ground by a hierarchical grid system with 40 1-ha (100×100 m) blocks, 160 50×50 m quadrats, and 640 25×25 m subquadrats.

When the data were collected in 1983-1987, the most common vegetation cover types (based primarily on dominant tree species in the stand and secondarily on moisture conditions, Witham et al. 1993) were mixed-mesic, coniferous, and pine-dominated stands, which covered 51, 12, and 10% of the study area respectively (Fig. 3.1). The latter two cover types occurred in the northern half of the study area along with small dense stands of young white pines planted 40-50 years ago on the northern edge of the study area and stands of small white pines with juniper ground cover on exposed rock ledges. In the southern half of the study area, the drier, ledge-dominated sites contained mixed vegetation and there was a small red maple swamp surrounding by deciduous forest near the center of the study area.

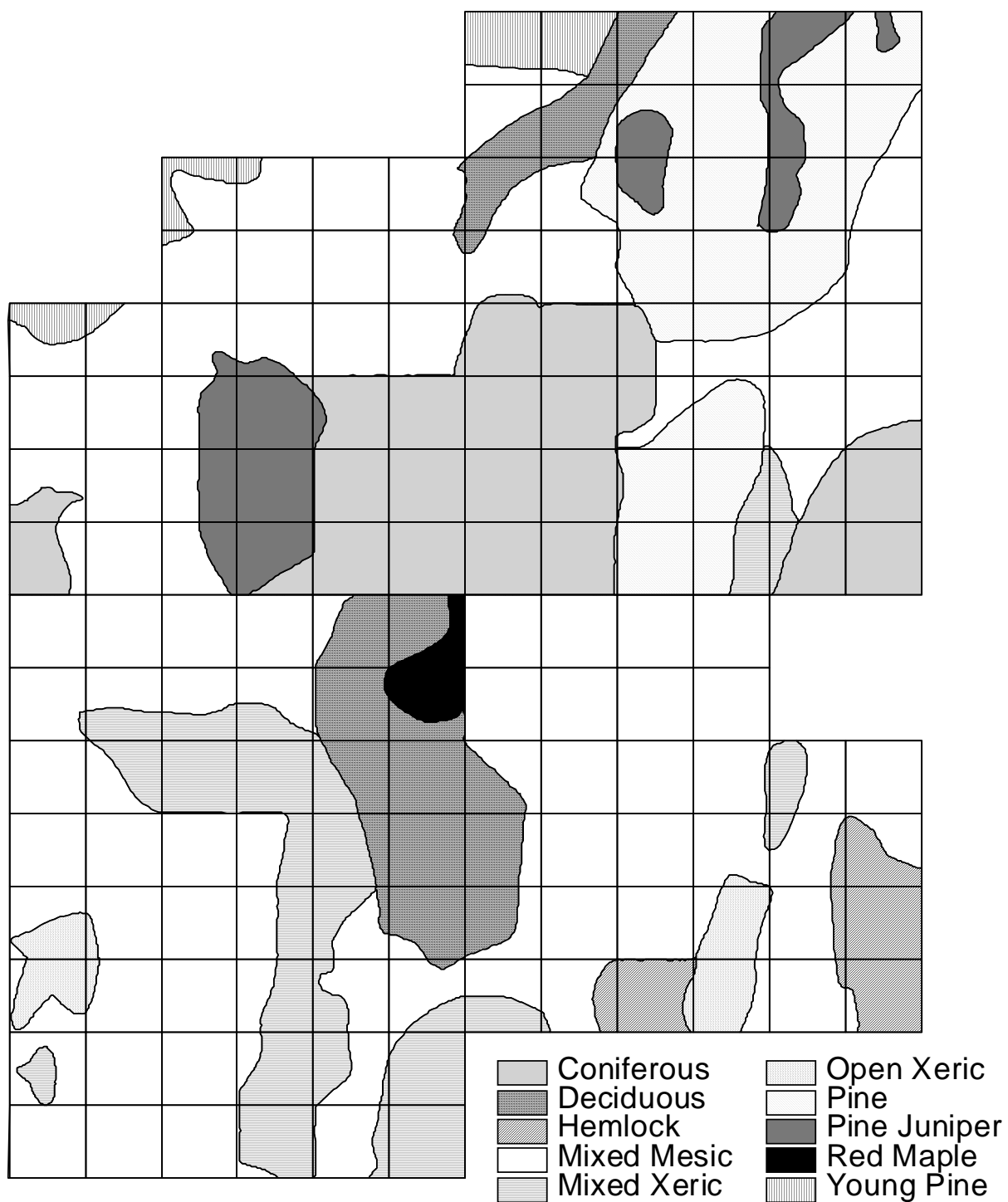


Figure 3.1. Distribution of vegetation cover types at the Holt Research Forest over the 50 m \times 50 m quads. Cover types are described in Witham et al. (1993).

Conceptual Approach

Haila et al. (1996) previously examined the role of stochasticity in habitat use within a boreal forest bird community in southern Finland. Therefore, I adopted their approach as well as some of their terminology. Namely, I used an *a posteriori* explanatory approach in which I tried to match pattern with process by comparing observed distribution patterns with those derived by stochastic processes. Similar to Haila et al. (1996), I considered stochastic processes to be the summation of factors that influenced bird occupancy patterns independent of the structural features of the vegetation (e.g., climatic fluctuations, food availability, regional population fluctuations). These can also include factors such as individual variability in how birds evaluate their environment and responses to year-to-year variations in habitat structure that are too subtle to be detected by human observers. While birds are not necessarily behaving randomly with respect to these factors, the summation of their responses to these factors may create variability in the spatial distribution patterns that is apparently random.

I examined variation in habitat use among years with “frequency landscapes” (*sensu* Haila et al. 1989). A frequency landscape is an area divided into a grid, where each grid cell contains a value that represents the number of years the cell was occupied. Here, I use the quadrats (hereafter quads) of the study area as the grid cells. The consistency with which quads are used over multiple years acts as a measure of relative preference for the features of that area (Haila et al. 1989) and thus indicates determinism in habitat occupancy. In contrast, significant variability in the quads used among years provides evidence for a greater role of stochasticity.

To assess the degree of stochasticity I first generated frequency landscapes for each species with null models in which certain elements were held constant while all others were allowed to vary randomly, and then I compared these to the observed frequency landscapes. If null models generated patterns of variability similar to the observed patterns, I concluded that the variability was predominantly stochastic. If I was unable to recreate the patterns with a null model, I concluded that the variability was largely caused by deterministic processes.

As with any model, confidence in the acceptance or rejection of the null model depends on its careful construction. For example, a completely random model of quad occupancy is probably unrealistic given the variation that exists in the vegetation of the quads and the ecology of the birds (e.g., habitat preferences, abundance, territoriality, site fidelity) (Haila et al. 1996). In other words, if a model is “too null” and does not incorporate realistic biological constraints, it can generate patterns that are very different from patterns seen in real communities (Gotelli and Graves 1996), making the rejection of a null model trivial or false. For example, if a bird species clearly prefers coniferous forest, it would be unrealistic to assume that quads dominated by coniferous trees and quads dominated by deciduous trees would be occupied with equal probability. Therefore, I incorporated various constraints to make the null models more realistic. However, care also needs to be taken when including constraints because a null model may not be rejected if its constraint incorporates the process it was designed to detect.

Data Collection

Bird Location and Territory Data

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 (late-May through early-July) each year. Each visit consisted of sampling the entire length of all north-south transects through block centers or all north-south transects along block borders between 0430 to 1030 hr (Fig. 3.1). Only one observer (J. W. Witham) collected the data for all years. All locations were digitized into a geographic information system (Witham and Kimball 1996). Data for all 16 visits were compiled and composite maps were made for each species in each year.

Territory numbers were determined from the maps in all years by J. W. Witham. A minimum of 5 registrations was required to denote a territory, and an emphasis was placed on observations of counter-singing males. Territories that straddled the boundary of the study area were counted if a majority of their points fell within the study area.

Although data have been collected since 1983, I limit my consideration to the first 5 years of the study, because in the winter of 1987-1998 the western half of the study area was experimentally disturbed. Because I am interested in the relative contributions of deterministic and stochastic processes in determining habitat use, the strongly deterministic shifts I observed in the distributions of birds after the disturbance (Chapter 2) is likely to overwhelm stochastic influences and thus make them difficult to detect.

Vegetation Data

Vegetation data were collected using two methods: timber inventory and relevé (Witham et al. 1993). A complete timber inventory was conducted in every quad in 1984. The resulting data consisted of the species, diameter at breast height (DBH), and condition (e.g., living or dead) of every tree with a DBH greater than 9.5 cm. From these data, for each quad I derived the total number of trees, total basal area of all trees, and the basal area of all coniferous trees, all deciduous trees, oaks (red and white [*Quercus alba*]), eastern white pine, birches (paper [*Betula papyrifera*], yellow [*Betula alleghaniensis*], and gray [*Betula populifolia*]), red maple, hemlock (*Tsuga canadensis*), balsam fir, and red spruce. These 10 species are the most abundant species and comprise 98% of the trees and 99% of the basal area (Table C.1).

Vegetation data from the relevé method were collected in every subquad in 1985 and consisted of the estimated percent coverage of each plant species (i.e., percentage of the ground that a species would cover if projected into a horizontal plane) in five strata (<0.25 m, 0.25-1 m, 1-5 m, 5-10 m, >10 m). Percent coverage was categorized into one of eight coverage classes: absent (0%), rare, <1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-100%. I limited my consideration to the same tree species and species groups (e.g., deciduous trees and oaks) of the timber inventory that occurred in the three highest strata.

Because the timber inventory was conducted at the quad level, I was restricted to this scale of resolution for my analysis of the frequency landscapes. Consequently, I scaled percent coverages to the quad level by averaging the midpoints of the coverage categories of each subquad. I arbitrarily selected 0.0025% and 0.25% to represent the midpoints of the rare and < 1% coverage categories. Using the relevé data I also

determined the total species richness of ferns and herbs, trees and shrubs, and all plants in each quad.

Data Analysis

Generating Frequency Landscapes

Using the bird location data from each year, I determined the occupancy status of all 160 quads (1 = occupied or 0 = unoccupied) for each species. I summed occupancy status over the 5 years to obtain the frequency of occupation of each quad (i.e., 0-5 years) and an overall observed frequency landscape.

I generated null frequency landscapes in a similar manner: occupying quads in each year according to the rules (i.e., constraints) of the particular null model and summing the occupancy status over the 5 years. A description of each constraint and the means by which I operationalized it within the context of the null models follow:

Yearly sum - To account for variability in abundance within and among species, all the null models were constrained by the yearly sum of occupied quads for each species. Functionally, this means that the number of quads that are randomly occupied in a year must equal the observed number of occupied quads in that year.

Occupancy - Quads that were unoccupied in all 5 years were likely non-habitat for a species. Thus, I limited the quads available to be randomly occupied to those that were occupied in at least one of the 5 years.

Spatial autocorrelation - Because birds are territorial and have territories larger than 50×50 m, the occupancy status of adjacent quads is likely to be spatially autocorrelated. I incorporated spatial autocorrelation by randomly seeding the landscape

with the same number of quads as there were territories for a species in a year. These quads acted as nuclei around which I grew territories using two accretion methods: regular and irregular. The regular method filled the quads surrounding each nucleus in an ordered sequence, such that the resulting territories were approximately disk or square shaped. The irregular method filled a randomly-selected unoccupied quad that was adjacent to a randomly selected occupied quad within the territory. This had the potential to produce irregularly shaped territories. In both of these methods, each territory was grown one quad at a time until reaching the number of quads occupied in that year. Territories were not allowed to expand into a quad that was already occupied.

Dispersion - Accounting for the spatial autocorrelation that results from territoriality, does not account for the repelling influence of territorial males. The dispersion constraint prevents territory nuclei from being randomly seeded next to each other by requiring that at least one unoccupied quad occur between territory nuclei. Nevertheless, for some of the more abundant bird species this constraint had to be relaxed in order to fit the number of territories present in a year. In these cases, the territories were randomly seeded according to the constraint until no more could fit in the landscape. The remaining nuclei were randomly seeded into an empty quad regardless of the occupancy status of neighboring quads.

Temporal autocorrelation – The assumption that individuals can freely choose their territory locations in each year is probably not valid because site fidelity in birds will increase the probability that the same quad(s) will be occupied from one year to the next (O'Connor 1987), even if habitat quality declines (i.e., quad use will be temporally autocorrelated). To incorporate site fidelity, I seeded the landscape with territory nuclei

in the first year according to the rules of a spatially autocorrelated constraint. In subsequent years, I reseeded the landscape according to the following rules. I drew a uniform random number for each territory and compared it to s , a measure of the strength of site fidelity ($0 \leq s \leq 1$). If the random number was less than or equal to s , the territory nucleus was seeded in the same quad or in a quad adjacent to the quad containing the territory nucleus from the previous year. If the number was greater than s , the territory nucleus was seeded in a random location. Territories were grown around each of the nuclei in accordance with the rules of the spatially autocorrelated constraint. Note that the territoriality constraint is necessarily incorporated in this model because territories form the basis of site fidelity. To determine the degree of site fidelity that minimized the difference between observed and null frequency landscapes for the most species, I repeated this procedure for different levels of s , which I varied between 0 and 1 in increments of 0.2.

Habitat - Thus far I have assumed that all quads (except for those that were never occupied under the zero frequency constraint) were suitable for occupation. This is unrealistic given the variability in vegetation among the quads (Fig. 3.1) and habitat preferences of individual species. I incorporated species-specific habitat constraints into null models using a two-step process. First I used multiple logistic regression to build statistical models that related vegetative characteristics of quads (independent variables) to the frequency of quad occupation, which was modeled as the proportion of years a quad was occupied (dependent variable). Using these models I generated frequency landscapes from the fitted frequencies of quad occupation. Next, in each year I drew a

uniform random number for each quad and occupied a quad only if the random number was less than or equal to the fitted value of the quad.

Prior to model building, I removed coverage variables that never exceeded 1% and variables that were highly correlated ($r > 0.8$) with other variables. Fourteen variables were removed, leaving 30 variables for inclusion (Table 3.1). Because of the large number of variables and species for which models are being fit, I sacrificed *a priori* model selection and extensive model checking for automation of the model fitting process with the approach proposed by Shtatland et al. (2001). First, I performed stepwise logistic regression with probabilities for entry and removal from the model equal to one; these probabilities allowed all variables to be sequentially entered into the model and prevented their removal once they were in the model. The result was a stepwise sequence of models that ranged in size from 1 to all 30 variables. I used information criteria to determine which model in the stepwise sequence was optimally sized, because information criterion penalizes the likelihood of a model for its complexity (i.e., the number of variables in the model). Thus, as the number of variables increased in the stepwise sequence the information criterion decreased until the penalty of including more variables offset the information gained at which point it started to increase. The model with the lowest information criterion value was of optimal size (k) and models that contained $k \pm 1$ and $k \pm 2$ variables were of sub-optimal size. Because I was interested in developing models that identified vegetation features that explained the observed distribution of bird species, I used Schwarz information criterion (SIC; also called Bayesian information criterion [BIC]) instead of Akaike information criterion (AIC). SIC penalizes models with more parameters more severely than does AIC (Burnham and

Table 3.1. Names and descriptions of 30 vegetation variables used to describe the observed occupancy patterns of 50 m × 50 m quads by birds breeding in the Holt Research Forest, 1983-1987.

Variable	Description
tree_density	number of trees with a DBH > 9.5 cm
tot_ts_spp	number of tree and shrub species
tot_h_spp	number of herbaceous species
ba_####†	basal area of all tree species (all), deciduous tree species (dec), oak species (oak), white pine (wp), birch species (brch), red maple (rm), hemlock (hem), balsam fir (bf), and red spruce (rs)
avg_cov_####_3	average coverage of all tree species (all), deciduous tree species (dec), oak species (oak), and white pine (wp) in the 1-5 m stratum
avg_cov_####_4	average coverage of all tree species (all), deciduous tree species (dec), oak species (oak), white pine (wp), birch species (brch), red maple (rm), balsam fir (bf), and red spruce(rs) in 5-10 m stratum
avg_cov_####_5	average coverage of all tree species (all), coniferous tree species (con), deciduous tree species (dec), oak species (oak), white pine (wp), and red maple (rm) in the >10 m strata

Note: Average coverage variables represent the midpoint of the coverage class of each 25 m × 25 m subquad averaged over all subquads in a quad. Also, variables for some species or species groups are absent from some strata because they were highly correlated with another variable.

†#### represents a particular species or species group listed parenthetically under the variable description (e.g., ba_all, avg_cov_wp_3).

Anderson 2002), so it tends to select simpler models that are more useful for description and interpretation (Shtatland et al. 2001). In contrast, AIC selects larger models that are more useful for prediction (Shtatland et al. 2001).

Next I conducted best subset selection procedures to obtain the best 20 models of each optimal and sub-optimal size, where the best were those that had the highest likelihood score (chi-square) statistic for all possible models of that size (SAS Institute 2003). I ranked all the models for each species according to their values of SIC and considered models with $\Delta\text{SIC} \leq 2$ to be candidates for the best model (Burnham and Anderson 2002). I performed model averaging on the candidate models to obtain parameter estimates for the coefficients of the relevant vegetation variables and their corresponding unconditional standard errors. If a parameter estimate did not exist in one of the models being averaged it was considered to be present but equal to zero (Burnham and Anderson 2002). With these parameter estimates, I determined the fitted frequencies for each quad.

Comparing Observed and Null Frequency Landscapes

I generated 100 frequency landscapes for each species from null models containing one or more of the constraints outlined above (Table 3.2). For each frequency landscape of the simulation, I represented the variability in quad use with the frequency distribution of occupied quads (i.e., the number of quads that were occupied in 0, 1, 2, ... 5 years), and then I averaged the number in each frequency category over the 100 iterations.

Table 3.2. Names and defining constraints of null models that are used to simulate habitat use in birds breeding at the Holt Research Forest, 1983-1987.

Model Name	Null Model Constraints					
	Yearly Sum	Occupancy	Spatial Autocorrelation	Dispersion	Temporal Autocorrelation	Habitat
Free	X					
Occupied Free	X	X				
Regular	X		X			
Occupied Regular	X	X	X			
Irregular	X		X			
Occupied Irregular	X	X	X			
Dispersed Regular	X		X	X		
Site Fidelity	X		X		X	
Habitat	X					X

I considered a null model to fit the observed data if its resulting average frequency distribution matched the observed frequency distribution. I could not assess goodness of fit between the two frequency distributions using chi-square goodness-of-fit tests, because of the low number of quads that occurred in the 0 and 5 frequency classes of many species. Instead, I used 5000 iterations of a Monte-Carlo simulation to generate a distribution of the test statistic ($\sum_{i=0}^5 |O_i - E_i|$, where O_i and E_i are the observed and expected number of quads occurring in frequency class i) that was expected under the average frequency distribution. In each iteration, I randomly assigned quads to each frequency class based on the proportion of quads occurring in that class and calculated the test statistic based on the randomly generated observed frequencies and the expected frequencies. I compared the test statistic based on the actual data to this distribution and assessed its statistical significance at $\alpha = 0.05$.

I excluded from this analysis bird species that did not establish territories in two or more years and were not reliably counted by territory mapping because they 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*]).

RESULTS

Twenty species met the criteria for inclusion in the analyses. The total number of territories of all these species combined in a single year ranged from 133 to 163. The

Ovenbird, Black-throated Green Warbler, and Blackburnian Warbler were the most abundant species; each comprised an average of 21%, 19%, and 8% of the territories in a year respectively (Table 3.3). (Scientific names of birds are provided in Table 3.3.) All but one species was present in the study area in every year; there were no territories for the Nashville Warbler in 1986.

Patterns of Frequency Landscapes

The number of quads occupied within a year was positively related to the number of territories for most species ($r > 0.65$ for 17 species, $n = 5$ years), although only 8 of these were significantly correlated ($r > 0.95$, $p < 0.02$) because of the small number of years. When all species were combined the correlation was also significant ($r = 0.91$, $p < 0.0001$, $n = 100$ [20 species \times 5 years]). There was also a positive relationship between the number of quads occupied five times and the total number of quads occupied over the 5-year period ($r = 0.86$, $p < 0.0001$, $n = 20$ species). When the two most abundant species (Ovenbird and Black-throated Green Warbler) were excluded, this correlation was weaker but still significant ($r = 0.65$, $p = 0.0038$, $n = 18$).

There was a negative relationship between the number of quads per territory and the number of territories for all species combined ($r = -0.51$, $p < 0.0001$, $n = 99$). The number of quads per territory acts only as an index for territory size and it is probably biased high because of the inclusion of quads in the total that were used by non-territorial individuals or individuals making excursions outside of territories. When species were examined individually the relationship remained negative for 17 of the 20 species, 8 of which had $r < -0.70$. However, the relationships were statistically significant ($r < -0.91$,

Table 3.3. Numbers of occupied quads (Quad), territories (Terr) and occupied quads per territory (Quads/Terr) of 20 bird species at the Holt Research Forest, 1983-1987.

Bird Species		Year					Quads/Terr	
		1983	1984	1985	1986	1987	\bar{X}	SD
Hairy Woodpecker	Quad	14	16	14	10	10	10.4	4.62
(<i>Picoides villosus</i>)	Terr	1	1	2	1	2		
Eastern Wood-Pewee	Quad	29	41	58	18	29	8.1	3.58
(<i>Contopus virens</i>)	Terr	3	3	9	3	6		
Black-capped Chickadee	Quad	80	74	97	87	101	10.6	2.33
(<i>Poecile atricapilla</i>)	Terr	6	6	11	8	13		
Brown Creeper	Quad	53	85	84	66	60	11.5	2.11
(<i>Certhia americana</i>)	Terr	5	6	9	5	6		
Red-breasted Nuthatch	Quad	14	35	69	46	32	10.3	4.58
(<i>Sitta canadensis</i>)	Terr	4	4	6	4	2		
Golden-crowned Kinglet	Quad	16	4	23	22	45	6.5	1.64
(<i>Regulus satrapa</i>)	Terr	2	1	4	3	6		
Veery	Quad	44	50	31	42	27	8.8	0.83
(<i>Catharus fuscescens</i>)	Terr	5	5	4	5	3		
Hermit Thrush	Quad	55	55	69	65	67	8.9	0.68
(<i>Catharus guttatus</i>)	Terr	7	6	8	7	7		
Nashville Warbler	Quad	70	49	39	4	25	8.2	1.53
(<i>Vermivora ruficapilla</i>)	Terr	8	8	4	0	3		
Yellow-rumped Warbler	Quad	57	74	87	85	89	9.2	1.83
(<i>Dendroica coronata</i>)	Terr	7	6	10	11	10		
Black-and-white Warbler	Quad	76	56	56	48	27	9.1	0.65
(<i>Mniotilta varia</i>)	Terr	8	6	7	5	3		
Blackburnian Warbler	Quad	58	69	73	73	87	6.4	0.35
(<i>Dendroica fusca</i>)	Terr	9	11	11	11	15		
Black-throated Green Warbler	Quad	141	149	136	117	123	4.7	0.28
(<i>Dendroica virens</i>)	Terr	31	35	28	24	25		
Pine Warbler	Quad	27	11	7	11	6	9.7	3.11
(<i>Dendroica pinus</i>)	Terr	2	1	1	1	1		

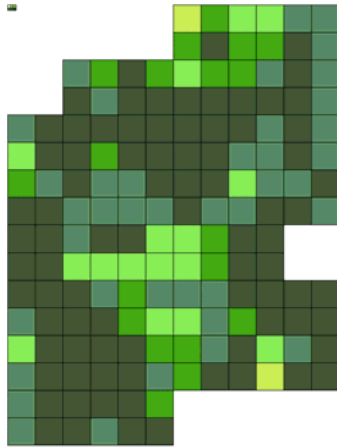
Table 3.3 (Continued).

Bird Species		Year					Quads/Terr	
		1983	1984	1985	1986	1987	\bar{X}	SD
Canada Warbler	Quad	17	11	19	13	7	11.5	3.77
(<i>Wilsonia canadensis</i>)	Terr	1	1	2	1	1		
Ovenbird	Quad	142	143	127	137	137	4.5	0.49
(<i>Seiurus aurocapillus</i>)	Terr	29	39	27	29	31		
Common Yellowthroat	Quad	52	44	29	25	30	5.17	2.41
(<i>Geothlypis trichas</i>)	Terr	8	5	9	7	8		
Scarlet Tanager	Quad	36	37	28	30	41	11.3	2.24
(<i>Piranga olivacea</i>)	Terr	3	3	2	3	5		
White-throated Sparrow	Quad	50	54	41	13	24	6.3	2.25
(<i>Zonotrichia albicollis</i>)	Terr	9	6	7	4	3		
Purple Finch	Quad	22	21	24	18	44	14.7	5.07
(<i>Carpodacus purpureus</i>)	Terr	2	2	2	1	2		

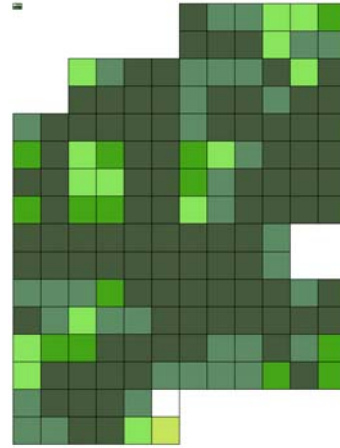
$p < 0.03$) for only four species (Black-capped Chickadee, Black-throated Green Warbler, Ovenbird, and Scarlet Tanager).

Variability in habitat use among the 20 species followed three general patterns that were apparent in the observed frequency landscapes (Figs. 3.2, C.1). Frequency landscapes of species that were very abundant and exhibited widespread use of the study area over the 5 years were characterized by a lack of unoccupied quads and a high frequency of use for most quads. Two species exhibited this pattern: Ovenbird and Black-throated Green Warbler (Figs. 3.2A, B); they occupied 59% and 52% of the quads in all 5 years, respectively. Species such as the Black-capped Chickadee and Hermit Thrush also showed widespread use but were of intermediate abundance (Figs. 3.2C, D). Consequently, frequency landscapes of these species also had very few quads that were never occupied or occupied in all years, with most quads occupied in 1-3 years. The third type of frequency landscape resulted from species that had low to intermediate abundance and were more stenotopic in their use of the study area; these frequency landscapes were characterized by many quads that were never occupied or only occupied once and very few quads that were occupied 4 or 5 years (Figs. 3.2E, F). These patterns were typical of species such as the Canada Warbler, which returned to the red maple swamp near the middle of the study area in all 5 years (Figs. 3.1, 3.2E), and the Common Yellowthroat, which occurred in the more open areas that were coincident with the exposed rock ledges (Figs. 3.1, 3.2F). The differences in the three types of frequency landscape were also reflected in the shapes of their frequency distribution of occupied quads (Fig. 3.3, Table C.2).

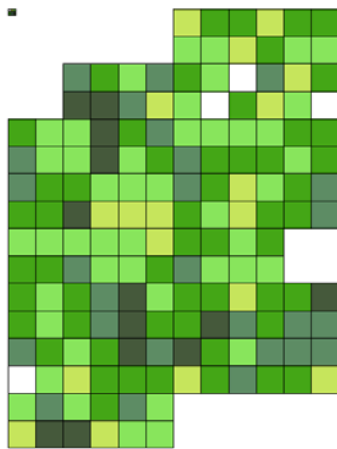
A. Black-throated Green Warbler



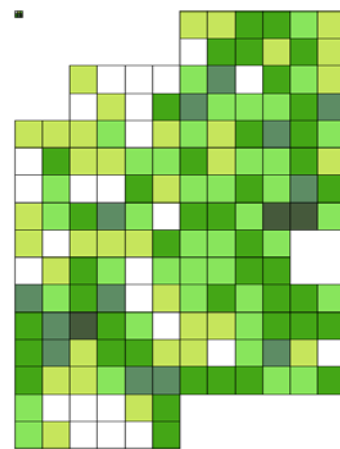
B. Ovenbird



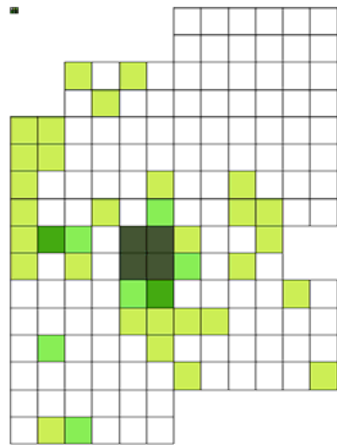
C. Black-capped Chickadee



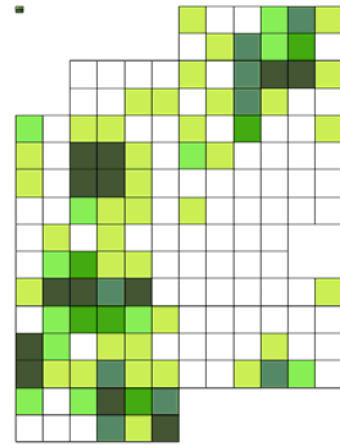
D. Hermit Thrush



E. Canada Warbler



F. Common Yellowthroat



Number of Years Occupied



Figure 3.2. Observed frequency landscapes for six bird species breeding at the Holt Research Forest, 1983-1987. Each grid cell is a 50×50 m quad. See Fig. C.1 for remaining species.

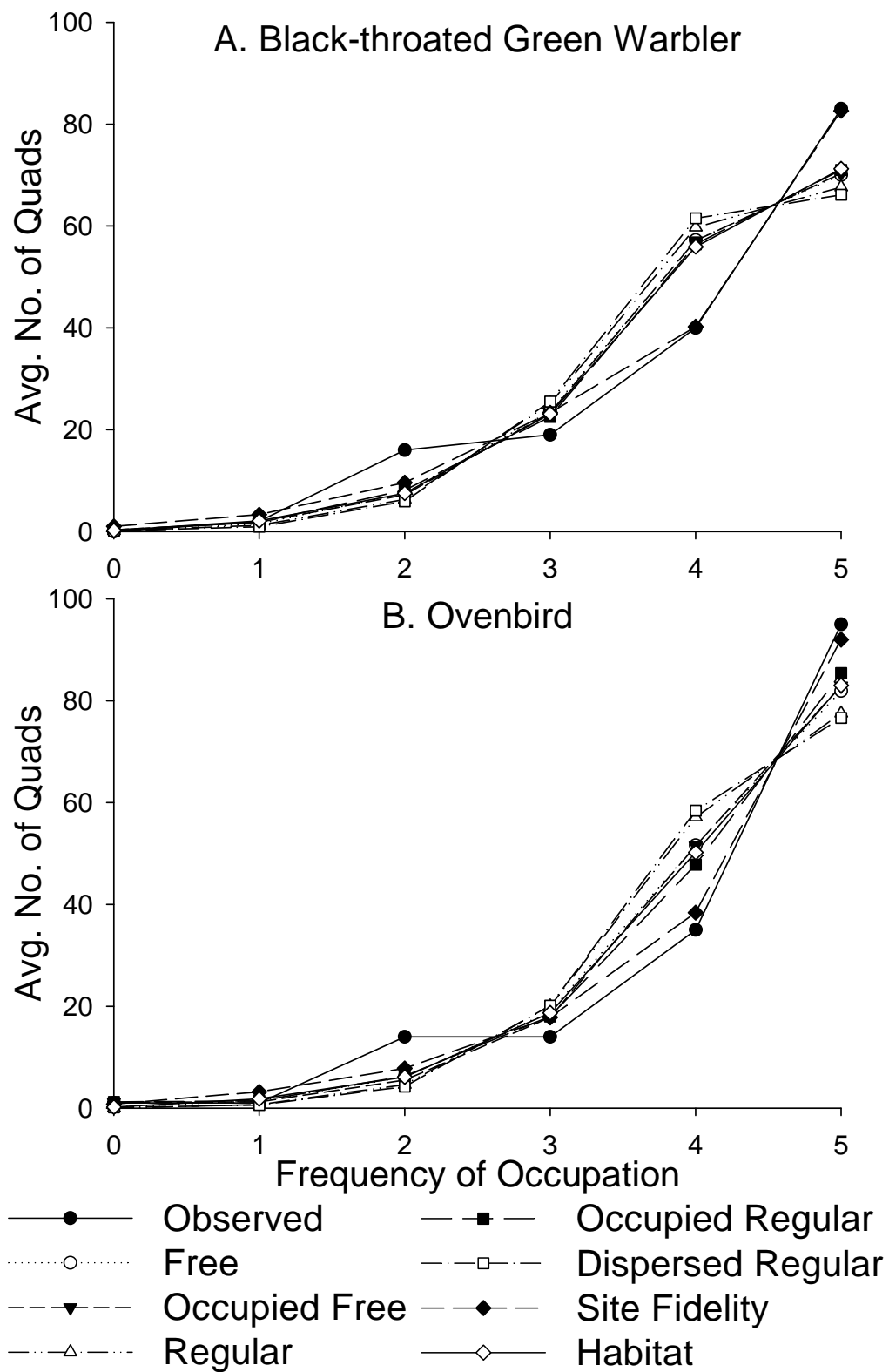


Figure 3.3. Frequency distributions of occupied quads based on observed data and various null models. See text and Table 3.2 for model descriptions.

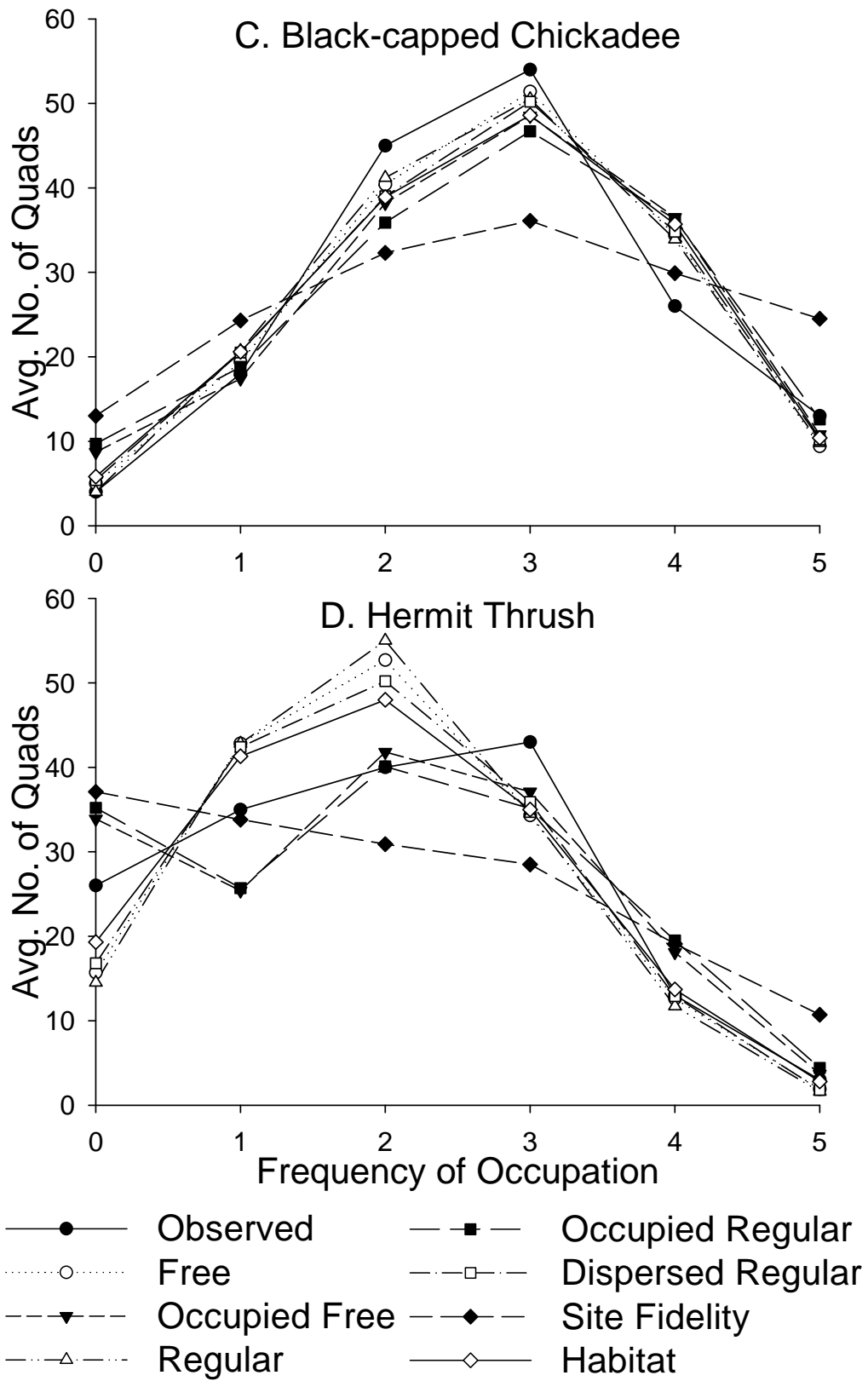


Figure 3.3 (Continued).

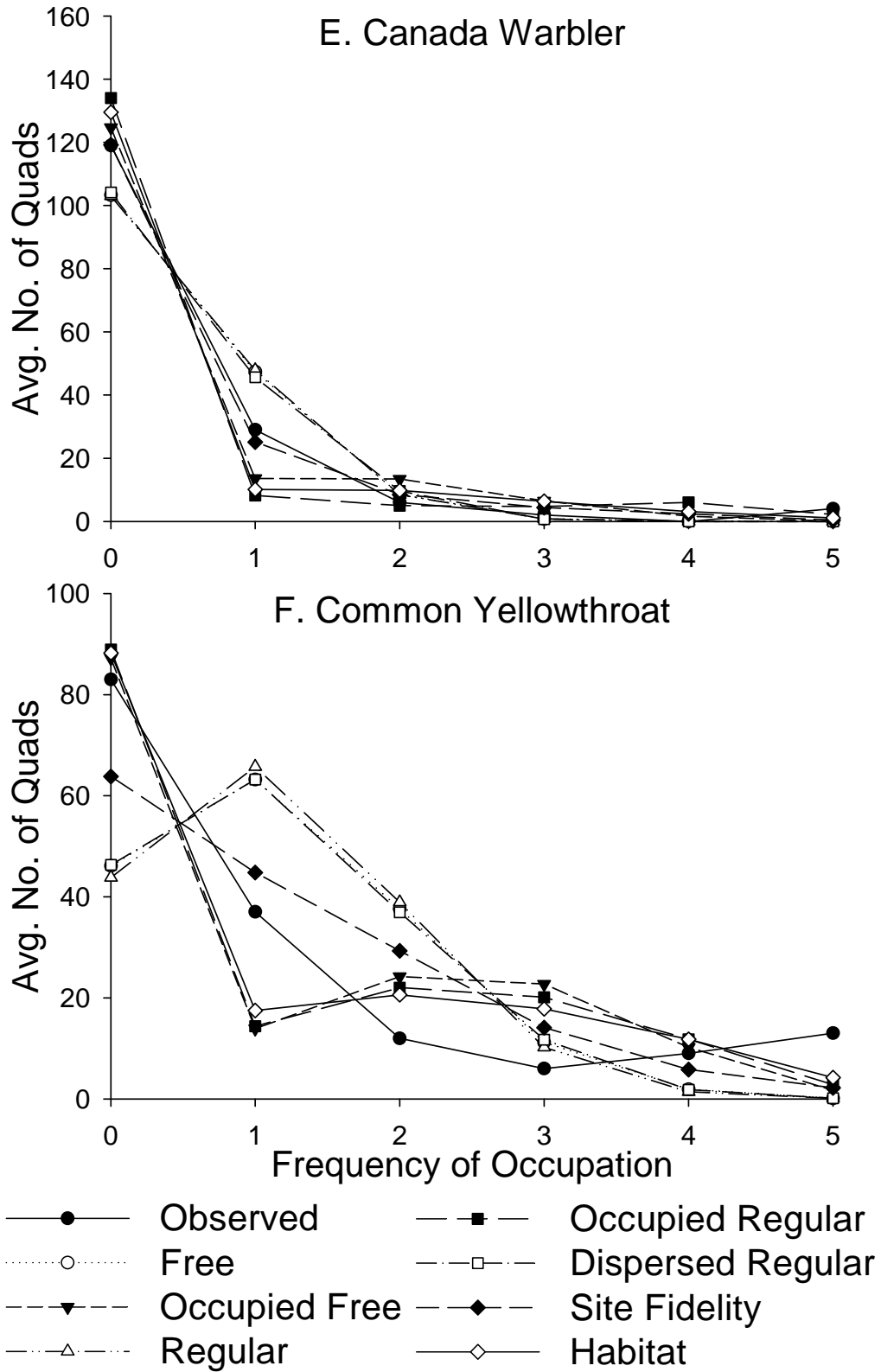


Figure 3.3 (Continued).

Fit between Observed and Null Frequency Distributions

I was able to recreate the patterns of variability in spatial distributions with one or more null models for 19 of 20 species. Frequency distributions from models that restricted quad occupation only by the annual number of occupied quads (i.e. free models) showed a poor fit to observed frequency distributions for 80% of the species (Table 3.4). Only the Hairy Woodpecker, Black-capped Chickadee, Brown Creeper, and Purple Finch had patterns of habitat occupancy that were consistent with this model. The additional incorporation of the occupancy constraint greatly improved the fit for most species (i.e., null frequency distributions more closely approximated the observed frequency distributions) (Table C.2), but only the frequency distributions from the occupied free model of the Black-capped Chickadee, Brown Creeper, Hermit Thrush, and Pine Warbler matched those of the observed data. In contrast, inclusion of the occupancy constraint resulted in poorer fits for the Hairy Woodpecker and Purple Finch because there was a higher frequency of quads occupied in multiple years. For widespread species such as the Ovenbird and the Black-throated Green Warbler, this constraint had no effect because these species only had one and zero quads, respectively, that were unoccupied in all 5 years (Figs. 3.2A, B). Consequently, the occupied free models were functionally the same as the free models for these two species.

Models including spatial autocorrelation in the form of territoriality performed nearly the same as the free models. Regular- and irregular-shaped territories were constrained to be of the same average size, but the variability in the sizes of the irregular-shaped territories was less than that of the regular-shaped territories. However, this dissimilarity caused little to no differences in the frequency distributions of occupied

Table 3.4. Results of goodness-of-fit tests between average frequency distributions of quad occupancy generated by the null models and the frequency distribution based on the observed data. Non-significant ($\alpha = 0.05$) p-values (in bold-face) indicate frequency distributions are not significantly different.

[illegible]

Table 3.4 (Continued).

Bird Species	Occupied			Occupied		Occupied		Dispersed	Site	
	Free	Free	Regular	Regular	Irregular	Irregular	Regular	Regular	Fidelity	Habitat
Scarlet Tanager	0.000	0.041	0.000	0.002	0.001	0.008	0.001		0.405	0.048
White-throated Sparrow	0.000	0.000	0.000	0.001	0.000	0.001	0.000		0.470	0.293
Purple Finch	0.304	0.001	0.758	0.000	0.280	0.000	0.432		0.025	0.318

Note: See text and Table 3.2 for model descriptions.

quads (Table C.2). Therefore, for the remainder of the paper I only present the results for those models that used regular-shaped territories. Similarly, preventing territory centers from occurring close to each other (i.e., dispersion constraint) resulted in frequency distributions that were almost identical to those without the constraint. While constraining the territorial models with the occupancy constraint improved the fit of those species not already fit by the free model, the differences in distributions were still significant (Table C.2).

Site fidelity models with a strength of site fidelity (s) equal to 0.6 maximized the number of species with a significant fit between observed and null frequency distributions (Table C.3). At this level of site fidelity, 13 species exhibited significant fits (Table 3.4); five of these were not fit by any other model.

The statistical habitat models varied considerably among species in both the number and identity of constituent variables, which suggests that species were idiosyncratic in their responses to vegetation structure (Table C.4). Of the 30 variables analyzed, 28 occurred in the final model of at least one species. Models ranged in size (excluding the intercept) from 2-10 variables. Variables that were consistently important among the species included basal area of all trees combined and basal area of white pine, which both occurred in models of 8 of the 20 bird species, and basal area of deciduous trees, which occurred in the models of 7 species (Tables 3.5, C.4).

The top models selected by Schwarz information criterion were very consistent in terms of their fit to the number of years a quad was actually occupied. The fitted frequency landscapes from the single best model, and from the average of models with $\Delta\text{SIC} \leq 2$ and $\Delta\text{SIC} \leq 4$ were nearly identical.

Table 3.5. Relationships between frequency of quad occupancy and vegetation structure variables that occur in models of more than 5 of the 20 bird species breeding at the Holt Research Forest, 1983-1987. Full models with parameter estimates and the standard errors for each species are in Table C.4.

Bird Species	Variables†										
	avg_cov_					avg_cov_	avg_cov_	avg_cov_	avg_cov_		
	ba_all	ba_wp	ba_dec	ba_rs	ba_bf	all_3	tot_h_spp	tree_density	dec_5	oak_3	wp_5
Hairy Woodpecker		-	+								-
Eastern Wood-Pewee			+		-				-		+
Black-capped Chickadee											
Brown Creeper	+										
Red-breasted Nuthatch	+	+		+	+			-		+	
Golden-crowned Kinglet				+			-				
Veery	+	-	+			+	+				
Hermit Thrush					-	+					
Nashville Warbler	-					-	-		-		
Yellow-rumped Warbler	+	+	-					-			
Black-and-white Warbler		-		-					-	-	
Blackburnian Warbler				+		+	-	-			+
Black-throated Green Warbler			-						+		
Pine Warbler	+	+						-			
Canada Warbler			+		-	+	+			-	-
Ovenbird						+					

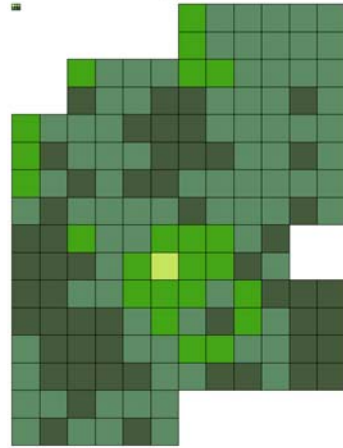
Table 3.5 (Continued).

Bird Species	Variables†										
	avg_cov_					avg_cov_		avg_cov_	avg_cov_		avg_cov_
	ba_all	ba_wp	ba_dec	ba_rs	ba_bf	all_3	tot_h_spp	tree_density	dec_5	oak_3	wp_5
Common Yellowthroat	-	+			-				-		
Scarlet Tanager								-		+	
White-throated Sparrow	-	-	-	-	-						
Purple Finch				+						-	+

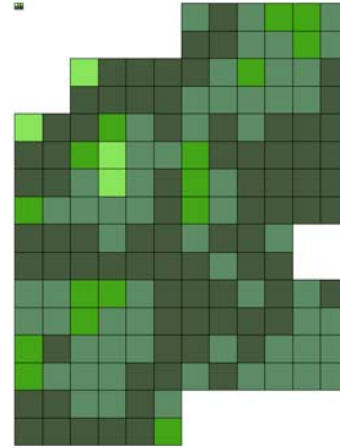
Note: ‘+’ indicates a positive relationship and ‘-’ indicates a negative relationship. Empty cells indicate that the variable was not important for that species.

† See Table 3.1 for variable descriptions.

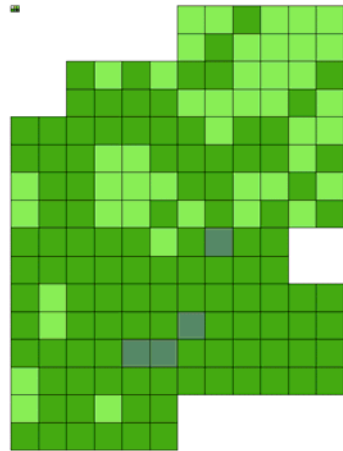
A. Black-throated Green Warbler



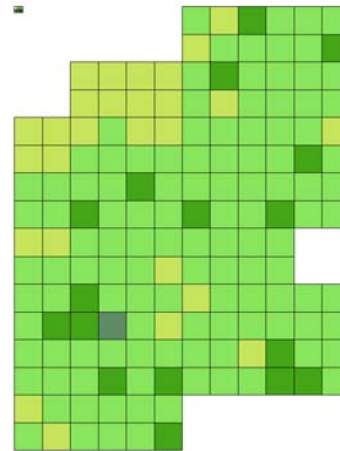
B. Ovenbird



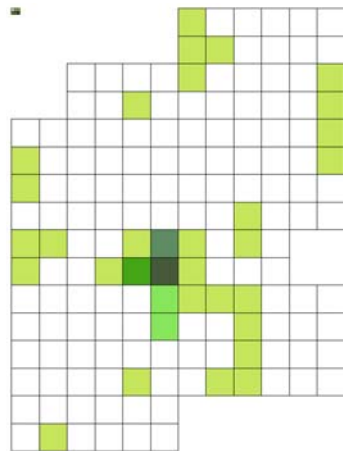
C. Black-capped Chickadee



D. Hermit Thrush



E. Canada Warbler



F. Common Yellowthroat

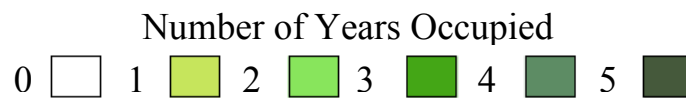
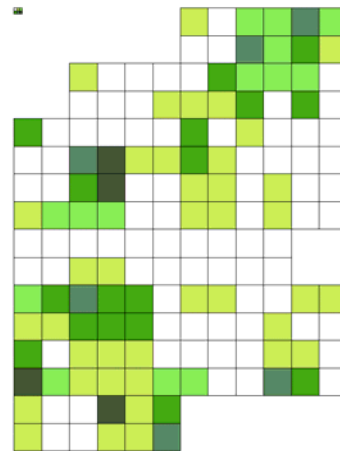


Figure 3.4. Frequency landscapes fit by the logistic regression models for six bird species breeding at the Holt Research Forest, 1983-1987. Each grid cell is a 50×50 m quad. See Fig. C.2 for remaining species.

The fitted frequency landscapes generated by the statistical habitat models were generally consistent with the observed frequency landscapes (compare Figs. 3.2 and 3.4; also see Fig. 3.3, Appendices B and E). The correspondence was higher for the species with observed frequency landscapes that had a high number of quads that were occupied in all or none of the years (A, B, E, and F of Figs. 3.2 and 3.4). However, the models tended to equalize the fitted frequencies, for species showing intermediate levels of quad use (C and D of Figs. 3.2 and 3.4).

When null frequency landscapes were generated from the fitted frequency landscapes, 12 of the 20 species had frequency distributions that were not significantly different from the observed distributions. In contrast to the site fidelity model, which also fit 12 species, only two species (Eastern-Wood Pewee and Red-breasted Nuthatch) were fit exclusively by the habitat model. For the species in which the fitted frequencies of quads was nearly equalized, the model converged in similarity to the free model. Thus, the habitat model was a good fit for three (Black-capped Chickadee, Brown Creeper, and Purple Finch) of the four species that were best described by the free model.

The Common Yellowthroat was the only species whose frequency distribution could not be matched by that of a null model (Table 3.4). This species, more than any other, had a frequency distribution that approached a bimodal distribution (Fig. 3.3). The high number of quads that were occupied in 5 years relative to the number of quads that were occupied for one and two years indicates the repeated use of certain areas and thus a low degree of stochastic variation.

DISCUSSION

Birds clearly exhibited variability in their spatial distribution patterns over the 5 years of this study (Figs. 3.2 and 3.3). If birds were invariant in their habitat use, the frequency landscapes and their corresponding distributions of occupied quads would have been dichotomous (i.e., quads would have been occupied in all or none of the years).

I was able to generate frequency distributions of quad use with one or more null models that matched the observed frequency distributions for all but one species (Common Yellowthroat), which suggests that the variability in spatial distribution patterns for nearly all species has a large stochastic component. Similarly, Haila et al. (1996) found that the territory locations of 11 of 17 forest bird species varied stochastically from year to year and Virkkala and Rajasärkkä (2006) found most bird species to be randomly distributed within areas of old-growth boreal forest in northern Finland.

The predicted frequency distribution of the free model was unrealistic for all but four species – Hairy Woodpecker, Black-capped Chickadee, Brown Creeper, and Purple Finch - suggesting that there was no pattern in the variability of these species. The poor fit of the free models for most species, however, was not because of a lack of spatial autocorrelation in quad occupancy. Although incorporating various forms of territoriality into null models probably better simulated distribution patterns within a year compared to the free model, it did not significantly improve the fit of the frequency landscapes to the observed landscapes because the randomization of territory locations in each year disrupted the spatial autocorrelation of occupied quads in the frequency landscape. The resulting frequency landscapes were similar to those generated by the free model, so the

species that were fit by the free model were also fit by models incorporating territoriality. When I further constrained the free and territorial models with the occupancy constraint (i.e., occupied free and occupied regular models), the null frequency distributions of most bird species better matched the observed frequency distributions. However, the distributions remained significantly different for all but four species.

In contrast to models with the occupancy constraint, the distributions from the habitat and site fidelity models fit the observed distributions of 12 and 13 species, respectively (eight were fit by both models). Importantly, this comparison distinguishes between two modes of habitat selection: preference and avoidance. The occupancy constraints incorporated avoidance and the site fidelity and habitat constraints incorporated preference. In the site fidelity models, preference was for previously occupied sites, and in the habitat models, preference was for sites with favorable vegetation structure. Preference and avoidance are not symmetrical alternatives (Haila et al. 1996). Preference implies that individuals seek to find an optimal habitat whereas avoidance allows individual to settle anywhere other than avoided areas. These alternatives have important consequences for interpreting variability in habitat use, because preference, such as that assumed by the Fretwell-Lucas model and the buffer effect, implies determinism in habitat use, whereas avoidance for a particular habitat allows variability in the use of the remaining habitats (Haila et al. 1996). Given the much larger number of species that were better fit by site fidelity and habitat models, habitat selection appears to be a result of preference. This finding contrasts with that of Haila et al. (1996) who found avoidance to be the prevailing mode of habitat selection.

Superficially, the site fidelity null model may appear to be invalid because it implicitly incorporates the mechanism I am trying to assess (i.e., deterministic tracking of habitat variation) (Gilpin and Diamond 1984, Gotelli and Graves 1996). However, in the model the increased probability of quad use in a year occurred strictly as a consequence of the presence in the previous year. The model assumes nothing about habitat quality when choosing or returning to a site. The initial locations were random and when site fidelity was not a factor (i.e., as when a new individual replaces a territory holder in the population) new territories were established in randomly selected locations.

Although I did not base my implementation of site fidelity on habitat, it could be argued that in reality site fidelity is a trait that evolved to tie the occurrence of an individual to habitat conditions. This argument would be valid if there was a high correspondence between site fidelity and habitat quality. However, site fidelity can actually inhibit transfers to vacant territories in intrinsically better habitat if knowledge of a particular territory confers a great enough advantage (Fretwell 1968, O'Connor 1985). Nevertheless, if an individual returns to a site and fails to successfully reproduce then an individual will be less likely to return to the same place in the following year (Haas 1998, Porneluzi 2003, Hoover 2003, Shutler and Clark 2003, Fisher and Wiebe 2006). Thus, site fidelity can cause spatial distribution patterns to become decoupled from habitat quality and, at best, site fidelity allows birds to track habitat conditions with a one-year time lag.

The conclusions from the site fidelity models were based on a probability of 0.6 that territories would occur at or very near to their previous location; this probability includes both overwinter survival and site tenacity. This probability is probably high

based on published adult survival rates (Martin and Li 1992) and return rates of select species (Haas 1998, Porneluzi 2003, Hartley 2003, Campbell, unpublished data).

Nevertheless, even if this probability is reduced to 0.4, the null frequency distributions fits the observed frequency distributions for 9 species (Table C.3), which still suggests that site fidelity plays an important role in describing variation in distribution patterns.

Although habitat models generated frequency distributions that fit the observed distributions for 12 species, this model may be biased in favor of matching the observed patterns because the fitted frequencies on which the simulations were based relied on the observed frequencies. Furthermore, the observed frequency landscapes to which the habitat models were fit implicitly include territoriality and site fidelity, so I may not be examining vegetation structure in isolation of these other factors.

It is also important to note that the habitat models only account for the vegetation structure in each quad. While vegetative structure is often assumed to be the primary proximate factor determining habitat use by birds, many other factors influence the decision of a bird to settle in an area: quantity, quality, and distribution of food, mate availability, abundance of competitors and predators, physiological constraints, weather, and past experience. These factors acting individually or together can overwhelm the influence of vegetation structure and make otherwise suitable habitats unavailable to birds (Block and Brennan 1993). In this study the habitat models for many species identify more “suitable” sites than are occupied in a single year and the high number of sites that were occupied only once is also suggestive of this possibility (Figs. 3.2 and 3.4, Appendices B and E). Haila et al. (1996) also found this pattern predominantly in scarce species.

If habitats are not fully saturated with individuals, populations may be non-equilibrial, which has important consequences for habitat use dynamics. If such populations are influenced by a wide array of underlying processes with a substantial stochastic component, dynamics in habitat use can appear random (Wiens 1984). Further, deterministic models such as those of Fretwell and Lucas (1969) are equilibrium-based theories that assume habitats are saturated, resources are limited, and populations are competitively structured. Wiens (1984) notes that “patterns” which are detected when equilibrium-based methods are applied to non-equilibrial populations are probably more myth than reality.

However, for some species habitats are probably saturated. For example, the two most abundant species (Ovenbird and Black-throated Green Warbler) had a significantly negative relationship between territory size (number of quads per territory) and the number of territories in a given year. This finding is consistent with crowding and territorial compression (i.e., smaller territories when abundances are higher). However, a possibility that can not be excluded is that the years of high abundance and smaller territories were years in which habitat quality was high enough that birds could meet their needs with smaller territories.

Effect of Scale

Although I found support for stochastic dynamics, we lack knowledge of the scale of habitat classification within which such dynamics operate (O'Connor 1986). In studies where the differences among habitats were very clear, predictions of deterministic models were corroborated (Kluyver and Tinbergen 1953, Udvardy 1953, Glas 1960,

O'Connor 1986, 1987, Petit and Petit 1996). However when available habitats increase in similarity the influence of deterministic processes is likely to decrease and stochastic processes are likely to play a larger role in determining patterns of occupancy (Milinski and Parker 1991). Habitat differences, and thus patterns of habitat selection, can also vary depending on the spatial scale at which they are measured (Sherry and Holmes 1985, Pulliam and Danielson 1991, Rotenberry 1986). Although all habitats are mosaics of different patches at some level of resolution, it is more likely that patterns of habitat selection would appear deterministic at a large spatial scale where differences in vegetation (e.g., forest vs. grassland) would be greater than the differences in the patches within an apparent vegetation type. Thus, the stochastic variation in habitat occupancy in this study may have resulted because the spatial extent of the study area was relatively small and the habitats relatively homogeneous. More work is needed to establish the boundary conditions between stochastic and deterministic habitat dynamics both in terms of differences in habitats and spatial scales at which the dynamics are investigated.

An additional issue that arises from spatial scale is the potential disparity between the scale at which I measured habitat selection and the scale at which it was actually occurring (Addicott et al. 1987, Orians and Wittenberger 1991). I chose 50×50 m quads as the scale to measure presence and absence largely because of limitations imposed by the vegetation data. If the spatial scale of the territories is considerably larger than that of the quads, stochasticity may appear as an artifact of this disparity. In other words, for some species quad occupancy may appear random within a deterministically located territory (Hanski et al. 1996). This may explain why four territorial bird species were best fit by the free model.

Study Limitations

Three limitation of my study require exposition. First, my approach is based on matching patterns from null models to those of the observed data. A failure to reject a null model does not necessarily imply that random processes created the pattern (Connor and Simberloff 1986). Rather, the factors that determine the patterns may be so variable in time and space that they can be represented as stochastic processes. In contrast, if the null model is rejected (i.e., the pattern is consistent with the theory's predictions), this provides positive, but not definitive, evidence in favor of the mechanism, because different mechanisms can produce similar ecological patterns. Further, a lack of detection does not imply that stochastic elements are not at work, rather they are of lesser importance than deterministic processes.

Second, quads are used as single observations even though they are not independent of each other. Spatial and temporal autocorrelation likely occur from territoriality and site fidelity, respectively. Both of these processes are parts of the system being modeled and not biases from data collection (Haila et al. 1996). Spatial dependence is lessened because I am examining distributions over 5 years. Temporal dependence reduces stochastic year-to-year variation, making the analysis of temporal variation conservative (Haila et al. 1996).

Third, to be able to distinguish between site fidelity and habitat quality as reason for returning to an area, enough time needs to elapse for individuals to intersperse and choose from all available environments (O'Connor 1987). Because birds were not marked, the degree to which areas of high occupancy resulted from individual site fidelity

or different individuals responding to habitat quality is unknown. While 5 years is probably long enough to ensure that there was turnover in the populations of most species, a longer time series would help to distinguish between these two models.

CONCLUSIONS

The year-to-year changes in spatial distribution patterns could be modeled as a purely stochastic process for only 4 of the 20 species I examined. In contrast, only one species exhibited such a high degree of determinism in habitat use that the variability in distribution patterns could not be matched with a null model. For most species, random variability had to be constrained in order for the patterns of variability in the observed data to be matched by null models, which suggests that the variability in most species has components of both deterministic and stochastic processes.

Territorial constraints did little to improve the correspondence between the patterns of variability generated from null models and those of the observed distributions. When random habitat use was limited to areas that were above some minimum threshold of suitability (i.e., avoided areas were excluded), the resulting variability more closely approximated the observed patterns of variability for most species, but the fits were significant for only 2 species. However, null models that incorporated habitat structure and site fidelity constraints fit the distribution patterns of 12 and 13 species, respectively. The high correspondence of habitat models suggested that habitat selection based on vegetation structure is able to recreate the observed patterns of variability, whereas the site fidelity models, in which site-tenacious territorial birds are using habitat randomly, indicate that these patterns can be reproduced independent of habitat structure.

Regardless of the mechanism, it is clear that any factor that causes birds to return to the same site repeatedly and limits the spatial extent of the variability can generate spatial distribution patterns similar to those observed in the 5-year data set.

Greater support for models with preference constraints (i.e. site fidelity and habitat models) over models with avoidance constraints suggested that preference was the primary mode of habitat selection. Despite this relatively deterministic influence on habitat use patterns, there appeared to be enough of a stochastic component to their decisions to prevent preference from creating largely deterministic distribution patterns.

Although there appeared to be a stochastic component to the year-to-year changes in habitat use, in reality it was unlikely that birds were making random decisions about where to settle. Habitat selection was probably tied deterministically to environmental cues, but the response to the combination of multiple cues and individual variation in response to these cues may have created patterns of habitat use that appeared random. Given the stochasticity present in the system, from a practical standpoint it was easier to model variation in habitat use as a constrained random process rather than trying to account for the multitude of environmental factors that influenced the habitat selection of birds.

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APPENDICES

APPENDIX A. Supplementary Data and Analyses for Chapter 1

Table A.1. Abundance (No.), ranked abundance (Rank), and percent abundance (%) of the 26 most common bird species in the Holt Research Forest in 1983-2002. Abundances are based on the number of territories and are reported for managed and control halves of the study area and the total study area. Note that total managed and control abundances do not always sum to total abundance because in some cases there were territories that straddled the managed and control boundaries and could not be placed definitively in one half of the study area or the other.

Bird Species	1983								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	22	0.00	1	18	1.37	1	20	0.66
Eastern Wood-Pewee	0	22	0.00	3	10	4.11	3	15	1.99
Blue-headed Vireo	0	22	0.00	0	23	0.00	0	24	0.00
Tufted Titmouse	0	22	0.00	0	23	0.00	0	24	0.00
Black-capped Chickadee	3	11	3.90	3	10	4.11	6	10	3.97
Brown Creeper	3	11	3.90	2	14	2.74	5	12	3.31
White-breasted Nuthatch	0	22	0.00	0	23	0.00	0	24	0.00
Red-breasted Nuthatch	3	11	3.90	1	18	1.37	4	13	2.65
Winter Wren	0	22	0.00	0	23	0.00	0	24	0.00
Golden-crowned Kinglet	2	14	2.60	0	23	0.00	2	17	1.32
Veery	3	11	3.90	2	14	2.74	5	12	3.31
Hermit Thrush	4	6	5.19	3	10	4.11	7	9	4.64
Nashville Warbler	4	6	5.19	4	7	5.48	8	6	5.30
Yellow-rumped Warbler	2	14	2.60	5	4	6.85	7	9	4.64
Black-and-white Warbler	4	6	5.19	4	7	5.48	8	6	5.30
Black-throated Blue Warbler	0	22	0.00	1	18	1.37	1	20	0.66
Blackburnian Warbler	4	6	5.19	5	4	6.85	9	4	5.96
Black-throated Green Warbler	18	1	23.38	12	2	16.44	31	1	20.53
Pine Warbler	0	22	0.00	2	14	2.74	2	17	1.32
Canada Warbler	1	16	1.30	0	23	0.00	1	20	0.66
Ovenbird	15	2	19.48	14	1	19.18	29	2	19.21
Common Yellowthroat	6	3	7.79	2	14	2.74	8	6	5.30
Scarlet Tanager	0	22	0.00	3	10	4.11	3	15	1.99
White-throated Sparrow	4	6	5.19	5	4	6.85	9	4	5.96
Purple Finch	1	16	1.30	1	18	1.37	2	17	1.32
American Goldfinch	0	22	0.00	0	23	0.00	0	24	0.00

Table A.1 (Continued).

Bird Species	1984								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	23	0.00	0	22	0.00	1	20	0.62
Eastern Wood-Pewee	1	17	1.23	2	13	2.53	3	16	1.85
Blue-headed Vireo	4	6	4.94	3	8	3.80	7	5	4.32
Tufted Titmouse	0	23	0.00	0	22	0.00	0	24	0.00
Black-capped Chickadee	4	6	4.94	2	13	2.53	6	9	3.70
Brown Creeper	3	10	3.70	3	8	3.80	6	9	3.70
White-breasted Nuthatch	0	23	0.00	0	22	0.00	0	24	0.00
Red-breasted Nuthatch	2	13	2.47	2	13	2.53	4	14	2.47
Winter Wren	0	23	0.00	0	22	0.00	0	24	0.00
Golden-crowned Kinglet	1	17	1.23	0	22	0.00	1	20	0.62
Veery	4	6	4.94	1	16	1.27	5	13	3.09
Hermit Thrush	1	17	1.23	5	4	6.33	6	9	3.70
Nashville Warbler	5	3	6.17	3	8	3.80	8	4	4.94
Yellow-rumped Warbler	2	13	2.47	4	5	5.06	6	9	3.70
Black-and-white Warbler	3	10	3.70	3	8	3.80	6	9	3.70
Black-throated Blue Warbler	0	23	0.00	0	22	0.00	0	24	0.00
Blackburnian Warbler	4	6	4.94	7	3	8.86	11	3	6.79
Black-throated Green Warbler	17	2	20.99	18	2	22.78	35	2	21.60
Pine Warbler	0	23	0.00	1	16	1.27	1	20	0.62
Canada Warbler	1	17	1.23	0	22	0.00	1	20	0.62
Ovenbird	20	1	24.69	19	1	24.05	39	1	24.07
Common Yellowthroat	3	10	3.70	2	13	2.53	5	13	3.09
Scarlet Tanager	1	17	1.23	1	16	1.27	3	16	1.85
White-throated Sparrow	3	10	3.70	3	8	3.80	6	9	3.70
Purple Finch	2	13	2.47	0	22	0.00	2	17	1.23
American Goldfinch	0	23	0.00	0	22	0.00	0	24	0.00

Table A.1 (Continued).

Bird Species	1985								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	23	0.00	0	23	0.00	2	18	1.20
Eastern Wood-Pewee	3	11	3.66	6	5	7.32	9	7	5.42
Blue-headed Vireo	0	23	0.00	2	13	2.44	2	18	1.20
Tufted Titmouse	0	23	0.00	0	23	0.00	0	25	0.00
Black-capped Chickadee	5	6	6.10	6	5	7.32	11	4	6.63
Brown Creeper	5	6	6.10	4	10	4.88	9	7	5.42
White-breasted Nuthatch	0	23	0.00	0	23	0.00	0	25	0.00
Red-breasted Nuthatch	3	11	3.66	3	12	3.66	6	12	3.61
Winter Wren	0	23	0.00	0	23	0.00	0	25	0.00
Golden-crowned Kinglet	3	11	3.66	1	17	1.22	4	14	2.41
Veery	4	7	4.88	0	23	0.00	4	14	2.41
Hermit Thrush	3	11	3.66	5	7	6.10	8	9	4.82
Nashville Warbler	3	11	3.66	1	17	1.22	4	14	2.41
Yellow-rumped Warbler	3	11	3.66	7	3	8.54	10	5	6.02
Black-and-white Warbler	3	11	3.66	4	10	4.88	7	11	4.22
Black-throated Blue Warbler	0	23	0.00	0	23	0.00	0	25	0.00
Blackburnian Warbler	6	4	7.32	5	7	6.10	11	4	6.63
Black-throated Green Warbler	15	1	18.29	13	2	15.85	28	1	16.87
Pine Warbler	0	23	0.00	1	17	1.22	1	22	0.60
Canada Warbler	2	16	2.44	0	23	0.00	2	18	1.20
Ovenbird	14	2	17.07	13	2	15.85	27	2	16.27
Common Yellowthroat	6	4	7.32	3	12	3.66	9	7	5.42
Scarlet Tanager	1	18	1.22	1	17	1.22	2	18	1.20
White-throated Sparrow	2	16	2.44	5	7	6.10	7	11	4.22
Purple Finch	1	18	1.22	1	17	1.22	2	18	1.20
American Goldfinch	0	23	0.00	1	17	1.22	1	22	0.60

Table A.1 (Continued).

Bird Species	1986								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	23	0.00	1	16	1.54	1	20	0.72
Eastern Wood-Pewee	0	23	0.00	3	7	4.62	3	15	2.16
Blue-headed Vireo	1	16	1.37	2	10	3.08	3	15	2.16
Tufted Titmouse	0	23	0.00	0	23	0.00	0	25	0.00
Black-capped Chickadee	5	5	6.85	3	7	4.62	8	5	5.76
Brown Creeper	3	9	4.11	2	10	3.08	5	9	3.60
White-breasted Nuthatch	0	23	0.00	0	23	0.00	1	20	0.72
Red-breasted Nuthatch	2	13	2.74	2	10	3.08	4	12	2.88
Winter Wren	0	23	0.00	0	23	0.00	0	25	0.00
Golden-crowned Kinglet	1	16	1.37	2	10	3.08	3	15	2.16
Veery	4	6	5.48	1	16	1.54	5	9	3.60
Hermit Thrush	3	9	4.11	4	5	6.15	7	7	5.04
Nashville Warbler	0	23	0.00	0	23	0.00	0	25	0.00
Yellow-rumped Warbler	3	9	4.11	8	3	12.31	11	4	7.91
Black-and-white Warbler	3	9	4.11	2	10	3.08	5	9	3.60
Black-throated Blue Warbler	1	16	1.37	0	23	0.00	1	20	0.72
Blackburnian Warbler	6	4	8.22	5	4	7.69	11	4	7.91
Black-throated Green Warbler	14	2	19.18	10	2	15.38	24	2	17.27
Pine Warbler	0	23	0.00	1	16	1.54	1	20	0.72
Canada Warbler	1	16	1.37	0	23	0.00	1	20	0.72
Ovenbird	14	2	19.18	15	1	23.08	29	1	20.86
Common Yellowthroat	6	4	8.22	1	16	1.54	7	7	5.04
Scarlet Tanager	2	13	2.74	1	16	1.54	3	15	2.16
White-throated Sparrow	3	9	4.11	1	16	1.54	4	12	2.88
Purple Finch	1	16	1.37	0	23	0.00	1	20	0.72
American Goldfinch	0	23	0.00	1	16	1.54	1	20	0.72

Table A.1 (Continued).

Bird Species	1987								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	15	1.39	1	17	1.27	2	18	1.29
Eastern Wood-Pewee	1	15	1.39	5	6	6.33	6	9	3.87
Blue-headed Vireo	0	22	0.00	0	23	0.00	0	25	0.00
Tufted Titmouse	0	22	0.00	0	23	0.00	0	25	0.00
Black-capped Chickadee	7	4	9.72	6	5	7.59	13	4	8.39
Brown Creeper	3	8	4.17	2	12	2.53	6	9	3.87
White-breasted Nuthatch	0	22	0.00	0	23	0.00	1	21	0.65
Red-breasted Nuthatch	0	22	0.00	2	12	2.53	2	18	1.29
Winter Wren	0	22	0.00	0	23	0.00	0	25	0.00
Golden-crowned Kinglet	4	6	5.56	2	12	2.53	6	9	3.87
Veery	2	11	2.78	0	23	0.00	3	14	1.94
Hermit Thrush	3	8	4.17	4	8	5.06	7	7	4.52
Nashville Warbler	2	11	2.78	1	17	1.27	3	14	1.94
Yellow-rumped Warbler	3	8	4.17	7	4	8.86	10	5	6.45
Black-and-white Warbler	1	15	1.39	2	12	2.53	3	14	1.94
Black-throated Blue Warbler	0	22	0.00	0	23	0.00	0	25	0.00
Blackburnian Warbler	8	3	11.11	7	4	8.86	15	3	9.68
Black-throated Green Warbler	13	2	18.06	12	2	15.19	25	2	16.13
Pine Warbler	0	22	0.00	1	17	1.27	1	21	0.65
Canada Warbler	1	15	1.39	0	23	0.00	1	21	0.65
Ovenbird	14	1	19.44	17	1	21.52	31	1	20.00
Common Yellowthroat	6	5	8.33	2	12	2.53	8	6	5.16
Scarlet Tanager	1	15	1.39	4	8	5.06	5	11	3.23
White-throated Sparrow	2	11	2.78	1	17	1.27	3	14	1.94
Purple Finch	0	22	0.00	2	12	2.53	2	18	1.29
American Goldfinch	0	22	0.00	1	17	1.27	2	18	1.29

Table A.1 (Continued).

Bird Species	1988								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	23	0.00	1	19	1.22	1	21	0.63
Eastern Wood-Pewee	2	13	2.67	2	12	2.44	4	15	2.53
Blue-headed Vireo	1	17	1.33	1	19	1.22	2	18	1.27
Tufted Titmouse	0	23	0.00	0	24	0.00	0	25	0.00
Black-capped Chickadee	5	5	6.67	5	6	6.10	10	5	6.33
Brown Creeper	4	8	5.33	3	8	3.66	7	8	4.43
White-breasted Nuthatch	0	23	0.00	0	24	0.00	0	25	0.00
Red-breasted Nuthatch	3	11	4.00	2	12	2.44	5	12	3.16
Winter Wren	4	8	5.33	1	19	1.22	5	12	3.16
Golden-crowned Kinglet	2	13	2.67	2	12	2.44	5	12	3.16
Veery	0	23	0.00	1	19	1.22	1	21	0.63
Hermit Thrush	2	13	2.67	6	5	7.32	8	7	5.06
Nashville Warbler	1	17	1.33	2	12	2.44	3	16	1.90
Yellow-rumped Warbler	4	8	5.33	8	4	9.76	12	4	7.59
Black-and-white Warbler	3	11	4.00	2	12	2.44	5	12	3.16
Black-throated Blue Warbler	0	23	0.00	0	24	0.00	0	25	0.00
Blackburnian Warbler	5	5	6.67	8	4	9.76	13	3	8.23
Black-throated Green Warbler	12	2	16.00	14	2	17.07	26	2	16.46
Pine Warbler	0	23	0.00	1	19	1.22	1	21	0.63
Canada Warbler	0	23	0.00	0	24	0.00	0	25	0.00
Ovenbird	13	1	17.33	15	1	18.29	28	1	17.72
Common Yellowthroat	4	8	5.33	2	12	2.44	6	9	3.80
Scarlet Tanager	1	17	1.33	3	8	3.66	4	15	2.53
White-throated Sparrow	7	3	9.33	2	12	2.44	9	6	5.70
Purple Finch	1	17	1.33	1	19	1.22	2	18	1.27
American Goldfinch	1	17	1.33	0	24	0.00	1	21	0.63

Table A.1 (Continued).

Bird Species	1989								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	Total
Hairy Woodpecker	1	20	1.12	0	23	0.00	2	20	1.12
Eastern Wood-Pewee	3	12	3.37	3	10	3.41	6	11	3.35
Blue-headed Vireo	2	16	2.25	0	23	0.00	2	20	1.12
Tufted Titmouse	0	25	0.00	0	23	0.00	0	25	0.00
Black-capped Chickadee	7	4	7.87	4	7	4.55	12	5	6.70
Brown Creeper	5	7	5.62	4	7	4.55	9	8	5.03
White-breasted Nuthatch	1	20	1.12	1	18	1.14	2	20	1.12
Red-breasted Nuthatch	3	12	3.37	3	10	3.41	6	11	3.35
Winter Wren	2	16	2.25	3	10	3.41	5	13	2.79
Golden-crowned Kinglet	4	10	4.49	2	14	2.27	6	11	3.35
Veery	1	20	1.12	3	10	3.41	4	16	2.23
Hermit Thrush	5	7	5.62	5	5	5.68	10	7	5.59
Nashville Warbler	0	25	0.00	0	23	0.00	0	25	0.00
Yellow-rumped Warbler	4	10	4.49	12	3	13.64	16	3	8.94
Black-and-white Warbler	2	16	2.25	2	14	2.27	4	16	2.23
Black-throated Blue Warbler	0	25	0.00	0	23	0.00	0	25	0.00
Blackburnian Warbler	6	5	6.74	6	4	6.82	12	5	6.70
Black-throated Green Warbler	10	3	11.24	18	1	20.45	28	1	15.64
Pine Warbler	1	20	1.12	2	14	2.27	3	18	1.68
Canada Warbler	1	20	1.12	0	23	0.00	1	23	0.56
Ovenbird	11	1	12.36	15	2	17.05	26	2	14.53
Common Yellowthroat	5	7	5.62	1	18	1.14	6	11	3.35
Scarlet Tanager	2	16	2.25	2	14	2.27	4	16	2.23
White-throated Sparrow	10	3	11.24	0	23	0.00	10	7	5.59
Purple Finch	3	12	3.37	1	18	1.14	4	16	2.23
American Goldfinch	0	25	0.00	1	18	1.14	1	23	0.56

Table A.1 (Continued).

Bird Species	1990								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	2	13	2.50	1	14	1.27	3	15	1.86
Eastern Wood-Pewee	1	18	1.25	3	9	3.80	4	14	2.48
Blue-headed Vireo	1	18	1.25	1	14	1.27	2	17	1.24
Tufted Titmouse	0	24	0.00	0	22	0.00	0	25	0.00
Black-capped Chickadee	7	5	8.75	6	5	7.59	13	4	8.07
Brown Creeper	3	10	3.75	2	11	2.53	6	10	3.73
White-breasted Nuthatch	0	24	0.00	0	22	0.00	0	25	0.00
Red-breasted Nuthatch	2	13	2.50	5	6	6.33	7	9	4.35
Winter Wren	1	18	1.25	0	22	0.00	1	20	0.62
Golden-crowned Kinglet	2	13	2.50	2	11	2.53	4	14	2.48
Veery	0	24	0.00	1	14	1.27	1	20	0.62
Hermit Thrush	6	6	7.50	9	3	11.39	15	3	9.32
Nashville Warbler	1	18	1.25	0	22	0.00	1	20	0.62
Yellow-rumped Warbler	4	9	5.00	7	4	8.86	12	5	7.45
Black-and-white Warbler	4	9	5.00	1	14	1.27	5	12	3.11
Black-throated Blue Warbler	0	24	0.00	0	22	0.00	0	25	0.00
Blackburnian Warbler	5	7	6.25	4	7	5.06	9	6	5.59
Black-throated Green Warbler	11	1	13.75	18	1	22.78	29	1	18.01
Pine Warbler	2	13	2.50	3	9	3.80	5	12	3.11
Canada Warbler	0	24	0.00	0	22	0.00	0	25	0.00
Ovenbird	10	2	12.50	15	2	18.99	25	2	15.53
Common Yellowthroat	7	5	8.75	0	22	0.00	7	9	4.35
Scarlet Tanager	0	24	0.00	1	14	1.27	1	20	0.62
White-throated Sparrow	8	3	10.00	0	22	0.00	8	7	4.97
Purple Finch	2	13	2.50	0	22	0.00	2	17	1.24
American Goldfinch	1	18	1.25	0	22	0.00	1	20	0.62

Table A.1 (Continued).

Bird Species	1991								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	16	1.23	1	15	1.12	2	17	1.16
Eastern Wood-Pewee	2	13	2.47	1	15	1.12	4	14	2.31
Blue-headed Vireo	4	8	4.94	1	15	1.12	5	10	2.89
Tufted Titmouse	0	22	0.00	0	23	0.00	0	24	0.00
Black-capped Chickadee	3	10	3.70	3	7	3.37	7	7	4.05
Brown Creeper	2	13	2.47	5	6	5.62	7	7	4.05
White-breasted Nuthatch	0	22	0.00	0	23	0.00	0	24	0.00
Red-breasted Nuthatch	2	13	2.47	2	10	2.25	4	14	2.31
Winter Wren	0	22	0.00	0	23	0.00	0	24	0.00
Golden-crowned Kinglet	0	22	0.00	1	15	1.12	1	20	0.58
Veery	0	22	0.00	2	10	2.25	2	17	1.16
Hermit Thrush	5	6	6.17	8	5	8.99	13	5	7.51
Nashville Warbler	0	22	0.00	0	23	0.00	0	24	0.00
Yellow-rumped Warbler	3	10	3.70	10	3	11.24	13	5	7.51
Black-and-white Warbler	4	8	4.94	1	15	1.12	5	10	2.89
Black-throated Blue Warbler	0	22	0.00	0	23	0.00	0	24	0.00
Blackburnian Warbler	6	4	7.41	8	5	8.99	14	3	8.09
Black-throated Green Warbler	17	1	20.99	23	1	25.84	40	1	23.12
Pine Warbler	2	13	2.47	2	10	2.25	4	14	2.31
Canada Warbler	0	22	0.00	0	23	0.00	0	24	0.00
Ovenbird	16	2	19.75	17	2	19.10	33	2	19.08
Common Yellowthroat	5	6	6.17	0	23	0.00	5	10	2.89
Scarlet Tanager	1	16	1.23	2	10	2.25	4	14	2.31
White-throated Sparrow	7	3	8.64	0	23	0.00	7	7	4.05
Purple Finch	1	16	1.23	1	15	1.12	2	17	1.16
American Goldfinch	0	22	0.00	1	15	1.12	1	20	0.58

Table A.1 (Continued).

Bird Species	1992								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	24	0.00	0	23	0.00	0	24	0.00
Eastern Wood-Pewee	4	10	4.76	1	15	1.23	5	11	3.01
Blue-headed Vireo	1	20	1.19	2	9	2.47	3	16	1.81
Tufted Titmouse	0	24	0.00	0	23	0.00	0	24	0.00
Black-capped Chickadee	6	5	7.14	3	6	3.70	9	6	5.42
Brown Creeper	4	10	4.76	2	9	2.47	7	8	4.22
White-breasted Nuthatch	0	24	0.00	0	23	0.00	0	24	0.00
Red-breasted Nuthatch	2	15	2.38	2	9	2.47	4	12	2.41
Winter Wren	3	12	3.57	0	23	0.00	3	16	1.81
Golden-crowned Kinglet	1	20	1.19	1	15	1.23	2	20	1.20
Veery	2	15	2.38	1	15	1.23	3	16	1.81
Hermit Thrush	5	7	5.95	7	5	8.64	12	5	7.23
Nashville Warbler	1	20	1.19	0	23	0.00	1	21	0.60
Yellow-rumped Warbler	5	7	5.95	9	3	11.11	14	3	8.43
Black-and-white Warbler	3	12	3.57	2	9	2.47	5	11	3.01
Black-throated Blue Warbler	0	24	0.00	0	23	0.00	0	24	0.00
Blackburnian Warbler	5	7	5.95	8	4	9.88	13	4	7.83
Black-throated Green Warbler	11	2	13.10	21	1	25.93	32	1	19.28
Pine Warbler	1	20	1.19	2	9	2.47	3	16	1.81
Canada Warbler	0	24	0.00	0	23	0.00	0	24	0.00
Ovenbird	11	2	13.10	16	2	19.75	27	2	16.27
Common Yellowthroat	7	3	8.33	0	23	0.00	7	8	4.22
Scarlet Tanager	2	15	2.38	1	15	1.23	3	16	1.81
White-throated Sparrow	6	5	7.14	1	15	1.23	7	8	4.22
Purple Finch	2	15	2.38	1	15	1.23	3	16	1.81
American Goldfinch	2	15	2.38	1	15	1.23	3	16	1.81

Table A.1 (Continued).

Bird Species	1993								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	22	1.01	1	17	1.06	2	21	1.04
Eastern Wood-Pewee	6	6	6.06	3	10	3.19	9	7	4.66
Blue-headed Vireo	2	18	2.02	6	6	6.38	8	10	4.15
Tufted Titmouse	0	25	0.00	0	23	0.00	0	25	0.00
Black-capped Chickadee	7	4	7.07	2	12	2.13	9	7	4.66
Brown Creeper	2	18	2.02	4	8	4.26	6	13	3.11
White-breasted Nuthatch	0	25	0.00	0	23	0.00	0	25	0.00
Red-breasted Nuthatch	4	10	4.04	4	8	4.26	8	10	4.15
Winter Wren	3	13	3.03	0	23	0.00	3	18	1.55
Golden-crowned Kinglet	3	13	3.03	0	23	0.00	3	18	1.55
Veery	2	18	2.02	1	17	1.06	3	18	1.55
Hermit Thrush	3	13	3.03	8	4	8.51	11	5	5.70
Nashville Warbler	1	22	1.01	0	23	0.00	1	23	0.52
Yellow-rumped Warbler	5	8	5.05	7	5	7.45	12	4	6.22
Black-and-white Warbler	3	13	3.03	1	17	1.06	4	15	2.07
Black-throated Blue Warbler	0	25	0.00	0	23	0.00	0	25	0.00
Blackburnian Warbler	7	4	7.07	10	3	10.64	17	3	8.81
Black-throated Green Warbler	14	1	14.14	21	1	22.34	35	1	18.13
Pine Warbler	3	13	3.03	3	10	3.19	6	13	3.11
Canada Warbler	1	22	1.01	0	23	0.00	1	23	0.52
Ovenbird	12	2	12.12	16	2	17.02	28	2	14.51
Common Yellowthroat	5	8	5.05	1	17	1.06	6	13	3.11
Scarlet Tanager	1	22	1.01	2	12	2.13	3	18	1.55
White-throated Sparrow	7	4	7.07	2	12	2.13	9	7	4.66
Purple Finch	5	8	5.05	1	17	1.06	6	13	3.11
American Goldfinch	2	18	2.02	1	17	1.06	3	18	1.55

Table A.1 (Continued).

Bird Species	1994								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	23	0.00	0	22	0.00	0	24	0.00
Eastern Wood-Pewee	8	5	10.00	1	15	1.25	9	7	5.63
Blue-headed Vireo	0	23	0.00	2	11	2.50	2	18	1.25
Tufted Titmouse	0	23	0.00	0	22	0.00	0	24	0.00
Black-capped Chickadee	4	8	5.00	5	6	6.25	9	7	5.63
Brown Creeper	2	13	2.50	3	8	3.75	5	10	3.13
White-breasted Nuthatch	0	23	0.00	0	22	0.00	0	24	0.00
Red-breasted Nuthatch	2	13	2.50	2	11	2.50	4	12	2.50
Winter Wren	1	18	1.25	0	22	0.00	1	20	0.63
Golden-crowned Kinglet	1	18	1.25	0	22	0.00	1	20	0.63
Veery	1	18	1.25	2	11	2.50	3	15	1.88
Hermit Thrush	8	5	10.00	7	4	8.75	15	3	9.38
Nashville Warbler	0	23	0.00	0	22	0.00	0	24	0.00
Yellow-rumped Warbler	3	10	3.75	8	3	10.00	11	5	6.88
Black-and-white Warbler	2	13	2.50	1	15	1.25	3	15	1.88
Black-throated Blue Warbler	0	23	0.00	0	22	0.00	0	24	0.00
Blackburnian Warbler	9	3	11.25	5	6	6.25	14	4	8.75
Black-throated Green Warbler	9	3	11.25	19	1	23.75	28	2	17.50
Pine Warbler	1	18	1.25	3	8	3.75	4	12	2.50
Canada Warbler	2	13	2.50	0	22	0.00	2	18	1.25
Ovenbird	13	1	16.25	16	2	20.00	29	1	18.13
Common Yellowthroat	5	6	6.25	1	15	1.25	6	9	3.75
Scarlet Tanager	0	23	0.00	1	15	1.25	1	20	0.63
White-throated Sparrow	4	8	5.00	0	22	0.00	4	12	2.50
Purple Finch	3	10	3.75	3	8	3.75	6	9	3.75
American Goldfinch	2	13	2.50	1	15	1.25	3	15	1.88

Table A.1 (Continued).

Bird Species	1995								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	17	1.39	0	21	0.00	1	19	0.68
Eastern Wood-Pewee	7	4	9.72	1	14	1.33	8	7	5.41
Blue-headed Vireo	3	11	4.17	2	10	2.67	5	10	3.38
Tufted Titmouse	0	23	0.00	0	21	0.00	0	24	0.00
Black-capped Chickadee	4	8	5.56	6	6	8.00	10	6	6.76
Brown Creeper	0	23	0.00	4	7	5.33	4	12	2.70
White-breasted Nuthatch	0	23	0.00	0	21	0.00	0	24	0.00
Red-breasted Nuthatch	4	8	5.56	2	10	2.67	6	8	4.05
Winter Wren	0	23	0.00	0	21	0.00	0	24	0.00
Golden-crowned Kinglet	3	11	4.17	1	14	1.33	4	12	2.70
Veery	1	17	1.39	0	21	0.00	1	19	0.68
Hermit Thrush	7	4	9.72	7	4	9.33	14	4	9.46
Nashville Warbler	0	23	0.00	0	21	0.00	0	24	0.00
Yellow-rumped Warbler	5	6	6.94	8	3	10.67	14	4	9.46
Black-and-white Warbler	1	17	1.39	1	14	1.33	2	16	1.35
Black-throated Blue Warbler	0	23	0.00	0	21	0.00	0	24	0.00
Blackburnian Warbler	7	4	9.72	6	6	8.00	13	5	8.78
Black-throated Green Warbler	10	1	13.89	16	2	21.33	26	1	17.57
Pine Warbler	1	17	1.39	2	10	2.67	3	14	2.03
Canada Warbler	1	17	1.39	0	21	0.00	1	19	0.68
Ovenbird	7	4	9.72	16	2	21.33	23	2	15.54
Common Yellowthroat	2	14	2.78	0	21	0.00	2	16	1.35
Scarlet Tanager	3	11	4.17	2	10	2.67	5	10	3.38
White-throated Sparrow	2	14	2.78	0	21	0.00	2	16	1.35
Purple Finch	3	11	4.17	1	14	1.33	4	12	2.70
American Goldfinch	0	23	0.00	0	21	0.00	0	24	0.00

Table A.1 (Continued).

Bird Species	1996								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	19	1.37	0	21	0.00	1	21	0.76
Eastern Wood-Pewee	4	7	5.48	2	10	3.45	6	7	4.58
Blue-headed Vireo	3	10	4.11	1	13	1.72	4	10	3.05
Tufted Titmouse	0	24	0.00	0	21	0.00	0	25	0.00
Black-capped Chickadee	4	7	5.48	3	7	5.17	7	6	5.34
Brown Creeper	1	19	1.37	3	7	5.17	4	10	3.05
White-breasted Nuthatch	0	24	0.00	0	21	0.00	0	25	0.00
Red-breasted Nuthatch	1	19	1.37	2	10	3.45	3	14	2.29
Winter Wren	0	24	0.00	0	21	0.00	0	25	0.00
Golden-crowned Kinglet	1	19	1.37	0	21	0.00	1	21	0.76
Veery	1	19	1.37	0	21	0.00	1	21	0.76
Hermit Thrush	5	5	6.85	6	5	10.34	11	5	8.40
Nashville Warbler	2	14	2.74	0	21	0.00	2	17	1.53
Yellow-rumped Warbler	6	3	8.22	7	3	12.07	13	3	9.92
Black-and-white Warbler	3	10	4.11	0	21	0.00	3	14	2.29
Black-throated Blue Warbler	2	14	2.74	0	21	0.00	2	17	1.53
Blackburnian Warbler	5	5	6.85	6	5	10.34	11	5	8.40
Black-throated Green Warbler	11	2	15.07	12	1	20.69	23	1	17.56
Pine Warbler	0	24	0.00	1	13	1.72	1	21	0.76
Canada Warbler	1	19	1.37	0	21	0.00	1	21	0.76
Ovenbird	11	2	15.07	10	2	17.24	21	2	16.03
Common Yellowthroat	3	10	4.11	0	21	0.00	3	14	2.29
Scarlet Tanager	0	24	0.00	2	10	3.45	2	17	1.53
White-throated Sparrow	4	7	5.48	0	21	0.00	4	10	3.05
Purple Finch	2	14	2.74	2	10	3.45	4	10	3.05
American Goldfinch	2	14	2.74	1	13	1.72	3	14	2.29

Table A.1 (Continued).

Bird Species	1997								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	18	1.61	1	14	1.45	2	16	1.52
Eastern Wood-Pewee	4	5	6.45	6	5	8.70	10	5	7.58
Blue-headed Vireo	3	9	4.84	2	10	2.90	5	9	3.79
Tufted Titmouse	0	24	0.00	0	22	0.00	1	21	0.76
Black-capped Chickadee	4	5	6.45	4	6	5.80	8	6	6.06
Brown Creeper	1	18	1.61	3	8	4.35	4	11	3.03
White-breasted Nuthatch	0	24	0.00	1	14	1.45	1	21	0.76
Red-breasted Nuthatch	3	9	4.84	3	8	4.35	6	8	4.55
Winter Wren	0	24	0.00	0	22	0.00	0	25	0.00
Golden-crowned Kinglet	0	24	0.00	0	22	0.00	0	25	0.00
Veery	1	18	1.61	0	22	0.00	1	21	0.76
Hermit Thrush	4	5	6.45	2	10	2.90	6	8	4.55
Nashville Warbler	0	24	0.00	0	22	0.00	0	25	0.00
Yellow-rumped Warbler	4	5	6.45	8	3	11.59	12	3	9.09
Black-and-white Warbler	3	9	4.84	1	14	1.45	4	11	3.03
Black-throated Blue Warbler	2	13	3.23	0	22	0.00	2	16	1.52
Blackburnian Warbler	3	9	4.84	7	4	10.14	10	5	7.58
Black-throated Green Warbler	9	2	14.52	15	1	21.74	24	1	18.18
Pine Warbler	0	24	0.00	1	14	1.45	1	21	0.76
Canada Warbler	1	18	1.61	0	22	0.00	1	21	0.76
Ovenbird	10	1	16.13	12	2	17.39	22	2	16.67
Common Yellowthroat	2	13	3.23	0	22	0.00	2	16	1.52
Scarlet Tanager	2	13	3.23	1	14	1.45	3	13	2.27
White-throated Sparrow	2	13	3.23	0	22	0.00	2	16	1.52
Purple Finch	2	13	3.23	1	14	1.45	3	13	2.27
American Goldfinch	1	18	1.61	1	14	1.45	2	16	1.52

Table A.1 (Continued).

Bird Species	1998								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	20	1.18	1	18	1.20	2	21	1.18
Eastern Wood-Pewee	3	11	3.53	6	5	7.23	9	7	5.29
Blue-headed Vireo	5	7	5.88	4	8	4.82	9	7	5.29
Tufted Titmouse	1	20	1.18	2	15	2.41	3	18	1.76
Black-capped Chickadee	5	7	5.88	5	6	6.02	12	5	7.06
Brown Creeper	1	20	1.18	3	12	3.61	4	15	2.35
White-breasted Nuthatch	2	14	2.35	1	18	1.20	3	18	1.76
Red-breasted Nuthatch	1	20	1.18	4	8	4.82	5	12	2.94
Winter Wren	0	25	0.00	0	23	0.00	0	26	0.00
Golden-crowned Kinglet	1	20	1.18	3	12	3.61	4	15	2.35
Veery	5	7	5.88	1	18	1.20	6	10	3.53
Hermit Thrush	7	3	8.24	6	5	7.23	13	4	7.65
Nashville Warbler	0	25	0.00	0	23	0.00	0	26	0.00
Yellow-rumped Warbler	5	7	5.88	11	3	13.25	16	3	9.41
Black-and-white Warbler	5	7	5.88	0	23	0.00	5	12	2.94
Black-throated Blue Warbler	2	14	2.35	0	23	0.00	2	21	1.18
Blackburnian Warbler	6	4	7.06	3	12	3.61	9	7	5.29
Black-throated Green Warbler	12	2	14.12	11	3	13.25	23	2	13.53
Pine Warbler	2	14	2.35	3	12	3.61	5	12	2.94
Canada Warbler	1	20	1.18	0	23	0.00	1	24	0.59
Ovenbird	12	2	14.12	12	1	14.46	24	1	14.12
Common Yellowthroat	2	14	2.35	0	23	0.00	2	21	1.18
Scarlet Tanager	0	25	0.00	3	12	3.61	3	18	1.76
White-throated Sparrow	1	20	1.18	0	23	0.00	1	24	0.59
Purple Finch	3	11	3.53	3	12	3.61	6	10	3.53
American Goldfinch	2	14	2.35	1	18	1.20	3	18	1.76

Table A.1 (Continued).

Bird Species	1999								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	25	0.00	2	12	2.60	2	21	1.30
Eastern Wood-Pewee	3	8	4.11	5	6	6.49	8	7	5.19
Blue-headed Vireo	2	14	2.74	2	12	2.60	4	12	2.60
Tufted Titmouse	1	21	1.37	1	17	1.30	2	21	1.30
Black-capped Chickadee	3	8	4.11	5	6	6.49	9	5	5.84
Brown Creeper	3	8	4.11	4	8	5.19	7	8	4.55
White-breasted Nuthatch	0	25	0.00	1	17	1.30	2	21	1.30
Red-breasted Nuthatch	2	14	2.74	2	12	2.60	4	12	2.60
Winter Wren	2	14	2.74	0	23	0.00	2	21	1.30
Golden-crowned Kinglet	1	21	1.37	1	17	1.30	3	16	1.95
Veery	2	14	2.74	2	12	2.60	5	10	3.25
Hermit Thrush	7	3	9.59	2	12	2.60	9	5	5.84
Nashville Warbler	0	25	0.00	0	23	0.00	0	26	0.00
Yellow-rumped Warbler	6	4	8.22	9	3	11.69	15	3	9.74
Black-and-white Warbler	4	5	5.48	0	23	0.00	4	12	2.60
Black-throated Blue Warbler	2	14	2.74	0	23	0.00	2	21	1.30
Blackburnian Warbler	2	14	2.74	6	4	7.79	8	7	5.19
Black-throated Green Warbler	11	2	15.07	12	2	15.58	23	2	14.94
Pine Warbler	1	21	1.37	1	17	1.30	2	21	1.30
Canada Warbler	1	21	1.37	0	23	0.00	1	25	0.65
Ovenbird	11	2	15.07	15	1	19.48	26	1	16.88
Common Yellowthroat	2	14	2.74	0	23	0.00	2	21	1.30
Scarlet Tanager	2	14	2.74	1	17	1.30	3	16	1.95
White-throated Sparrow	3	8	4.11	0	23	0.00	3	16	1.95
Purple Finch	1	21	1.37	4	8	5.19	5	10	3.25
American Goldfinch	1	21	1.37	2	12	2.60	3	16	1.95

Table A.1 (Continued).

Bird Species	2000								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	26	0.00	0	23	0.00	1	24	0.66
Eastern Wood-Pewee	3	11	3.61	6	4	8.96	9	6	5.92
Blue-headed Vireo	4	9	4.82	1	16	1.49	5	10	3.29
Tufted Titmouse	1	21	1.20	0	23	0.00	1	24	0.66
Black-capped Chickadee	4	9	4.82	4	7	5.97	8	7	5.26
Brown Creeper	2	15	2.41	3	8	4.48	5	10	3.29
White-breasted Nuthatch	0	26	0.00	1	16	1.49	1	24	0.66
Red-breasted Nuthatch	2	15	2.41	1	16	1.49	3	17	1.97
Winter Wren	1	21	1.20	0	23	0.00	1	24	0.66
Golden-crowned Kinglet	1	21	1.20	1	16	1.49	3	17	1.97
Veery	5	6	6.02	1	16	1.49	6	8	3.95
Hermit Thrush	5	6	6.02	6	4	8.96	11	4	7.24
Nashville Warbler	4	9	4.82	0	23	0.00	4	13	2.63
Yellow-rumped Warbler	6	4	7.23	5	6	7.46	11	4	7.24
Black-and-white Warbler	4	9	4.82	1	16	1.49	5	10	3.29
Black-throated Blue Warbler	2	15	2.41	0	23	0.00	2	20	1.32
Blackburnian Warbler	6	4	7.23	5	6	7.46	11	4	7.24
Black-throated Green Warbler	12	1	14.46	12	2	17.91	24	1	15.79
Pine Warbler	1	21	1.20	2	11	2.99	3	17	1.97
Canada Warbler	1	21	1.20	0	23	0.00	1	24	0.66
Ovenbird	11	2	13.25	12	2	17.91	23	2	15.13
Common Yellowthroat	2	15	2.41	0	23	0.00	2	20	1.32
Scarlet Tanager	1	21	1.20	2	11	2.99	3	17	1.97
White-throated Sparrow	1	21	1.20	0	23	0.00	1	24	0.66
Purple Finch	2	15	2.41	2	11	2.99	4	13	2.63
American Goldfinch	2	15	2.41	2	11	2.99	4	13	2.63

Table A.1 (Continued).

Bird Species	2001								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	1	19	1.28	0	22	0.00	2	18	1.24
Eastern Wood-Pewee	2	13	2.56	5	6	6.25	7	8	4.35
Blue-headed Vireo	2	13	2.56	3	11	3.75	5	12	3.11
Tufted Titmouse	0	24	0.00	1	16	1.25	1	21	0.62
Black-capped Chickadee	4	7	5.13	5	6	6.25	9	6	5.59
Brown Creeper	2	13	2.56	4	9	5.00	6	10	3.73
White-breasted Nuthatch	1	19	1.28	1	16	1.25	2	18	1.24
Red-breasted Nuthatch	2	13	2.56	4	9	5.00	6	10	3.73
Winter Wren	0	24	0.00	0	22	0.00	0	25	0.00
Golden-crowned Kinglet	1	19	1.28	1	16	1.25	2	18	1.24
Veery	7	4	8.97	0	22	0.00	7	8	4.35
Hermit Thrush	6	5	7.69	5	6	6.25	12	5	7.45
Nashville Warbler	0	24	0.00	0	22	0.00	0	25	0.00
Yellow-rumped Warbler	4	7	5.13	11	3	13.75	15	3	9.32
Black-and-white Warbler	3	9	3.85	0	22	0.00	3	16	1.86
Black-throated Blue Warbler	0	24	0.00	0	22	0.00	0	25	0.00
Blackburnian Warbler	7	4	8.97	6	4	7.50	14	4	8.70
Black-throated Green Warbler	12	2	15.38	14	1	17.50	26	1	16.15
Pine Warbler	2	13	2.56	2	13	2.50	4	14	2.48
Canada Warbler	1	19	1.28	0	22	0.00	1	21	0.62
Ovenbird	13	1	16.67	12	2	15.00	25	2	15.53
Common Yellowthroat	1	19	1.28	0	22	0.00	1	21	0.62
Scarlet Tanager	3	9	3.85	1	16	1.25	4	14	2.48
White-throated Sparrow	0	24	0.00	0	22	0.00	0	25	0.00
Purple Finch	3	9	3.85	3	11	3.75	6	10	3.73
American Goldfinch	1	19	1.28	2	13	2.50	3	16	1.86

Table A.1 (Continued).

Bird Species	2002								
	Managed			Control			Total		
	No.	Rank	%	No.	Rank	%	No.	Rank	%
Hairy Woodpecker	0	22	0.00	0	22	0.00	1	20	0.66
Eastern Wood-Pewee	2	13	2.90	6	5	7.69	9	6	5.92
Blue-headed Vireo	3	10	4.35	4	8	5.13	7	9	4.61
Tufted Titmouse	0	22	0.00	0	22	0.00	1	20	0.66
Black-capped Chickadee	4	8	5.80	4	8	5.13	8	8	5.26
Brown Creeper	2	13	2.90	4	8	5.13	6	11	3.95
White-breasted Nuthatch	0	22	0.00	1	15	1.28	1	20	0.66
Red-breasted Nuthatch	1	16	1.45	1	15	1.28	3	15	1.97
Winter Wren	0	22	0.00	0	22	0.00	0	24	0.00
Golden-crowned Kinglet	1	16	1.45	0	22	0.00	1	20	0.66
Veery	6	3	8.70	0	22	0.00	6	11	3.95
Hermit Thrush	5	5	7.25	3	11	3.85	8	8	5.26
Nashville Warbler	0	22	0.00	0	22	0.00	0	24	0.00
Yellow-rumped Warbler	5	5	7.25	9	3	11.54	14	3	9.21
Black-and-white Warbler	4	8	5.80	1	15	1.28	5	12	3.29
Black-throated Blue Warbler	0	22	0.00	0	22	0.00	0	24	0.00
Blackburnian Warbler	5	5	7.25	6	5	7.69	11	4	7.24
Black-throated Green Warbler	11	2	15.94	12	2	15.38	23	2	15.13
Pine Warbler	0	22	0.00	3	11	3.85	3	15	1.97
Canada Warbler	0	22	0.00	0	22	0.00	0	24	0.00
Ovenbird	11	2	15.94	16	1	20.51	28	1	18.42
Common Yellowthroat	2	13	2.90	0	22	0.00	2	17	1.32
Scarlet Tanager	1	16	1.45	1	15	1.28	2	17	1.32
White-throated Sparrow	0	22	0.00	0	22	0.00	0	24	0.00
Purple Finch	4	8	5.80	5	6	6.41	9	6	5.92
American Goldfinch	2	13	2.90	2	12	2.56	4	13	2.63

Table A.2. Correlation between the number of territories / 40 ha at the Holt Research Forest and the average number of individuals detected per route of the BBS in the state of Maine for all 20 years (1983-2002), pre-harvest years (1983-1987) and post-harvest years (1988-2002). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Bird Species	All Years	Pre-harvest Years	Post-Harvest Years
Hairy Woodpecker	-0.025	0.334	-0.077
Eastern Wood-Pewee	-0.680 **	0.265	-0.760 **
Blue-headed Vireo	0.567 **	0.431	0.483
Black-capped Chickadee	0.211	0.133	0.217
Brown Creeper	-0.066	-0.462	0.033
Red-breasted Nuthatch	0.471 *	0.520	0.392
Winter Wren	-0.140	.	-0.486
Golden-crowned Kinglet	-0.048	0.434	0.010
Veery	-0.219	0.591	-0.685 **
Hermit Thrush	0.523 *	0.973 **	0.084
Nashville Warbler	0.040	-0.161	0.093
Yellow-rumped Warbler	0.408	0.018	0.084
Black-and-white Warbler	0.038	0.784	-0.126
Blackburnian Warbler	-0.434	-0.352	-0.519 *
Black-throated Green Warbler	0.123	0.400	0.258
Pine Warbler	0.307	-0.123	-0.203
Ovenbird	0.173	-0.096	0.164
Common Yellowthroat	0.658 **	-0.252	0.623 *
Scarlet Tanager	0.042	-0.093	0.045
White-throated Sparrow	0.073	0.895 *	-0.284
Purple Finch	-0.560 *	-0.046	-0.261
American Goldfinch	0.308	0.743	0.297

Table A.3. Percentage annual change in bird abundance at the Holt Research Forest and in Maine (1983-2002) of 16 bird species for which a zero-breakpoint (simple linear) regression model best described the trends at the Holt Research Forest.

Bird species	% Annual change ^a	
	Holt Research Forest	Maine BBS
Hairy Woodpecker	0.07	3.24
Eastern Wood-Pewee	4.71**	-3.21*
Blue-headed Vireo	8.37**	4.14*
Brown Creeper	-1.33	12.34*
Red-breasted Nuthatch	-0.16	-0.56
Golden-crowned Kinglet	-3.02	4.93*
Nashville Warbler	-9.72*	-0.75
Black-and-white Warbler	-2.25*	-3.49***
Blackburnian Warbler	-0.20	-0.08
Black-throated Green Warbler	-1.33*	3.29*
Pine Warbler	3.90	10.17***
Ovenbird	-1.42**	-0.41
Common Yellowthroat	-8.03***	-0.82
Scarlet Tanager	-0.40	2.29*
Purple Finch	6.78***	-0.03
American Goldfinch	8.89**	3.11***

^a Significance levels for percentage annual change in bird abundance: *P<0.05, **P<0.01, ***P<0.001.

Table A.4. Percentage annual changes in bird abundance at the Holt Research Forest and in Maine (1983-2002) of six bird species for which a one-breakpoint regression model best described the trends at the Holt Research Forest.

Bird Species	Holt Research Forest			Maine BBS	
	% Annual change1 ^a	Breakpoint ^b	% Annual change2 ^a	% Annual change1 ^c	% Annual change2 ^c
Black-capped Chickadee	14.84 *	1987	-1.90	-3.54	0.60
Winter Wren	38.19	1989	-10.29	5.17	-1.06
Veery	-15.44 *	1990	10.33 *	-4.49 *	-2.32 *
Hermit Thrush	9.57 **	1991	-2.87	8.27 *	3.74 ***
Yellow-rumped Warbler	19.04 *	1987	0.99	7.20	3.82 ***
White-throated Sparrow	1.751	1993	-24.27 ***	-5.90 ***	0.25

^a Significance levels for percentage annual changes in bird abundance at the Holt Research Forest for the time periods before (1) and after (2) the breakpoint (i.e., 1983-breakpoint and breakpoint-2002, respectively): *P<0.05, **P<0.01, ***P<0.001.

^b Estimated year (standard error) at which the regression slope changes.

^c Percentage annual change in bird abundance in Maine (n = 13-62 BBS routes) corresponding to the time periods defined by the breakpoint estimate; same significance levels as in footnote ^a.

APPENDIX B. Supplementary Data and Analyses for Chapter 2

Examples of occupied areas of the Ovenbird in 1986 and 1989.

Using all the observations of a species in a given year (including those outside the borders of the study area), we delineated the occupied area (aggregate of territories) (OA) using the 90% contour of the fixed ($h = 20$) kernel home range estimator and then restricted it to within the confines of the study area. By overlaying the occupied area with the map of the gaps we were able to calculate the proportion of gaps occurring in the occupied area. The OAs from Ovenbirds in 1986 and 1989 (two years before and two years after the disturbance, respectively) illustrate the change in the distributions and use of the disturbed areas. In 1986 Ovenbirds were using 91.6% of the area that was to become gaps (Fig. B1). By 1989 Ovenbirds were clearly avoiding the disturbed areas (Fig. B2); only 6.6% of the gap area occurred within their OA.

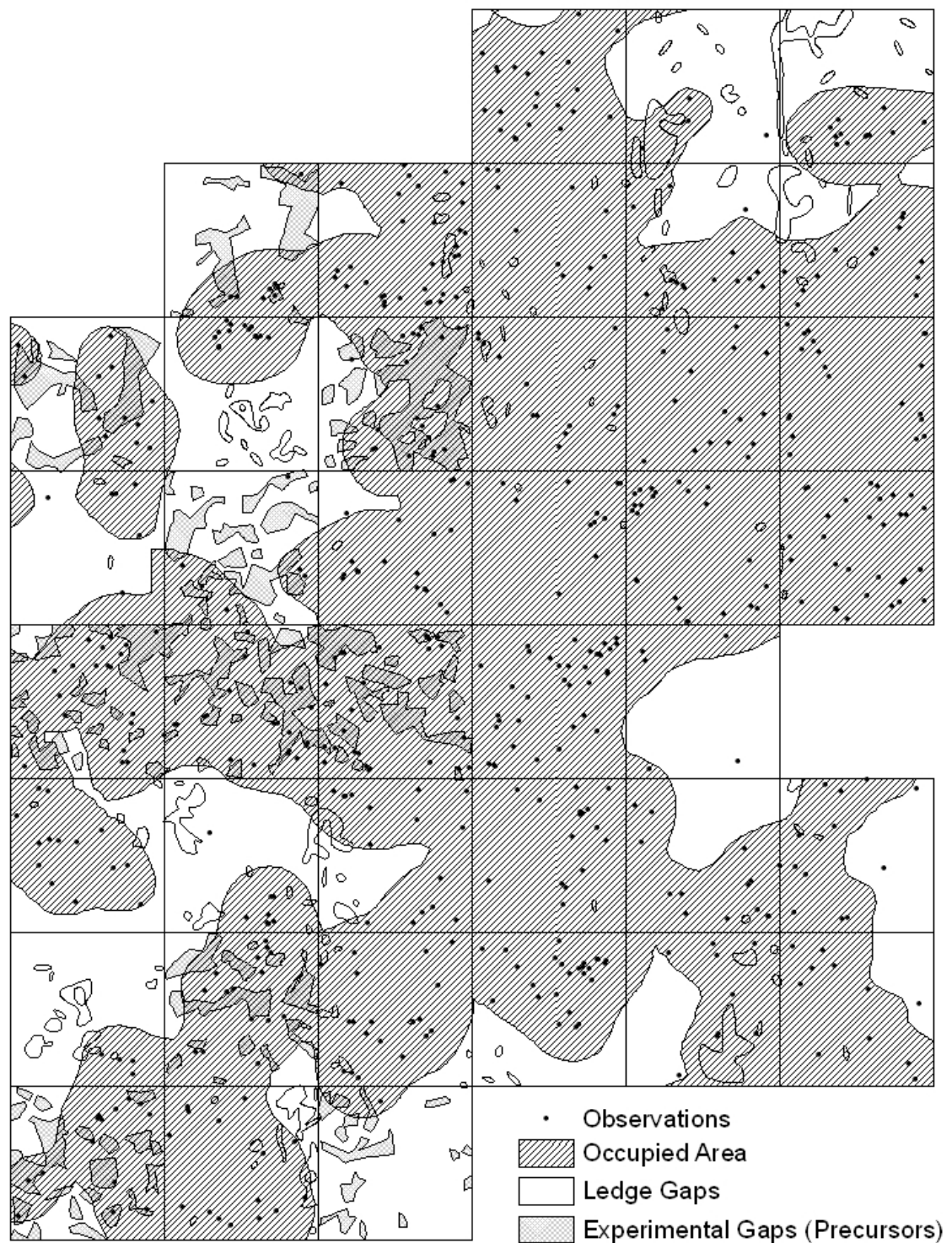


Figure B.1. The observations, occupied area, and the proportion of gaps in the occupied area of the Ovenbird in 1986. Note that in 1986 the experimental gaps did not yet exist; they are included to show how these areas of the forest were used prior to the disturbance. Since birds did not respond strongly to treefall gaps, they have been omitted for clarity.

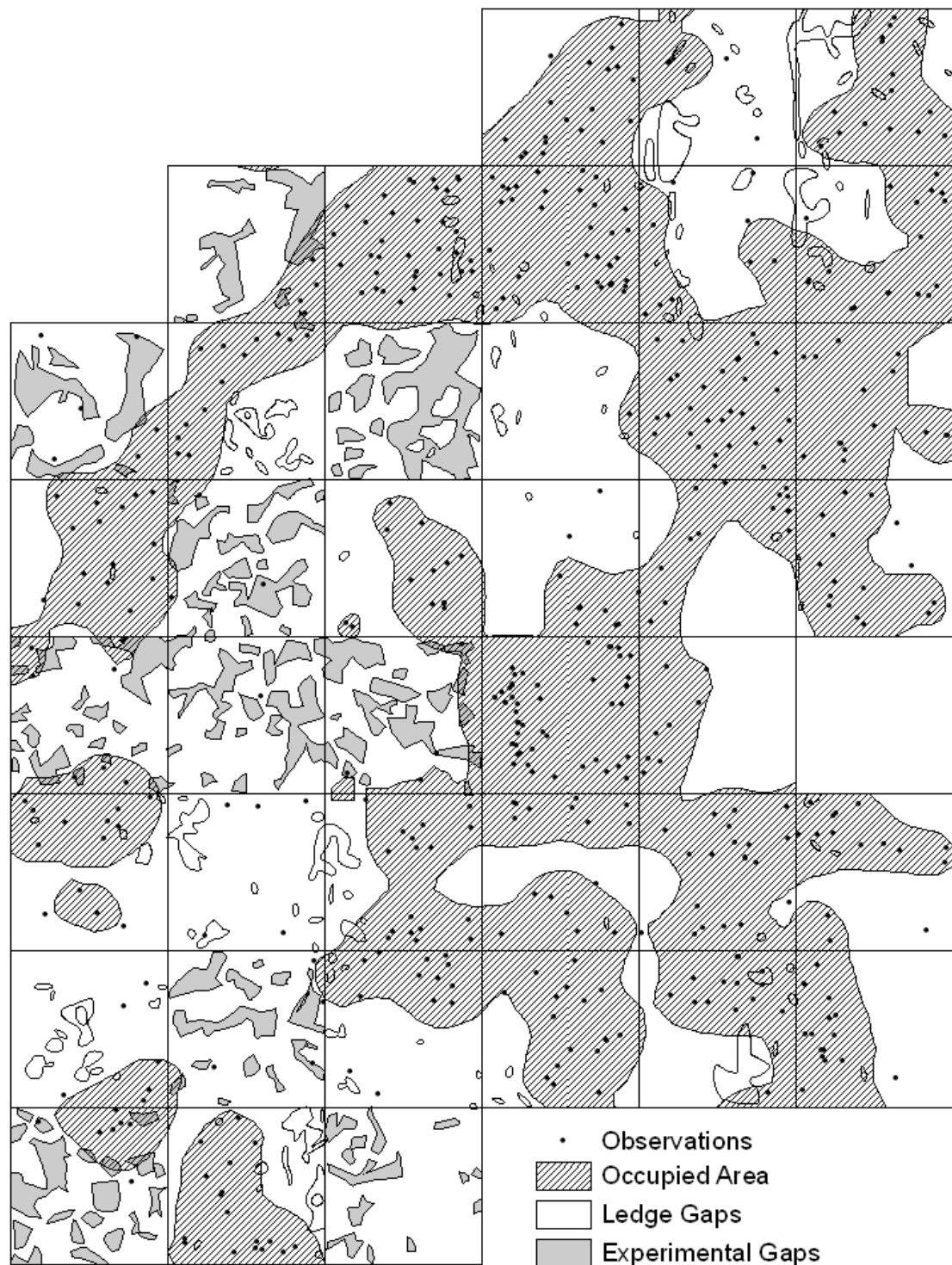


Figure B.2. The observations, occupied area, and the proportion of gaps in the occupied area of the Ovenbird in 1989. Since birds did not respond strongly to treefall gaps, they have been omitted for clarity.

Comparison of results from the Kolmogorov-Smirnov and “confidence band” tests used to evaluate the similarity in observed and expected (based on random use) cumulative distributions of distances from experimental gaps.

Because the critical value of the Kolmogorov-Smirnov test was sensitive to sample size, this test often detected differences ($\alpha = 0.05$) between the observed and expected cumulative distributions of distances from experimental gaps that were unlikely to be biologically significant. By comparison, we decided that the cumulative distribution curves were different if at least 10% of the points on the observed curve had corresponding points on the expected curve that fell outside the confidence bands of the observed curve. The different methods provided the same results for ~86% of the comparisons (Table B.1). Disagreement between the two methods generally occurred in years when a species was abundant and differences were small; in these cases the Kolmogorov-Smirnov test found the differences in distributions to be statistically significant but the “confidence band” method did not. We believe that this alternative method detected differences that were more biologically meaningful. For example, in 1983 the Ovenbird had 460 observations. The results of the Kolmogorov-Smirnov test indicated that the curves were statistically significantly different, when visual inspection shows that they were very similar. Using the “confidence band” test showed that the expected curve never occurred outside the 95% confidence band (Fig. B.3A). In 1998 the Black-throated Green Warbler had 454 observations. The Kolmogorov-Smirnov test also found these curves to be different. However, according to the “confidence band” method the expected curve occurred outside the 95% confidence bands for 6.7% of the observations, which approached but was still less than our 10% cutoff for significant differences (Fig. B.3B).

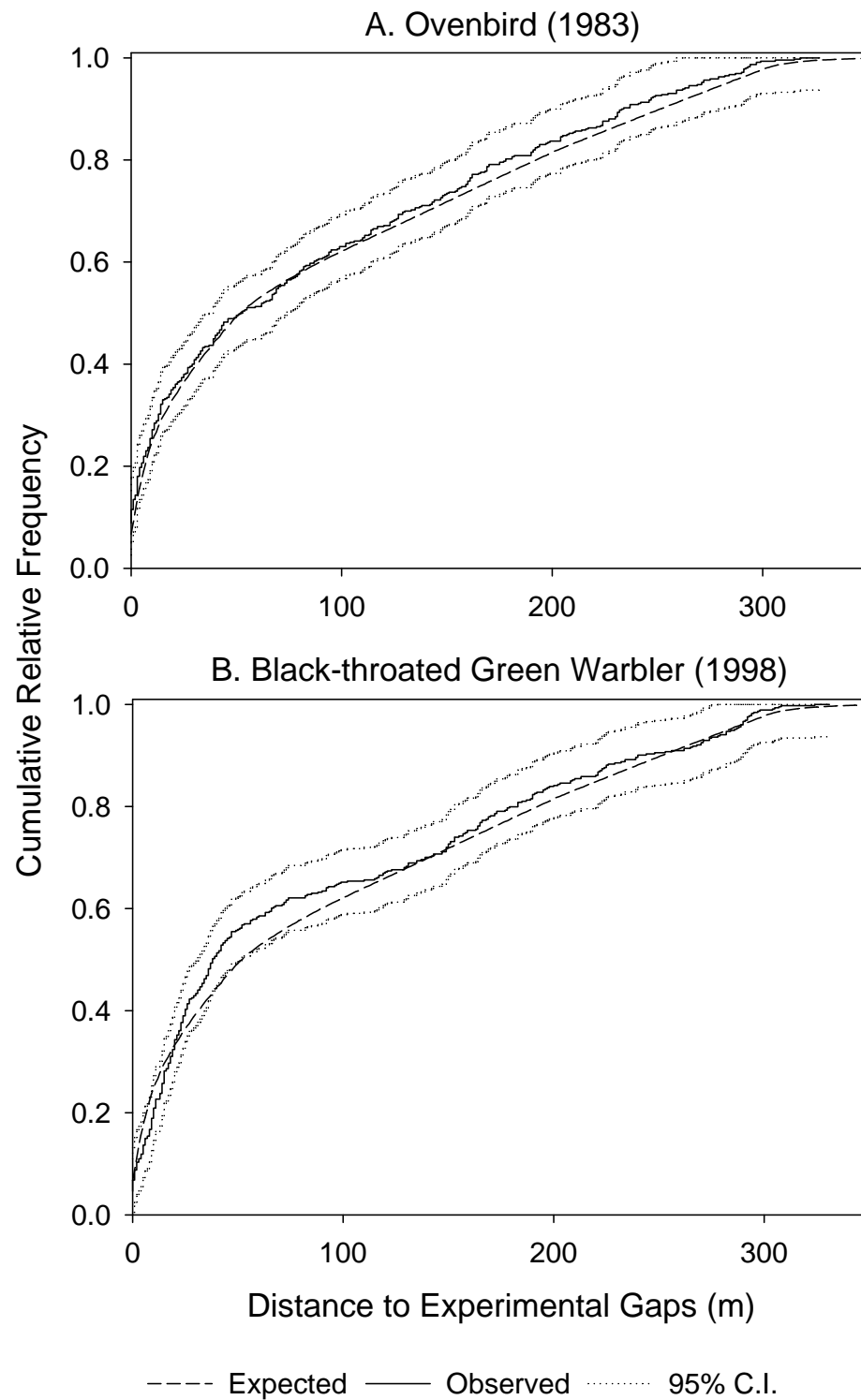


Figure B.3. Cumulative distribution curves of distances between observations and the nearest experimental gap for the Ovenbird in 1983 ($n = 460$) and the Black-throated Green Warbler in 1998 ($n = 454$). The observed curve is based on all the observations of a species in each year and is bounded by a 95% confidence band. The expected curve is based on all possible points spaced 5 m apart within the study area.

Table B.1. Comparison of the results from two tests which compare the cumulative distributions of distances of observations and random points from experimental gaps: Kolmogorov-Smirnov test (diff) and the “confidence band” test (pct^a) based on the percentage of observations with corresponding points on the expected curve falling outside the confidence bounds of the observed curve (see methods).

Bird Species	1983		1984		1985		1986		1987		1988		1989		1990		1991		1992	
	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct
Eastern Wood-Pewee	0.160	37.5	0.098	33.8	-0.007	0.0	0.272	68.4	0.232	82.2	-0.014	0.0	0.129	31.4	0.079	30.2	0.135	35.3	0.128	50.0
Blue-headed Vireo	-0.246	0.0	0.083	55.8	0.022	0.0	-0.006	0.0	-0.148	0.0	-0.071	0.0	0.085	26.9	0.019	0.0	0.132	62.5	-0.056	0.0
Black-capped Chickadee	-0.016	0.0	-0.040	0.0	0.023	13.2	-0.023	0.0	-0.027	0.0	0.065	46.1	-0.018	0.0	0.061	44.1	-0.043	0.0	-0.041	0.0
Brown Creeper	-0.053	0.0	0.074	32.3	0.003	0.0	0.019	6.2	-0.005	0.0	0.067	35.3	-0.033	0.0	-0.032	0.0	0.044	31.5	-0.030	0.0
Red-breasted Nuthatch	-0.112	0.0	-0.078	0.0	-0.016	0.0	0.064	24.6	0.034	2.5	-0.060	0.0	-0.026	0.0	0.040	3.2	-0.027	0.0	0.012	1.3
Winter Wren	0.239	89.5	0.143	83.0	0.375	86.7	.	.	0.451	94.1
Golden-crowned Kinglet	0.084	44.0	0.073	20.0	0.024	9.7	0.051	10.8	0.048	40.8	0.116	18.2	0.039	10.8	0.078	11.1	0.229	41.7	-0.033	0.0
Veery	0.133	71.4	0.221	81.8	0.246	72.4	0.025	7.7	0.139	46.4	0.069	35.1	0.000	0.0	-0.061	0.0	-0.027	0.0	-0.108	0.0
Hermit Thrush	0.001	0.0	0.108	59.8	0.065	14.1	-0.028	0.0	0.014	0.0	0.078	43.9	0.065	37.6	0.027	15.8	-0.006	0.0	0.035	7.3
Nashville Warbler	0.023	12.4	0.002	0.0	0.102	31.5	-0.154	0.0	0.044	4.1	0.001	0.0	0.021	7.1	0.152	41.2	-0.246	0.0	0.210	47.4
Yellow-rumped Warbler	0.054	21.2	0.041	12.4	0.086	35.7	0.051	31.7	0.104	41.0	0.089	63.3	0.108	64.6	0.110	34.8	0.127	69.9	0.053	52.4
Black-and-white Warbler	-0.052	0.0	-0.036	0.0	-0.035	0.0	0.081	44.6	0.019	0.0	0.016	6.0	-0.009	0.0	-0.027	0.0	0.065	33.3	0.120	47.8
Blackburnian Warbler	0.016	0.0	0.014	5.0	-0.007	0.0	0.006	0.0	0.032	20.1	0.016	0.8	0.096	61.7	0.068	51.1	0.045	10.2	0.028	7.8
Black-throated Green Warbler	0.096	41.5	0.027	19.8	0.019	17.2	0.003	0.0	0.004	0.0	0.047	50.9	0.091	72.4	0.117	65.2	0.091	68.9	0.097	83.5
Pine Warbler	0.211	55.0	0.482	50.0	0.187	40.0	0.389	46.7	0.332	42.9	-0.044	0.0	0.216	48.6	0.020	5.2	0.235	38.9	0.063	21.1
Ovenbird	0.004	0.0	0.007	8.7	0.011	0.0	0.012	0.0	0.010	0.0	0.058	22.5	0.139	44.1	0.123	24.8	0.089	26.9	0.070	9.6
Common Yellowthroat	0.056	17.2	-0.004	0.0	0.047	11.4	0.137	30.6	0.072	16.9	0.044	13.2	0.161	46.9	0.297	76.9	0.306	89.7	0.239	94.3
Scarlet Tanager	0.040	5.4	-0.123	0.0	-0.078	0.0	-0.109	0.0	0.125	33.3	0.033	8.2	0.020	9.6	0.058	5.3	0.041	59.3	0.134	40.0
White-throated Sparrow	-0.001	0.0	0.014	1.4	0.151	35.3	0.129	30.0	0.002	4.2	0.261	57.9	0.412	81.8	0.401	100.0	0.412	100.0	0.198	58.6
Purple Finch	-0.027	0.0	0.077	35.0	-0.089	0.0	-0.191	0.0	0.008	0.0	-0.117	0.0	0.197	58.3	0.203	70.6	-0.100	0.0	0.093	26.3

Table B.1 (Continued).

Bird Species	1993		1994		1995		1996		1997		1998		1999		2000		2001		2002	
	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct	diff	pct
Eastern Wood-Pewee	0.233	46.8	0.277	75.9	0.228	66.2	0.096	30.1	0.018	11.3	0.049	18.3	0.060	16.3	0.047	32.3	-0.036	0.0	0.068	16.1
Blue-headed Vireo	0.074	61.5	0.393	63.2	-0.010	0.0	0.127	63.2	-0.034	0.0	-0.002	0.0	-0.058	0.0	0.000	1.8	0.146	62.5	0.061	33.3
Black-capped Chickadee	0.098	54.0	-0.039	0.0	0.024	20.7	0.024	16.2	0.014	3.5	0.032	16.8	-0.016	0.0	-0.019	0.0	-0.012	0.0	-0.036	0.0
Brown Creeper	-0.013	0.0	-0.064	0.0	0.111	40.3	-0.019	0.0	-0.001	0.0	0.095	40.3	0.056	22.8	0.010	1.1	0.028	5.7	0.013	1.0
Red-breasted Nuthatch	0.078	54.3	-0.005	0.0	-0.028	0.0	-0.080	0.0	-0.036	0.0	0.136	62.5	0.008	0.0	-0.034	0.0	0.045	27.4	0.020	3.9
Winter Wren	-0.038	0.0	0.305	87.5	0.182	53.3	0.226	40.0	-0.337	0.0	.	.
Golden-crowned Kinglet	0.193	37.0	0.003	4.2	0.073	34.2	0.136	17.6	.	.	0.177	44.1	0.029	4.8	0.045	17.4	-0.060	0.0	-0.083	0.0
Veery	-0.125	0.0	-0.093	0.0	0.190	55.6	0.104	55.6	0.149	53.3	0.145	80.4	0.223	94.3	0.062	63.2	0.194	88.0	0.255	86.0
Hermit Thrush	0.020	3.7	-0.017	0.0	0.021	11.7	-0.026	0.0	0.044	26.0	-0.031	0.0	0.065	50.0	-0.026	0.0	0.022	24.1	-0.043	0.0
Nashville Warbler	0.023	10.0	0.190	33.3	.	.	0.273	91.7	-0.197	0.0	.	.	0.336	66.7	0.229	67.7
Yellow-rumped Warbler	0.051	42.7	0.148	68.2	0.100	73.5	0.078	49.1	0.057	59.6	0.108	68.6	-0.023	0.0	-0.044	0.0	0.114	72.5	0.047	28.8
Black-and-white Warbler	0.075	38.7	0.103	68.3	0.161	37.1	0.293	88.2	0.333	69.6	0.403	89.3	0.352	96.3	0.252	72.1	0.367	86.4	0.270	85.7
Blackburnian Warbler	0.042	11.5	0.033	9.6	0.058	34.2	0.055	21.8	0.078	14.4	0.031	3.8	0.133	46.7	0.036	26.9	0.063	18.5	0.030	17.2
Black-throated Green Warbler	0.095	60.3	0.094	58.9	0.065	48.0	0.023	1.7	0.067	44.6	0.019	6.7	0.015	0.0	0.035	26.8	0.024	2.0	0.016	2.2
Pine Warbler	0.085	33.3	0.147	42.6	0.201	40.4	0.109	17.4	0.133	37.5	0.148	31.0	0.243	40.5	0.205	34.3	0.155	41.9	0.360	64.0
Ovenbird	0.092	40.6	0.054	28.1	0.119	48.1	0.090	16.8	0.068	13.7	0.038	24.4	0.006	0.0	-0.001	0.0	0.026	11.9	0.006	0.5
Common Yellowthroat	0.203	50.7	0.231	80.5	0.217	52.9	0.311	64.0	0.389	88.9	0.361	86.7	0.420	84.6	0.247	37.5	0.291	60.0	0.298	86.7
Scarlet Tanager	-0.013	0.0	-0.088	0.0	-0.072	0.0	0.128	32.6	-0.084	0.0	-0.110	0.0	-0.054	0.0	-0.005	0.0	-0.070	0.0	0.013	11.4
White-throated Sparrow	0.313	76.6	0.341	96.9	0.315	100.0	0.358	81.0	0.412	94.1	0.208	25.0	0.320	88.2	0.284	75.0	-0.107	0.0	.	.
Purple Finch	0.132	54.2	-0.058	0.0	-0.015	0.0	-0.062	0.0	-0.064	0.0	-0.024	0.0	-0.042	0.0	-0.031	0.0	-0.060	0.0	-0.025	0.0

Note: diff = $D - D_{0.05,n}$, where D is the test statistic for Kolmogorov-Smirnov test (i.e., the the maximum difference between the distributions) and $D_{0.05,n}$ is the critical value for the Kolmogorov-Smirnov test for $\alpha=0.05$ and n observations. If diff ≥ 0 then the Kolmogorov-Smirnov tests indicates that a significant difference exists between the distributions. If diff < 0 then the test indicates that the distributions are not significantly different. Under the alternate method, if pct > 10 the distributions are considered different.

Table B.2. Sizes (in ha) of occupied areas of birds species breeding at the Holt Research Forest, 1983-2002. Occupied areas are the portion of the study area that a species use and were determined using the 90% contour of a fixed kernel density estimator with a smoothing parameter of 20 on all observations of a species. Years without range sizes are years in which there were no territories in the study area.

Bird Species	Year																			
	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Hairy Woodpecker	4.05	4.41	3.19	2.45	3.04	2.44	5.48	6.84	2.98	.	4.84	.	4.38	3.25	5.31	4.56	6.05	3.12	4.13	2.69
Eastern Wood-Pewee	6.72	7.53	9.08	3.02	3.67	8.08	3.43	5.16	4.82	6.29	7.84	8.54	9.29	8.28	9.87	9.72	8.73	9.48	7.83	10.73
Blue-headed Vireo	.	6.20	3.75	8.91	.	10.12	5.79	5.79	8.13	7.40	7.45	4.11	12.71	9.51	10.73	10.20	2.76	10.13	7.00	11.15
Tufted Titmouse	3.75	9.30	7.50	4.61	6.80	4.72
Black-capped Chickadee	18.78	14.82	14.18	12.43	21.66	18.53	22.54	23.13	16.18	16.00	23.01	20.07	21.37	18.68	23.44	29.78	24.42	16.34	27.49	21.77
Brown Creeper	11.68	15.98	16.16	10.74	14.07	14.01	15.94	16.61	10.04	18.95	16.96	16.70	11.87	10.99	15.58	15.03	17.08	13.05	16.26	15.02
White-breasted Nuthatch	.	.	.	1.84	2.61	.	6.41	3.91	9.97	6.26	3.99	7.60	4.82
Red-breasted Nuthatch	3.73	5.35	10.63	10.31	6.31	10.90	10.63	16.46	9.31	9.94	23.22	13.49	11.61	11.45	22.12	15.81	13.06	11.45	17.93	9.82
Winter Wren	7.12	10.53	3.66	.	4.07	3.67	2.04	3.09	1.90	.	.
Golden-crowned Kinglet	2.85	0.91	5.10	2.75	6.67	6.79	7.04	5.67	2.84	5.59	4.19	3.09	3.27	1.08	.	6.80	5.69	7.03	5.34	1.74
Veery	6.03	9.82	6.31	7.47	6.57	6.20	6.17	4.05	3.54	6.03	4.73	4.79	5.00	6.47	4.16	8.90	7.23	9.08	10.10	9.46
Hermit Thrush	14.30	12.56	11.19	9.83	6.58	12.85	11.19	16.38	19.04	17.88	19.41	25.77	14.81	14.74	12.98	14.91	19.50	21.09	17.68	17.76
Nashville Warbler	11.65	9.94	3.72	.	3.14	2.64	.	2.82	.	3.14	1.59	.	.	2.46	.	.	.	7.50	.	.
Yellow-rumped Warbler	10.54	14.36	16.36	11.02	15.34	17.35	23.05	12.13	14.04	13.29	15.79	10.65	11.86	16.97	16.26	14.96	21.66	13.04	16.14	19.11

Table B.2 (Continued).

Bird Species	Year																			
	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Black-and-white Warbler	18.06	12.77	10.57	9.34	5.39	10.76	10.57	9.45	11.48	8.00	10.58	4.35	6.82	8.36	6.10	7.06	8.13	9.58	6.38	7.70
Black-throated Blue Warbler	2.20	.	.	5.82	3.16	2.57	1.74	2.35	2.16	.	.
Blackburnian Warbler	11.80	9.16	12.09	15.13	9.61	9.15	8.02	3.47	12.51	10.86	11.38	12.54	3.70	8.56	7.40	9.36	6.99	7.19	8.04	9.49
Black-throated Green Warbler	23.78	25.87	15.96	16.90	19.58	19.40	18.11	17.08	20.79	17.77	18.42	10.66	10.70	14.39	13.58	12.24	12.63	15.93	18.09	13.57
Pine Warbler	6.41	2.48	1.53	2.32	1.50	2.03	6.03	7.93	4.92	9.51	8.91	6.89	8.77	3.90	3.46	7.92	5.29	5.18	7.97	4.53
Canada Warbler	2.21	2.36	2.78	1.79	1.42	.	1.79	.	.	.	0.98	2.08	1.02	1.17	0.85	0.65	0.98	0.57	1.07	.
Ovenbird	33.46	31.98	21.49	28.27	31.74	22.43	18.03	16.02	23.30	17.29	15.58	21.12	15.04	19.16	18.08	25.59	21.74	21.41	25.16	22.89
Common Yellowthroat	6.66	7.94	4.21	5.11	4.09	2.86	3.96	6.27	2.96	4.30	3.83	3.49	1.17	2.89	1.62	3.10	1.37	1.30	1.09	2.40
Scarlet Tanager	8.94	8.33	6.96	5.81	7.57	5.99	3.56	3.55	5.71	7.08	5.56	5.21	7.82	7.37	9.99	4.76	10.18	11.51	14.37	8.86
White-throated Sparrow	10.26	9.81	8.46	2.96	4.01	10.64	8.64	7.86	4.56	5.15	7.49	5.64	4.25	2.42	3.83	2.74	4.55	1.62	.	.
Purple Finch	5.46	6.38	6.68	4.78	10.57	7.86	6.96	4.93	7.47	10.41	11.98	14.68	12.08	9.92	8.28	10.21	11.21	15.50	15.67	14.54
American Goldfinch	.	.	5.67	3.00	1.88	4.86	3.87	3.85	4.12	6.06	9.26	9.32	.	9.08	6.28	11.81	10.57	16.67	14.73	17.78

Table B.3. Comparison of bird habitat use during the first five years (1983-1987) and the last five years (1998-2002) of the time series at the Holt Research Forest. Habitat use metrics are the proportion of experimental and ledge gap in an OA and the average distance (m) to the nearest experimental and ledge gap. Average differences are the differences between the averages of each time period and P-values are from Mann-Whitney tests of difference between the two time periods.

Bird Species	Proportion				Distance (m)			
	Experimental		Ledge		Experimental		Ledge	
	Avg. Diff.	P-value	Avg. Diff.	P-value	Avg. Diff.	P-value	Avg. Diff.	P-value
Eastern Wood-Pewee	-0.13	0.095	-0.07	0.222	31.74	0.222	6.73	0.032
Blue-headed Vireo	-0.01	0.841	-0.09	0.151	2.11	1.000	6.53	0.008
Black-capped Chickadee	-0.22	0.056	-0.28	0.016	-3.29	0.310	-2.00	0.222
Brown Creeper	0.08	0.310	-0.13	0.032	-25.28	0.032	2.36	0.310
Red-breasted Nuthatch	-0.15	0.032	-0.14	0.095	-5.83	0.841	-2.14	0.548
Winter Wren	---†	---	---	---	---	---	---	---
Golden-crowned Kinglet	0.04	0.310	-0.04	0.310	-21.51	0.222	2.26	1.000
Veery	-0.10	0.222	-0.02	0.421	7.13	0.690	11.34	0.008
Hermit Thrush	-0.27	0.008	-0.35	0.008	22.29	0.151	2.12	0.310
Nashville Warbler	-0.13	0.786	0.26	0.250	69.84	0.095	-17.80	0.095
Yellow-rumped Warbler	0.02	1.000	-0.14	0.095	3.74	0.841	-4.27	0.056
Black-and-white Warbler	-0.26	0.008	0.15	0.095	67.23	0.008	-10.69	0.016
Blackburnian Warbler	0.12	0.016	0.10	0.016	-1.73	1.000	-0.46	0.841
Black-throated Green Warbler	0.25	0.008	0.08	0.548	-7.56	0.222	-0.16	0.548
Pine Warbler	-0.15	0.008	-0.12	0.056	61.85	0.032	4.36	0.421
Ovenbird	0.28	0.008	-0.07	0.548	-8.77	0.151	6.81	0.008
Common Yellowthroat	-0.03	0.690	0.55	0.008	66.94	0.008	-40.03	0.008
Scarlet Tanager	-0.07	0.421	-0.11	0.310	11.19	0.548	-0.24	0.690

Table B.3 (Continued).

Bird Species	Proportion				Distance (m)			
	Experimental		Ledge		Experimental		Ledge	
	Avg. Diff.	P-value	Avg. Diff.	P-value	Avg. Diff.	P-value	Avg. Diff.	P-value
White-throated Sparrow	-0.04	0.905	0.38	0.032	90.85	0.016	-21.81	0.016
Purple Finch	-0.17	0.016	-0.19	0.095	-18.04	0.222	-2.52	0.548

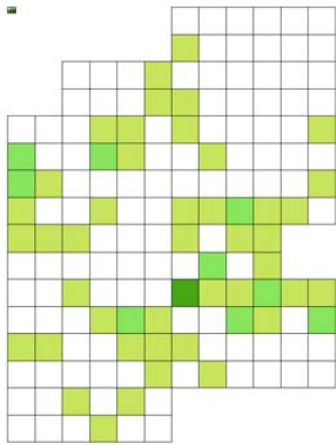
† Insufficient data for analyses.

APPENDIX C. Supplementary Data and Analyses for Chapter 3

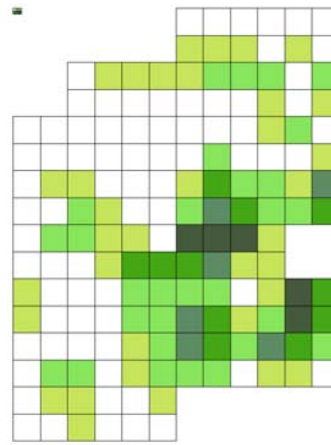
Table C.1. Numbers of individuals (DBH > 9.5 cm) and basal area (m²) of each tree species and their percentages of the total number of trees and total basal areas of all trees in the Holt Research Forest, 1984.

Species	Individuals		Basal Area	
	Count	%	Area	%
White Pine (<i>Pinus strobus</i>)	10989	33.6	684.5	50.0
Red Maple (<i>Acer rubrum</i>)	6756	20.6	194.5	14.2
Red Oak (<i>Quercus rubra</i>)	5664	17.3	194.7	14.2
Red Spruce (<i>Piceas rubens</i>)	2835	8.7	98.8	7.2
Balsam Fir (<i>Abies balsamea</i>)	1697	5.2	28.0	2.1
Hemlock (<i>Tsuga canadensis</i>)	1361	4.2	71.3	5.2
White Oak (<i>Quercus alba</i>)	1160	3.5	33.8	2.5
Paper Birch (<i>Betula papyrifera</i>)	658	2.0	20.2	1.5
Yellow Birch (<i>Betula alleghaniensis</i>)	595	1.8	18.0	1.3
Gray Birch (<i>Betula populifolia</i>)	460	1.4	7.5	0.5
Pitch Pine (<i>Pinus rigida</i>)	195	0.6	7.3	0.5
White Ash (<i>Fraxinus americana</i>)	144	0.4	4.1	0.3
Black Cherry (<i>Prunus serotina</i>)	107	0.3	1.7	0.1
Beech (<i>Fagus grandifolia</i>)	67	0.2	2.2	0.2
Bigtooth Aspen (<i>Populus grandidentata</i>)	23	0.1	1.0	0.1
Quaking Aspen (<i>Populus tremuloides</i>)	19	0.1	0.4	0.0
Apple (<i>Pyrus malus</i>)	13	0.0	0.2	0.0
Red Pine (<i>Pinus resinosa</i>)	5	0.0	0.4	0.0
Witch Hazel (<i>Hamamelis virginiana</i>)	2	0.0	0.0	0.0
Striped Maple (<i>Acer pensylvanicum</i>)	1	0.0	0.0	0.0

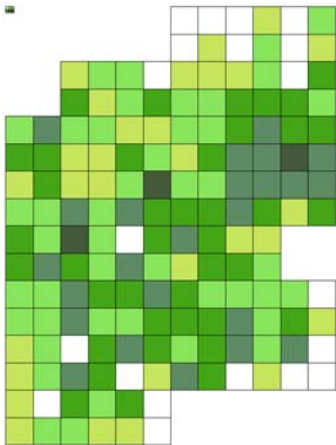
A. Hairy Woodpecker



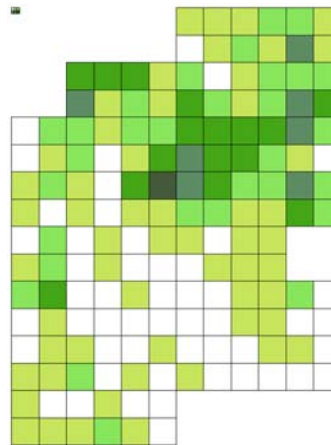
B. Eastern Wood-Pewee



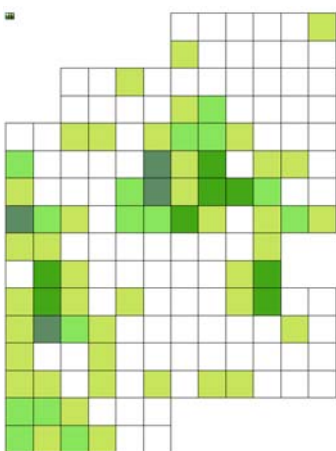
C. Brown Creeper



D. Red-breasted Nuthatch



E. Golden-crowned Kinglet



F. Veery

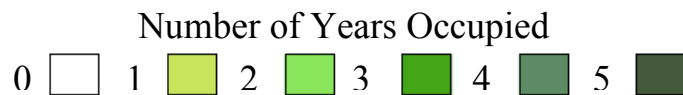
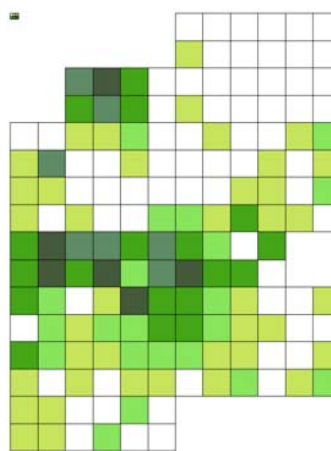
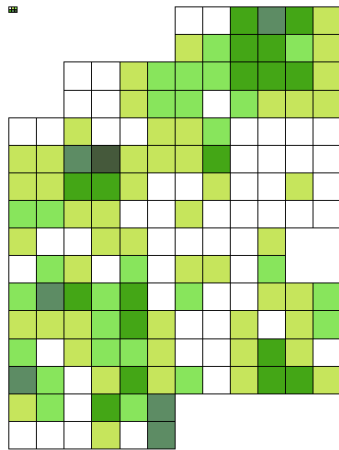
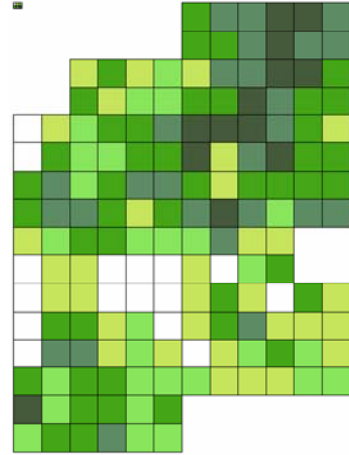


Figure C.1. Observed frequency landscapes for six bird species breeding at the Holt Research Forest, 1983-1987. Each grid cell is a 50×50 m quad. See Figure 2 for remaining species.

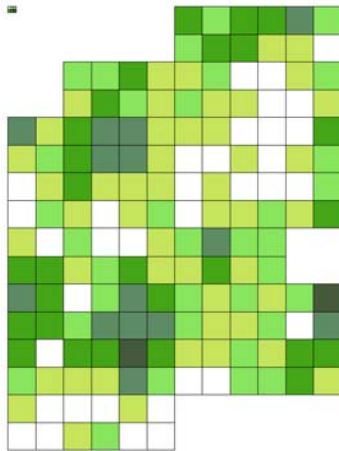
G. Nashville Warbler



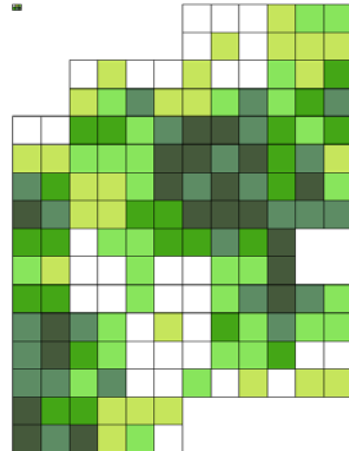
H. Yellow-rumped Warbler



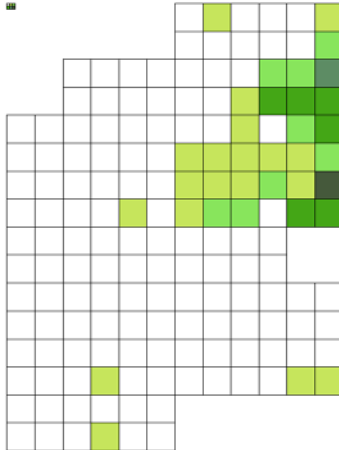
I. Black-and-white Warbler



J. Blackburnian Warbler



K. Pine Warbler



L. Scarlet Tanager

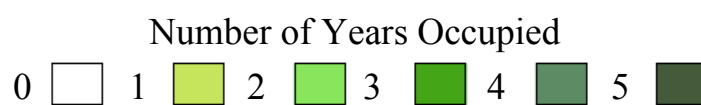
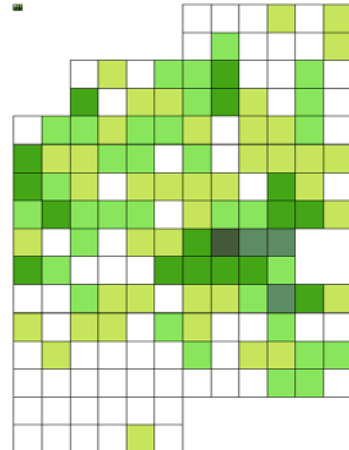
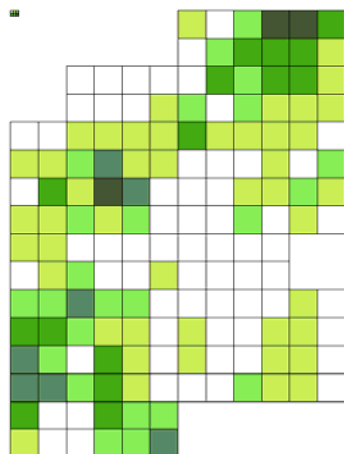


Figure C.1 (Continued).

M. White-throated Sparrow



N. Purple Finch

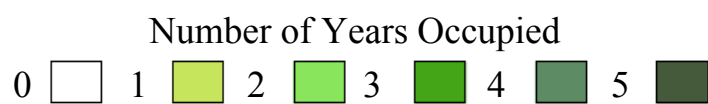
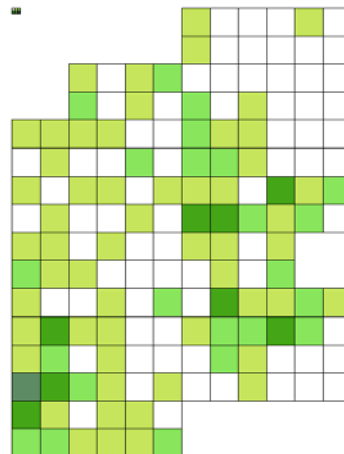


Figure C.1 (Continued).

Table C.2. Frequency distributions of occupied quads based on observed data and various null models and p-values from goodness-of-fit tests (see text) comparing each distribution to the observed distribution.

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
Hairy Woodpecker	Observed	107	43	9	1	0	0	.
	Free	106	45	8	1	0	0	0.877
	Occupied Free	121	21	13	5	1	0	0.000
	Regular	106	45	8	1	0	0	0.880
	Occupied Regular	128	14	8	6	3	1	0.000
	Irregular	106	46	8	1	0	0	0.851
	Occupied Irregular	125	16	11	6	1	0	0.000
	Dispersed Regular	106	46	8	1	0	0	0.863
	Site Fidelity	120	25	9	4	2	1	0.002
	Habitat	137	3	7	8	5	1	0.000
Eastern Wood-Pewee	Observed	74	35	29	11	6	5	.
	Free	47	64	37	11	1	0	0.000
	Occupied Free	80	21	31	21	7	1	0.024
	Regular	46	66	37	10	1	0	0.000
	Occupied Regular	84	20	27	20	9	1	0.003
	Irregular	47	65	36	11	1	0	0.000
	Occupied Irregular	82	20	29	20	8	1	0.008
	Dispersed Regular	49	62	37	11	2	0	0.000
	Site Fidelity	65	48	24	14	6	3	0.046
	Habitat	69	38	30	15	6	1	0.555
Black-capped Chickadee	Observed	4	18	45	54	26	13	.
	Free	5	19	40	51	34	9	0.402
	Occupied Free	9	17	38	49	37	11	0.124
	Regular	4	21	41	51	34	10	0.455
	Occupied Regular	10	19	36	47	36	13	0.057
	Irregular	4	19	42	51	34	10	0.503
	Occupied Irregular	7	18	41	49	35	11	0.345
	Dispersed Regular	5	21	39	50	35	10	0.262

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
Brown Creeper	Site Fidelity	13	24	32	36	30	25	0.000
	Habitat	6	20	40	48	35	11	0.225
	Observed	20	29	44	40	24	3	.
	Free	11	35	52	42	17	3	0.081
	Occupied Free	26	22	41	43	23	5	0.457
	Regular	11	36	52	41	17	3	0.076
	Occupied Regular	28	23	39	39	24	7	0.378
	Irregular	10	35	54	42	16	3	0.023
	Occupied Irregular	26	23	42	43	23	5	0.509
	Dispersed Regular	12	36	51	40	18	4	0.145
	Site Fidelity	28	32	35	30	23	13	0.017
Red-breasted Nuthatch	Habitat	16	34	45	41	20	4	0.698
	Observed	51	55	30	16	7	1	.
	Free	39	64	41	14	2	0	0.005
	Occupied Free	63	33	37	22	6	1	0.000
	Regular	39	64	42	13	2	0	0.003
	Occupied Regular	66	32	32	21	8	1	0.000
	Irregular	38	66	41	13	2	0	0.001
	Occupied Irregular	64	33	36	21	6	1	0.000
	Dispersed Regular	39	64	42	13	2	0	0.002
	Site Fidelity	62	41	27	19	9	2	0.037
	Habitat	51	50	38	18	4	0	0.502
Golden-crowned Kinglet	Observed	93	40	15	8	4	0	.
	Free	76	61	20	3	0	0	0.000
	Occupied Free	101	22	23	11	2	0	0.004
	Regular	76	62	19	3	0	0	0.000
	Occupied Regular	103	21	22	11	3	0	0.002

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
Veery	Irregular	77	61	20	3	0	0	0.000
	Occupied Irregular	104	20	22	12	3	0	0.000
	Dispersed Regular	77	60	20	3	0	0	0.000
	Site Fidelity	90	43	17	8	2	1	0.717
	Habitat	105	20	19	11	4	0	0.001
	Observed	68	40	21	18	7	6	.
	Free	41	63	39	14	2	0	0.000
	Occupied Free	75	21	30	23	9	1	0.001
	Regular	42	61	41	14	2	0	0.000
	Occupied Regular	78	21	26	21	11	3	0.001
	Irregular	41	62	40	14	3	0	0.000
	Occupied Irregular	78	20	27	22	11	2	0.001
	Dispersed Regular	43	61	39	14	3	0	0.000
	Site Fidelity	68	36	29	15	9	4	0.487
Hermit Thrush	Habitat	63	39	31	18	8	2	0.358
	Observed	26	35	40	43	13	3	.
	Free	16	43	53	34	13	2	0.009
	Occupied Free	34	25	42	37	18	4	0.097
	Regular	15	43	55	35	12	2	0.003
	Occupied Regular	35	26	40	35	20	4	0.054
	Irregular	16	43	52	35	12	2	0.009
	Occupied Irregular	33	26	43	37	18	4	0.116
	Dispersed Regular	17	42	50	36	13	2	0.036
	Site Fidelity	37	34	31	29	19	11	0.001
	Habitat	20	40	49	34	14	3	0.090

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied							p
		0	1	2	3	4	5		
Nashville Warbler	Observed	58	50	27	18	6	1	.	
	Free	42	66	41	11	1	0	0.000	
	Occupied Free	67	30	38	20	4	0	0.001	
	Regular	41	67	42	10	1	0	0.000	
	Occupied Regular	68	30	37	21	4	0	0.001	
	Irregular	42	67	40	11	1	0	0.000	
	Occupied Irregular	69	30	37	21	4	0	0.000	
	Dispersed Regular	42	66	41	11	1	0	0.000	
	Site Fidelity	55	50	34	18	3	0	0.646	
	Habitat	56	48	37	16	3	0	0.389	
Yellow-rumped Warbler	Observed	16	32	28	45	26	13	.	
	Free	8	27	47	48	25	6	0.004	
	Occupied Free	21	18	38	46	30	8	0.025	
	Regular	7	27	48	48	24	5	0.002	
	Occupied Regular	20	19	38	46	29	9	0.042	
	Irregular	7	27	48	48	24	5	0.001	
	Occupied Irregular	20	18	38	47	29	8	0.034	
	Dispersed Regular	9	28	46	46	26	7	0.031	
	Site Fidelity	22	27	31	34	27	18	0.112	
	Habitat	12	29	40	41	28	9	0.165	
Black-and-white Warbler	Observed	35	48	34	27	14	2	.	
	Free	23	53	51	27	6	1	0.003	
	Occupied Free	44	29	41	33	12	2	0.005	
	Regular	22	54	52	26	7	1	0.001	
	Occupied Regular	46	29	39	31	13	3	0.009	
	Irregular	22	53	52	26	6	1	0.001	

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
Blackburnian Warbler	Occupied Irregular	44	29	42	30	12	2	0.006
	Dispersed Regular	24	52	50	27	7	1	0.012
	Site Fidelity	44	41	32	22	15	6	0.182
	Habitat	29	48	46	27	9	1	0.281
	Observed	33	27	32	23	25	20	.
	Free	10	33	50	43	20	4	0.000
	Occupied Free	36	14	30	40	30	9	0.001
	Regular	9	34	52	42	20	4	0.000
	Occupied Regular	37	16	29	37	31	11	0.002
	Irregular	8	33	53	44	19	3	0.000
	Occupied Irregular	36	14	31	40	30	9	0.001
	Dispersed Regular	11	33	50	44	20	4	0.000
	Site Fidelity	25	32	33	32	25	14	0.207
	Habitat	22	31	37	34	25	10	0.010
Black-throated Green Warbler	Observed	0	2	16	19	40	83	.
	Free	0	2	8	24	57	70	0.002
	Occupied Free	0	2	7	23	57	70	0.002
	Regular	0	1	6	25	60	68	0.000
	Occupied Regular	0	2	8	23	56	71	0.005
	Irregular	0	1	6	25	61	67	0.000
	Occupied Irregular	0	1	6	25	60	68	0.000
	Dispersed Regular	0	1	6	26	62	66	0.000
	Site Fidelity	1	3	10	23	40	83	0.671
	Habitat	0	2	8	24	55	72	0.005

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
Pine Warbler	Observed	125	19	8	6	1	1	.
	Free	106	46	7	1	0	0	0.000
	Occupied Free	128	11	13	6	2	0	0.195
	Regular	106	46	7	1	0	0	0.000
	Occupied Regular	131	9	11	7	2	1	0.076
	Irregular	106	47	7	0	0	0	0.000
	Occupied Irregular	132	7	12	8	2	0	0.013
	Dispersed Regular	106	46	7	1	0	0	0.000
	Site Fidelity	120	27	8	3	2	1	0.225
	Habitat	128	11	12	6	2	0	0.188
Canada Warbler	Observed	119	29	6	2	0	4	.
	Free	103	47	9	1	0	0	0.001
	Occupied Free	125	14	13	7	2	0	0.000
	Regular	103	48	8	1	0	0	0.001
	Occupied Regular	134	8	5	5	6	2	0.000
	Irregular	104	47	9	1	0	0	0.001
	Occupied Irregular	132	7	9	7	5	1	0.000
	Dispersed Regular	104	46	10	1	0	0	0.001
	Site Fidelity	119	25	9	4	2	0	0.350
	Habitat	130	9	9	7	3	1	0.000
Ovenbird	Observed	1	1	14	14	35	95	.
	Free	0	1	6	19	52	82	0.001
	Occupied Free	1	1	6	18	52	83	0.002
	Regular	0	1	5	20	57	78	0.000
	Occupied Regular	1	1	6	18	48	85	0.019
	Irregular	0	1	5	20	57	78	0.000

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						
		0	1	2	3	4	5	p
Common Yellowthroat	Occupied Irregular	1	1	4	18	57	79	0.000
	Dispersed Regular	0	1	4	20	58	77	0.000
	Site Fidelity	1	3	8	18	38	92	0.330
	Habitat	0	2	7	18	49	84	0.006
	Observed	83	37	12	6	9	13	.
	Free	46	63	38	11	2	0	0.000
	Occupied Free	87	14	24	23	10	2	0.000
	Regular	44	66	39	10	1	0	0.000
	Occupied Regular	89	14	22	20	12	3	0.000
	Irregular	45	65	37	11	2	0	0.000
	Occupied Irregular	88	14	23	22	11	2	0.000
	Dispersed Regular	46	63	37	12	2	0	0.000
	Site Fidelity	64	45	29	14	6	2	0.000
	Habitat	88	18	20	18	12	5	0.000
Scarlet Tanager	Observed	66	41	33	16	3	1	.
	Free	49	64	35	10	2	0	0.000
	Occupied Free	77	27	31	19	6	1	0.041
	Regular	50	64	34	11	2	0	0.000
	Occupied Regular	81	24	27	19	8	1	0.002
	Irregular	49	64	35	11	2	0	0.001
	Occupied Irregular	79	26	28	19	7	1	0.008
	Dispersed Regular	51	62	34	11	2	0	0.001
	Site Fidelity	75	37	25	14	7	4	0.072
	Habitat	55	57	33	12	3	0	0.048

Table C.2 (Continued).

Bird Species	Model†	Number of Years Occupied						p
		0	1	2	3	4	5	
White-throated Sparrow	Observed	65	46	24	15	7	3	.
	Free	45	64	38	12	2	0	0.000
	Occupied Free	74	25	32	22	6	1	0.000
	Regular	43	66	39	11	2	0	0.000
	Occupied Regular	75	24	32	22	7	1	0.001
	Irregular	43	66	39	11	1	0	0.000
	Occupied Irregular	74	25	32	21	7	1	0.001
	Dispersed Regular	45	62	39	12	2	0	0.000
	Site Fidelity	64	44	28	17	6	2	0.855
	Habitat	64	40	33	17	5	1	0.293
Purple Finch	Observed	73	55	23	8	1	0	.
	Free	67	63	25	5	1	0	0.304
	Occupied Free	88	32	27	11	2	0	0.001
	Regular	70	59	25	6	1	0	0.758
	Occupied Regular	93	27	23	13	3	1	0.000
	Irregular	67	63	25	5	1	0	0.280
	Occupied Irregular	91	29	25	12	3	0	0.000
	Dispersed Regular	68	61	25	5	1	0	0.432
	Site Fidelity	87	40	18	10	4	2	0.003
	Habitat	67	63	24	5	1	0	0.318

†See text and Table 3.2 for model descriptions.

Table C.3. Results of goodness-of-fit tests between average frequency distributions of quad occupancy generated by site fidelity models with varying strengths of site fidelity and the frequency distributions based on the observed data. Non-significant ($\alpha = 0.05$) p-values (in bold-face) indicate frequency distributions are not significantly different.

Bird Species	Strength of Site Fidelity					
	0	0.2	0.4	0.6	0.8	1
Hairy Woodpecker	0.826	0.781	0.110	0.008	0.000	0.000
Eastern Wood-Pewee	0.000	0.000	0.000	0.026	0.112	0.279
Black-capped Chickadee	0.388	0.279	0.008	0.000	0.000	0.000
Brown Creeper	0.124	0.333	0.544	0.284	0.001	0.000
Red-breasted Nuthatch	0.004	0.368	0.733	0.475	0.001	0.000
Golden-crowned Kinglet	0.000	0.000	0.019	0.248	0.909	0.606
Veery	0.000	0.000	0.003	0.558	0.210	0.000
Hermit Thrush	0.004	0.078	0.202	0.022	0.000	0.000
Nashville Warbler	0.000	0.000	0.020	0.539	0.307	0.036
Yellow-rumped Warbler	0.002	0.048	0.143	0.337	0.027	0.000
Black-and-white Warbler	0.001	0.108	0.676	0.693	0.008	0.000
Blackburnian Warbler	0.000	0.000	0.000	0.044	0.729	0.219
Black-throated Green Warbler	0.000	0.001	0.015	0.192	0.520	0.003
Pine Warbler	0.000	0.000	0.018	0.112	0.525	0.659
Canada Warbler	0.001	0.013	0.203	0.381	0.144	0.008
Ovenbird	0.000	0.000	0.005	0.076	0.564	0.041
Common Yellowthroat	0.000	0.000	0.000	0.000	0.000	0.016
Scarlet Tanager	0.001	0.042	0.561	0.405	0.017	0.000
White-throated Sparrow	0.000	0.000	0.025	0.470	0.779	0.016
Purple Finch	0.428	0.997	0.777	0.025	0.000	0.000

Table C.4. Model averaged parameter estimates of vegetation variables and their associated unconditional standard errors (SE) and relative variable importance (RVI) for habitat models of 20 bird species breeding at the Holt Research Forest, 1983-1987.

Bird Species	Variable†	Estimate	SE	RVI	# of Models
Hairy Woodpecker	intercept	-3.40	1.519	1.00	4
	avg_cov_wp_5	-0.01	0.012	0.21	1
	ba_wp	-0.03	0.024	0.20	1
	ba_dec	0.06	0.051	0.27	1
	tot_ts_spp	0.03	0.020	0.32	1
Eastern Wood-Pewee	intercept	-4.30	0.627	1.00	7
	avg_cov_dec_5	-0.02	0.013	0.37	3
	avg_cov_oak_5	-0.01	0.008	0.11	1
	avg_cov_tot_4	-0.09	0.023	1.00	7
	avg_cov_wp_3	0.33	0.256	0.36	3
	avg_cov_wp_5	0.15	0.032	1.00	7
	ba_bf	-0.27	0.257	0.17	1
	ba_rm	-0.06	0.059	0.10	1
	ba_dec	0.68	0.223	1.00	7
	ba_oak	0.59	0.156	0.90	6
Black-capped Chickadee	intercept	-1.22	1.015	1.00	2
	ba_oak	0.28	0.078	1.00	2
	tot_ts_spp	0.03	0.016	0.56	1
Brown Creeper	intercept	-1.15	0.410	1.00	1
	avg_cov_wp_4	-0.21	0.053	1.00	1
	ba_hem	-0.37	0.091	1.00	1
	ba_all	0.15	0.045	1.00	1
Red-breasted Nuthatch	intercept	-1.04	0.470	1.00	4
	avg_cov_oak_3	0.33	0.300	0.21	1
	ba_bf	0.87	0.431	0.58	2
	ba_rs	0.38	0.148	0.83	3
	ba_wp	0.12	0.056	0.58	2
	ba_oak	-0.17	0.113	0.42	2
	ba_all	0.10	0.063	0.42	2

Table C.4 (Continued).

Bird Species	Variable†	Estimate	SE	RVI	# of Models
Golden-crowned Kinglet	tree_density	-0.01	0.002	1.00	4
	intercept	-0.84	0.645	1.00	2
	avg_cov_dec_3	0.36	0.281	0.33	1
	ba_rs	1.17	0.125	1.00	2
	tot_h_spp	-0.02	0.005	1.00	2
Veery	intercept	-3.89	0.758	1.00	3
	avg_cov_bf_4	0.25	0.144	0.55	2
	avg_cov_brch_4	0.24	0.066	1.00	3
	avg_cov_con_5	-0.02	0.013	0.17	1
	avg_cov_dec_3	-0.87	0.512	0.45	1
	avg_cov_tot_3	0.05	0.032	0.45	1
	ba_wp	-0.07	0.056	0.17	1
	ba_dec	0.20	0.127	0.37	1
	ba_oak	0.28	0.157	0.45	1
	ba_all	0.09	0.074	0.17	1
	tot_h_spp	0.01	0.005	0.45	1
	intercept	-0.72	0.175	1.00	2
	avg_cov_oak_4	0.19	0.050	1.00	2
Hermit Thrush	avg_cov_tot_3	0.02	0.016	0.33	1
	ba_bf	-1.28	0.444	1.00	2
	intercept	3.91	0.792	1.00	4
	avg_cov_dec_5	-0.03	0.012	0.84	3
Nashville Warbler	avg_cov_tot_3	-0.11	0.053	0.78	3
	avg_cov_wp_4	0.02	0.017	0.16	1
	ba_all	-0.39	0.059	1.00	4
	tot_h_spp	-0.01	0.004	0.74	3
	intercept	0.03	0.446	1.00	3
Yellow-rumped Warbler	avg_cov_rm_5	0.07	0.021	1.00	3
	avg_cov_wp_3	0.66	0.216	1.00	3
	ba_wp	0.03	0.027	0.26	1

Table C.4 (Continued).

Bird Species	Variable†	Estimate	SE	RVI	# of Models
Black-and-white Warbler	ba_dec	-0.60	0.100	1.00	3
	ba_all	0.12	0.049	0.74	2
	tree_density	0.00	0.001	0.23	1
	intercept	0.97	0.465	1.00	3
	avg_cov_dec_5	-0.02	0.009	0.74	2
	avg_cov_oak_3	-0.86	0.649	0.37	1
	ba_rs	-0.40	0.112	1.00	3
Blackburnian Warbler	ba_wp	-0.22	0.047	1.00	3
	intercept	-1.29	0.903	1.00	1
	avg_cov_tot_3	0.09	0.031	1.00	1
	avg_cov_wp_5	0.10	0.020	1.00	1
	ba_rm	0.44	0.130	1.00	1
	ba_rs	1.60	0.162	1.00	1
	tree_density	-0.01	0.002	1.00	1
Black-throated Green Warbler	tot_h_spp	-0.03	0.005	1.00	1
	tot_ts_spp	0.09	0.024	1.00	1
	intercept	1.12	0.289	1.00	1
	avg_cov_dec_5	0.09	0.021	1.00	1
	ba_hem	2.97	0.592	1.00	1
	ba_brch	-1.28	0.386	1.00	1
	ba_dec	-0.56	0.104	1.00	1
Pine Warbler	intercept	-5.22	1.079	1.00	4
	avg_cov_brch_4	-0.29	0.195	0.42	2
	avg_cov_rm_5	0.19	0.057	1.00	4
	ba_hem	0.44	0.261	0.47	2
	ba_wp	0.28	0.153	0.47	2
	ba_brch	-1.94	1.047	0.58	2
	ba_all	0.39	0.192	0.53	2
	tree_density	-0.02	0.005	1.00	4

Table C.4 (Continued).

Bird Species	Variable†	Estimate	SE	RVI	# of Models
Canada Warbler	intercept	-6.18	1.053	1.00	7
	avg_cov_brch_4	0.02	0.020	0.09	1
	avg_cov_dec_3	-0.63	0.477	0.32	2
	avg_cov_oak_3	-0.46	0.451	0.10	1
	avg_cov_tot_3	0.10	0.045	0.72	5
	avg_cov_wp_5	-0.02	0.016	0.18	1
	ba_bf	-1.03	0.716	0.42	3
	ba_rm	0.72	0.180	1.00	7
	ba_dec	0.04	0.038	0.10	1
	tot_h_spp	0.02	0.008	0.90	6
Ovenbird	intercept	0.35	0.398	1.00	2
	avg_cov_oak_4	-0.06	0.043	0.37	1
	avg_cov_rm_5	0.13	0.029	1.00	2
	avg_cov_tot_3	0.70	0.210	1.00	2
	avg_cov_wp_4	-0.14	0.048	1.00	2
Common Yellowthroat	intercept	4.75	0.710	1.00	2
	avg_cov_dec_3	0.33	0.262	0.33	1
	avg_cov_dec_5	-0.07	0.017	1.00	2
	avg_cov_tot_4	0.12	0.030	1.00	2
	ba_bf	-2.07	0.692	1.00	2
	ba_wp	0.44	0.084	1.00	2
	ba_all	-0.93	0.105	1.00	2
Scarlet Tanager	intercept	-1.05	0.732	1.00	12
	avg_cov_bf_4	-0.49	0.181	0.94	11
	avg_cov_brch_4	0.11	0.055	0.65	7
	avg_cov_dec_4	0.01	0.007	0.06	1
	avg_cov_oak_3	0.43	0.361	0.25	3
	avg_cov_tot_4	-0.01	0.006	0.11	2
	avg_cov_wp_3	0.75	0.272	1.00	12
	avg_cov_wp_4	-0.04	0.036	0.27	3

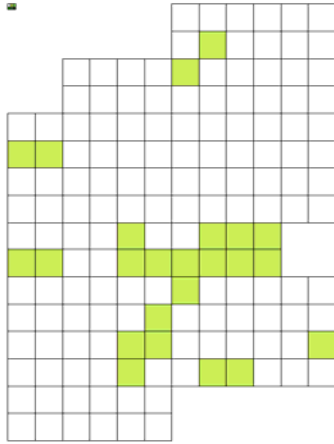
Table C.4 (Continued).

Bird Species	Variable†	Estimate	SE	RVI	# of Models
White-throated Sparrow	ba_brch	1.32	0.290	1.00	12
	tree_density	0.00	0.002	0.61	7
	intercept	3.07	1.228	1.00	6
	avg_cov_con_5	-0.02	0.017	0.21	1
	avg_cov_tot_4	0.02	0.014	0.21	1
	ba_bf	-1.86	0.612	1.00	6
	ba_rs	-0.19	0.121	0.47	3
	ba_wp	-0.04	0.032	0.16	1
	ba_dec	-0.59	0.148	1.00	6
	ba_all	-0.16	0.068	0.63	4
Purple Finch	tot_ts_spp	-0.02	0.015	0.28	2
	intercept	-1.98	0.203	1.00	3
	avg_cov_oak_3	-0.81	0.663	0.26	1
	avg_cov_rs_4	0.04	0.030	0.20	1
	avg_cov_wp_5	0.02	0.015	0.26	1
	ba_rs	0.28	0.103	0.80	2

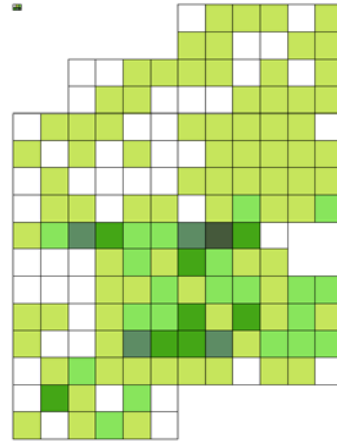
Note: The number of models in which each variable occurred was not equal, so the relative importance of a variable reflects both the posterior model probabilities (i.e., weights) and the number of models in which it occurs. I included the number of models in which each variable to aid in the interpretation of the relative variable importance.

† See Table 3.1 for variable descriptions.

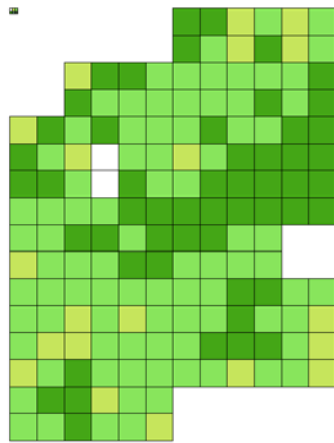
A. Hairy Woodpecker



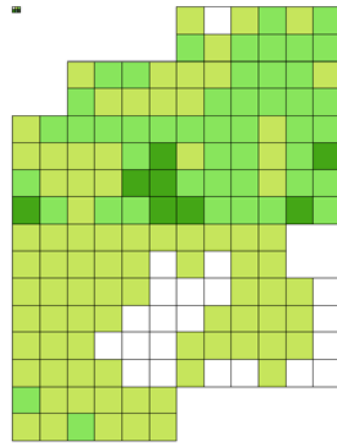
B. Eastern Wood-Pewee



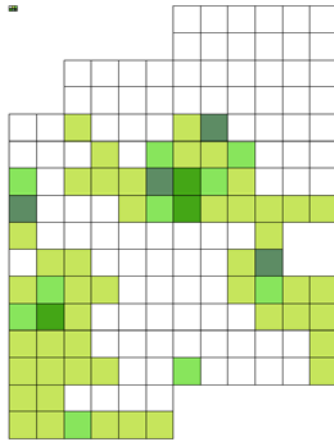
C. Brown Creeper



D. Red-breasted Nuthatch



E. Golden-crowned Kinglet



F. Veery

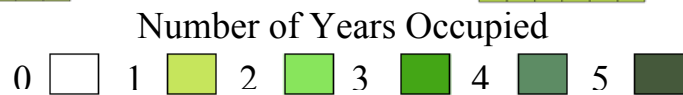
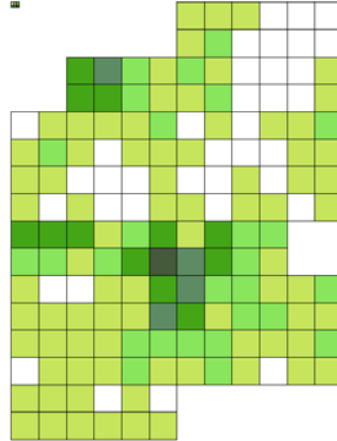
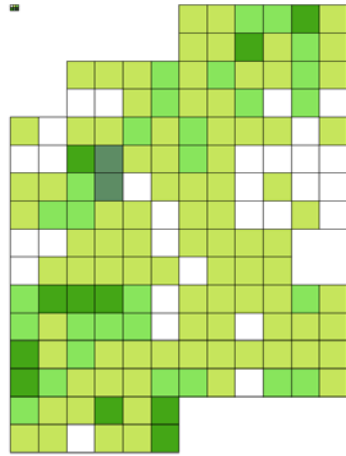
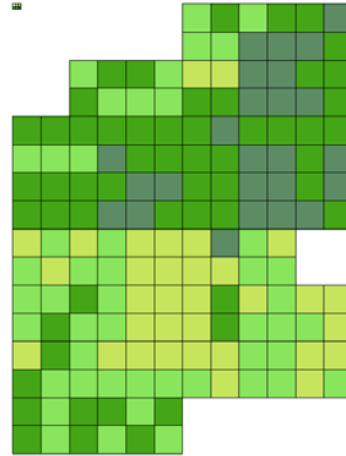


Figure C.2. Frequency landscapes fit by the logistic regression models for six bird species breeding at the Holt Research Forest, 1983-1987. Each grid cell is a 50×50 m quad. See Figure 4 for remaining species.

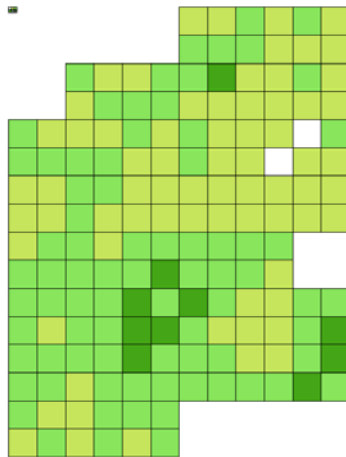
G. Nashville Warbler



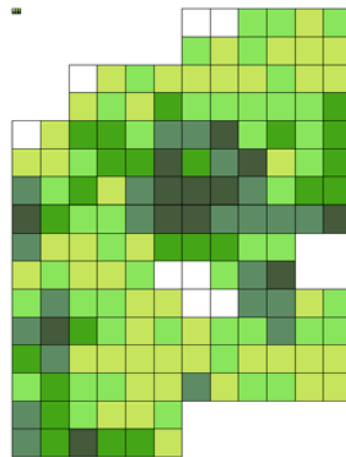
H. Yellow-rumped Warbler



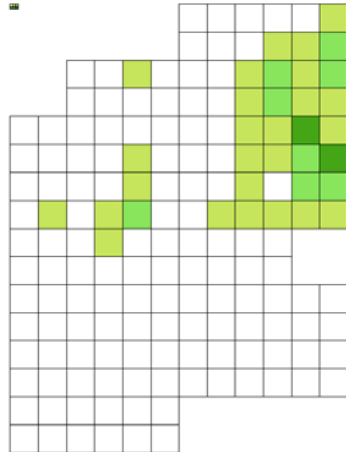
I. Black-and-white Warbler



J. Blackburnian Warbler



K. Pine Warbler



L. Scarlet Tanager

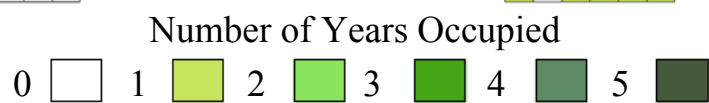
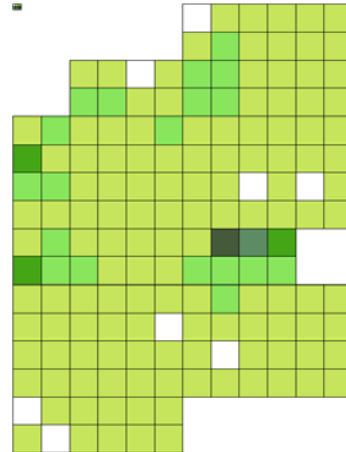
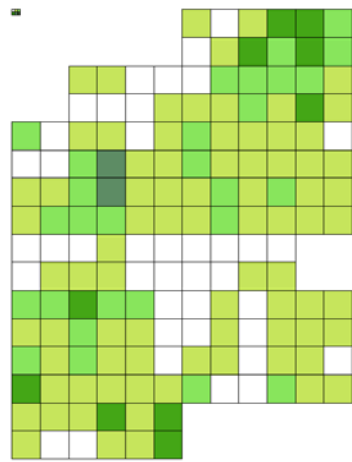
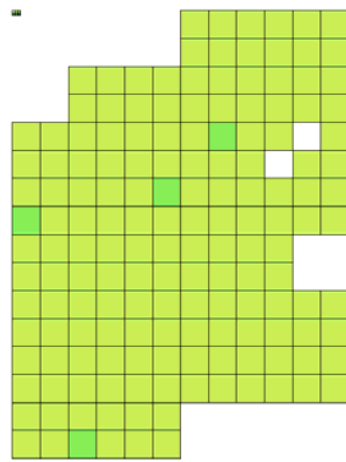


Figure C.2 (Continued).

M. White-throated Sparrow



N. Purple Finch



Number of Years Occupied

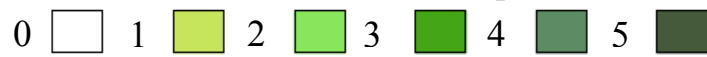


Figure C.2 (Continued).

BIOGRAPHY OF AUTHOR

Steven Paul Campbell was born in Syracuse, New York on November 22, 1972. He was raised in East Syracuse, New York and graduated from East Syracuse-Minoa High School in 1990. He attended the State University of New York College of Environmental Science and Forestry at Syracuse University and graduated as Salutatorian in 1994 with a B.S. degree in Environmental and Forest Biology. He earned two M.S. degrees from New Mexico State University in 1998, one in Biology and one in Experimental Statistics. Steven is a candidate for a Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in August 2007.