BREEDING BIRD COMMUNITIES OF THE HARDWOOD ECOSYSTEM EXPERIMENT

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Abstract.—Declining population trends of breeding birds associated with mature forests of the eastern and central United States have been a major concern for conservationists and land managers. As a landscape-scale, long-term, manipulative experiment, the Hardwood Ecosystem Experiment (HEE) in Indiana may provide important insights into factors associated with these declines. Accordingly, we quantified the characteristics of the breeding bird community at the HEE sites using 3 years of pre-treatment data. We also compared the HEE breeding bird community to similar data collected for the long-term monitoring program of the nearby Hoosier National Forest (HNF). From 2006 through 2008, we observed 74 species of birds across 240 survey points within the HEE sites, for a total of 17,806 detections. Of these, 62 species representing 17,340 detections were known to breed in the area. We adjusted the maximum counts at each survey point for differences in detectability, with small changes in adjusted density estimates for most species. Of the covariates used in modeling detectability, only sampling period (early/late in the morning) appeared consistently in the better fitting models. Abundance rankings showed that the HEE breeding avifauna was very similar to that of the HNF. Overall, the results suggested that the HEE sites supported a breeding bird community typical of mature Central Hardwood Forests and that these pre-treatment data will be useful to detect changes associated with the HEE treatments.

INTRODUCTION

The decline of Neotropical migrant birds has concerned researchers for at least three decades (Finch and Stangel 1993, Herkert 1995, Peterjohn et al. 1995, Robbins et al. 1989, Terborgh 1980). This concern has been especially focused on forest songbirds of the eastern and central United States. A reduction in the quality and/or quantity of the breeding grounds of these birds has been hypothesized as a contributing factor to this decline. Loss of wintering habitat or stopover migration habitat might also contribute to the decline, but research has been less conclusive on those impacts (Clawson et al. 1997, Packett and Dunning 2009).

Concerns over these declines have prompted considerable research examining the effects of forest management on avian communities (Duguay et al. 2000). However, much of the current published research consists of studies that were conducted with limited spatial and temporal scales (Mitchell et al. 2001) or limited replication (Thompson et al. 2000). Such studies lack utility because of their limited experimental design (Gram et al. 2003, Marzluff et al. 2000, Sallabanks et al. 2000). There is a need for more long-term studies (Collins 2001) as well as more manipulative experiments in heavily forested landscapes in the Central Hardwoods Region (Sallabanks et al. 2000, Thompson et al. 2000).

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Although several researchers have studied effects of forest management on migratory birds in forest-dominated landscapes (Annand and Thompson 1997, Thompson et al. 1992), these studies were not manipulative experiments and hence the researchers were able to examine only correlative or observational effects.

There also has been considerably less research investigating the effects of uneven-aged silvicultural schemes compared to even-aged management (Campbell et al. 2007). Other avian ecologists have conducted studies in fragmented habitats, and the results might not be applicable to more forested regions (Hartley and Hunter 1998, Robinson and Robinson 1999). Forest tracts in fragmented regions generally show decreased nesting success of mature forest birds, due to higher rates of brood parasitism by brown-headed cowbird (see Table 3 for list of common and scientific names of bird species) and increased nest predation by mammals, snakes, American crow, blue jay, and common grackle (Gates and Gysel 1978, Robbins 1979, Robinson et al. 1995, Wilcove 1985). Several studies have found that nest parasitism and predation are ameliorated when the forest tracts are part of a larger forested region (Donovan et al. 1997, Hanski 1996, Hartley and Hunter 1998, Temple and Cary 1988). Conversely, Flaspohler et al. (2001), King et al. (1996), and Manolis et al. (2002) have found decreased nesting success in relation to distance from clearcut edges even in heavily forested habitats. Landscape-level factors might determine the severity of local-level factors (Robinson et al. 1995).

In addition to declines in species that prefer mature forests, a decline of disturbance-dependent species is a concern (Brawn et al. 2001, Herkert 1995). These species can benefit from forest management, but to varying degrees (Schlossberg and King 2009). Some species prefer very young forests and peak in abundance immediately after harvest; other species have the highest abundance roughly 10 years after harvest (Schlossberg and King 2009). After about 20 years, most disturbance-dependent species are absent because the canopy has closed and shade eliminates understory vegetation (DeGraaf 1991).

The Hardwood Ecosystem Experiment (HEE) is located in the Central Hardwoods Region of the midwestern United States and is designed as a landscape-scale, long-term, manipulative research experiment. The project will examine the ecological and social impacts of forest management through a replicated series of study areas in south-central Indiana. The HEE is designed as a 100-year project to study the effects of even-aged management, uneven-aged management, and no timber harvest (control) on fauna and flora. There are three replicates of each management type spread over 30 linear kilometers and a total research area of more than 3,600 ha. Pre-treatment data collection began in 2006 and continued for 3 years prior to any manipulation. This process allowed us to study the spatial distribution of species in the region in the absence of treatments and will enable us to compare those findings to post-treatment data at each stage of the experiment. The silvicultural prescriptions of the HEE provide an opportunity to test the impacts of forest management strategies on mature forest-dwelling Neotropical migrants as well as those associated with early-successional habitat.

South-central Indiana is one of the few largely forested regions remaining in the midwestern United States, and it is possible that the area serves as a source population for other, more fragmented, areas of the Midwest (Robinson et al. 1995). Even though the research sites of the HEE are not located in a fully contiguous tract of forest, they are part of an overall forest region and are not isolated patches within agricultural land (Kalb and Mycroft, this publication: Fig. 1). The oak-hickory (*Quercus-Carya*) dominance of the HEE and elsewhere in the Central Hardwoods Region is threatened by altered disturbance regimes, increased white-tailed deer (*Odocoileus virginianus*) populations, and introduced diseases and pathogens (Kalb and Mycroft, this publication; McShea et al.

2007). The decline of oaks and hickories would have a profound impact on ecological and economic factors in Indiana, and the HEE will provide insight on possible methods of supporting oak-hickory forests.

Our objective was to compare conditions across management regimes before treatment to provide a baseline that shows how bird populations fluctuate over space and time. The long-term objective in this study is to determine the effects of forest management on breeding birds by assessing population differences among even-aged, uneven-aged, and no harvest management regimes.

A second objective in this paper is to compare our results to those of similar surveys conducted in mature forest communities in nearby areas. The U.S. Department of Agriculture, Forest Service has conducted breeding bird monitoring surveys in the nearby Hoosier National Forest (HNF) since 1991[2] (Thompson et al. 2002). The HNF surveys are conducted in mature forest stands and both projects use similar survey protocols. Therefore we expect the bird communities to be similar. By comparing HEE and HNF data from the same years, we expect to show that, prior to the HEE harvest treatments, the HEE sites supported bird communities typical of mature forests as measured in other long-term monitoring projects in the region.

STUDY AREA

This study took place in Morgan-Monroe and Yellowwood State Forests in south-central Indiana. The landscape consists of an oak-hickory forest type with steep hills and valleys in bedrock-derived soils (Jenkins, this publication). The area was once dominated by agriculture but began regenerating into forest in the early 1900s when the land became incorporated into the HNF and state forests (Jenkins, this publication). Kalb and Mycroft (this publication) give greater details of the HEE research area and study design.

The HEE uses nearly 20 percent of the Morgan-Monroe and Yellowwood State Forests and covers 3,603 ha. There are nine management units, and each includes a core research area and a buffer area (Kalb and Mycroft, this publication: Fig 1). These units are divided into three control (no harvest) units, three even-aged management units (i.e., clearcut and shelterwood methods), and three uneven-aged management units (i.e., single-tree selection and patch cuts). The management units range from 303 to 483 ha and the research cores range from 78 to 110 ha (Kalb and Mycroft, this publication: Table 1).

The HNF is located in southern Indiana, beginning approximately 20 km south of Yellowwood State Forest and extending to the Ohio River. It encompasses about 80,900 ha divided into four sections that are surrounded by other forested properties. Some sections also have open habitats such as farmland and pasture in the surrounding landscape. Historically, there have been some differences in the management of HNF and state forests (e.g., single-tree harvesting has been more prevalent in the state forests). HNF has a few more areas consisting of early successional habitat, but both regions are largely dominated by middle-aged to mature deciduous hardwood forests. Essentially, the HNF is part of a landscape similar to that of the HEE.

MATERIALS AND METHODS

Sampling

Survey points were placed in a manner to analyze breeding bird distributions and abundances at several spatial scales within the nine research cores. At the local scale, we classified points as being within a proposed harvest area (“harvest” sites), in the forest but within 100 m of a proposed harvest (“edge” sites), or greater than 100 m from a proposed harvest and

[2] HNF breeding bird survey (2006-2008) data on file with Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN

within the unharvested portion of the research core ("landscape" sites). At a broader scale, we classified the points according to the planned silvicultural treatments being implemented at HEE: control units, even-aged units (i.e., clearcuts and shelterwoods), and uneven-aged units (i.e., single-tree selection and patch cuts). After placing at least one point within each area receiving a clearcut, shelterwood, or patch cut harvest, and 2-4 points within 50 m of the edge of each of those areas, we systematically distributed points on a 150m x 150m grid throughout each management unit. Any grid-based points within 100 m of a harvest edge, within 100 m of the research core boundary, or within 100 m of an existing point were ignored (see Kalb and Mycroft, this publication: Fig. 2 for an example). All survey points were witnessed by marking a nearby large tree with paint and an aluminum tag, and were located to the most accurate possible meter (usually 6-10 m) using a Garmin GPS 12 (GARMIN International, Inc., Olathe, KS) handheld global positioning system (GPS) receiver.

Each management unit contained a different number of survey points due to the variation in size of the units and the number and size of the treatment sites (Kalb and Mycroft, this publication: Table 1). There were 240 survey points across the nine management units, with an average of 26.7 points per unit (Table 1).

Table 1.—Sample sizes of avian survey points within each management unit.

Management unit	Treatment type	No. of survey points
1	uneven-aged	31
2	control	19
3	even-aged	31
4	control	25
5	control	21
6	even-aged	27
7	uneven-aged	28
8	uneven-aged	32
9	even-aged	26
Total		240

We used aural point count surveys to determine densities of individual species of breeding birds at each of the survey points throughout the management units. We employed standard point count protocol, which can be an effective means of demonstrating changes in relative abundance of forest birds (Dawson 1981, Thompson et al. 2002). These surveys were conducted annually from 20 May - 20 June from 0600 to 1100 EDT. Each season, we hired 4-6 field workers who were trained before beginning the sampling. We sent compact discs of bird songs/calls of southern Indiana birds to field workers as soon as they were hired. If the technicians lived locally, we began training them in early May. Prior to the field sampling, technicians then underwent 1 week of intensive training within the HEE sites on song identification, distance estimation, and GPS usage. Fortunately, the same two expert birders trained the staff for the first 5 years of the study, which reduced potential inconsistency in the training. As the surveys were completed, the field technician coordinator reviewed the results to identify potential errors, and conducted re-training exercises as necessary.

We sampled each point twice per season using a different field technician to help minimize observer bias. After arriving at each survey point, the technician recorded wind speed, air temperature, and sky cover. The observer allowed a minute to pass for the birds to "settle" and then conducted a 10-minute survey. During the survey, the technician recorded each species of bird, sex of bird, estimated distance from technician, and whether identification was made through song, call, and/or sight. To use mark-recapture analysis to estimate differences in detectability for each species, we also recorded the minute period of the 10-minute survey in which the bird was detected (Farnsworth et al. 2002, Moore et al. 2004).

Data Analysis

Point-count surveys are a popular method of monitoring bird populations by estimating abundance and trends in abundance (Rosenstock et al. 2002). To make reliable comparisons among data sets and between species, raw counts should be adjusted for differences in species detectability (Farnsworth et al. 2002, Thompson and La Sorte 2008). To adjust our survey counts, we employed a capture-removal model that uses the same methodology as removal modeling of closed populations (Otis et al. 1978). Farnsworth et al. (2002) developed a method where individual covariates can be used to explain variation in detection probability by calculating maximum-likelihood estimates of model parameters.

Using a standardized point-count protocol controls for variation in seasonal and weather differences among survey periods, but other factors cannot be easily controlled (Moore et al. 2004). Therefore we added year, management unit (each unit was identified individually as a categorical variable), harvest type (local-scale - described in the Sampling section: harvest, edge, or landscape), observer rank (rank 4 = average, rank 3 = good, rank 2 = excellent, or rank 1 = expert), and binary time of day (detected before or after 0745 hours) as covariates to the analysis. We analyzed the data using a Huggins closed-capture model (Huggins 1989, 1991) in program MARK (White and Burnham 1999).

During each 10-minute survey period, the technician recorded the 1-minute time interval in which each individual was initially detected. After dividing the survey period into five 2-minute intervals (assuming equal per-minute detection probabilities within the survey), these intervals are treated as trapping occasions. Each detected individual was considered "removed" from the population (i.e., was not recorded in subsequent time periods within the same survey) after its initial detection period by setting recapture probability at 0. The most general model we tested was $M_{y+u+h+o+t}$ (*y* = year, *u* = management unit, *h* = harvest type, *o* = observer rank, *t* = binary time of day). Reduced models included all possible additive combinations of covariates (e.g., M_{y+h} and M_{h+o+t}) and all single-variable models. We did not separate the two sampling occasions for each survey point when building these models because we had no expectation that the sampling occasion periods would affect detectability, as all surveys were conducted within a short time period.

A unique goodness-of-fit procedure was not available for closed-population capture-recapture models in MARK, so we used a variance inflation factor, *c*, to assess the fit of each species' global model. The parameter *c* is estimated from a goodness-of-fit chi-square statistic and divided by its degrees of freedom, $\hat{c} = \chi^2/\text{df}$. The values for the models were $2.54 < c < 3.14$, which indicates that some overdispersion was present but not a structural lack of fit (Burnham and Anderson 1998). To correct for overdispersion, we conducted a second capture-recapture analysis for each species, where the $\hat{c}$ from the global or subglobal model was incorporated into calculations of best-fit models for all models in the set. This approach does not affect the values of the parameters, but it can change the ordering of the best-fit models because it favors models with fewer parameters. This procedure also inflates the standard errors of the parameters by a value of $\sqrt{\hat{c}}$ to account for the uncertainty due to overdispersion (White et al. 2001).

We used the Akaike information criterion (AIC) to compare our models. When adjustments to $\hat{c}$ are employed, the following equation is used to calculate a modified version of AIC:

$$\text{QAIC}_c = -\left[2\log\left(\mathcal{L}\left(\hat{\theta}\right)\right)/\hat{c}\right] + 2\text{K} + \frac{2K\ (K+1)}{n-K-1}$$

We found substantial model uncertainty for most species where there was no clear single model that best fit the data (Table 2). We used a weighted average of parameter estimates to conduct full-model averaging in which all subsets of the candidate set of models are included (Table 2) (Symonds and Moussalli 2011), calculated by:

$$\tilde{\bar{\beta}} = \sum_{i=1}^{R} w_i \hat{\beta}_i$$

Table 2.—Best-ranked models for detection probability estimates when individual covariates are considered. For covariates with asterisk (*), the individual covariate was found to be significant because its 95-percent confidence interval did not include zero.

Species	Model[a]	$QAIC_c$ weights	Covariate[b]	$\tilde{\tilde{\beta}}$	SE
Acadian flycatcher	M_y	0.35	2006	-0.53	0.30
			2007	0.09	0.16
			2008	-0.15	0.17
Brown-headed cowbird	M_t	0.56	TOD > 0745	-0.10	0.30
Carolina wren	M_t	0.57	TOD > 0745	-0.43	0.64
Cerulean warbler	M_t	0.63	TOD > 0745	-0.21	0.27
Hooded warbler	M_t	0.36	TOD > 0745	-0.02	0.14
Indigo bunting	M_h	0.34	Landscape	-0.20	0.51
			Edge	-0.03	0.37
Ovenbird	M_h	0.32	Landscape	-0.05	0.16
			Edge	-0.02	0.17
Red-eyed vireo	M_{y+o}	0.42	2006	0.34	0.23
			2007*	0.48	0.18
			2008*	-0.38	0.19
			Rank 1	-0.30	0.27
			Rank 2	0.21	0.27
			Rank 3*	-0.45	0.22
Eastern towhee	M_t	0.67	TOD > 0745	-0.56	0.41
Scarlet tanager	M_t	0.42	TOD > 0745	-0.35	0.21
Worm-eating warbler	M_{o+t}	0.32	Rank 1*	-0.65	0.26
			Rank 2	-0.17	0.25
			Rank 3	-0.30	0.22
			TOD > 0745	-0.12	0.12
Wood thrush	M_t	0.52	TOD > 0745	-0.19	0.16

[a] Models tested for effects of the following covariates on species detectability: *y* = year, *u* = management unit, *h* = harvest type, *o* = observer rank, *t* = binary time of day (TOD).
[b] See Materials and Methods section for detailed description of individual covariates.

A formula for estimating the unconditional variance of a model-averaged parameter has not yet been developed. Burnham and Anderson (1998) recommend using the following equation:

$$\widehat{var}\left(\tilde{\tilde{\beta}}\right) = \sum w_i \left[\widehat{var}\left(\hat{\beta}_i\right) + \left(\beta_i - \tilde{\tilde{\beta}}\right)^2\right]$$

Covariate $\tilde{\tilde{\beta}}$ values were calculated as a logit function and then converted into real values during the probability detection calculations.

Let p_i = the probability a bird is detected in any given detection interval. We evaluated each species separately and each interval was of equal length, so we assumed equal detection probabilities for each "capture occasion" ($p_1 = p_2 = p_3 = p_4 = p_5$). After we calculated a detection probability for each time period, the combined detection probability for the entire count was calculated by $\hat{p} = 1 - (1 - p_i)^5$. Dividing the observed count by the combined detection probability ($\hat{p}$) yielded the adjusted abundance estimate (Moore et al. 2004). In addition to program MARK, we used Microsoft Excel 2010 (Microsoft Corporation, Redmond, WA) for calculations and model manipulation.

For the initial pretreatment analysis, we placed a number of species into two habitat guilds. For the mature-forest guild, we chose acadian flycatcher, cerulean warbler, ovenbird, red-eyed vireo, scarlet tanager, worm-eating warbler, and wood thrush. These species were selected because they were comparatively easy to detect with vocal, territorial males, and were present in relatively high numbers in our study area. For the early successional guild, we chose brown-headed cowbird, Carolina wren, indigo bunting, and eastern towhee. Brown-headed cowbirds were also selected because they are nest parasites and can have interspecific effects (Friesen et al. 1999). Although hooded warblers are usually considered a mature forest species, they are often associated with small gaps within mature forest. Therefore, they may respond positively to harvest treatments much like the early successional species. Across both guilds, hooded warbler, worm-eating warbler, and cerulean warbler are species of concern in Indiana.

Upon reviewing the multi-year database, we noticed an unusual pattern in the observations of worm-eating warbler and chipping sparrow. Although the combined totals of these species were similar across years, their relative detections changed annually. Specifically, we detected many more chipping sparrows than worm-eating warblers in 2007, but the reverse was true in all other years. Field technicians often had difficulties with the similar-sounding songs of these two species. We believe that in 2007 most of our technicians had the species' songs interchanged. Therefore, we combined the chipping sparrow detections and worm-eating warbler detections for each year and re-classified the combined total as worm-eating warbler. Since chipping sparrow detections were a small fraction of those for worm-eating warbler in most years (e.g., 13 sparrows, 406 warblers in 2006), we feel that our approach reduced overall error across the analysis.

Comparison with HNF

The HNF monitoring survey has the same protocol as the HEE and concentrates on mature forest birds, thereby providing a comparison to the pre-treatment HEE data.[3] Using HNF data for 2006-08, we summarized the total detections recorded in these years. HNF data have not been adjusted for detectability, and different points are surveyed in odd and even years. Thus, we compared the total raw detections across all survey points in the HNF and HEE to determine if the relative abundance rankings of breeding species were similar and if the same overall trends in total detections were apparent in both databases.

RESULTS

General

From 2006 through 2008, we observed 74 bird species, of which 62 were breeding species, and recorded 17,806 total detections, of which 17,340 were of breeding species. Each year we detected some nonbreeding birds, most commonly migrants that were still in the HEE area during the first week of the survey period. As expected, our most abundant species were birds that use mature forest habitat, whereas typical early-successional species were recorded in relatively small numbers (Table 3). The red-eyed vireo was the most abundant species with 12.9 percent of all detections, followed by worm-eating warbler (7.6 percent), acadian flycatcher (7.4 percent), eastern wood-pewee (7.3 percent), and ovenbird (6.3 percent). Other commonly detected species included tufted titmouse, wood thrush, hooded warbler, scarlet tanager, American crow, and brown-headed cowbird. Together these 11 species accounted for 67.6 percent of detections for pre-treatment years.

[3] HNF breeding bird survey (2006-2008) data on file with Purdue University, Department of Forestry and Natural Resources, West Lafayette, IN

Table 3.—Total detections for all HEE survey points during each pre-treatment sampling year.

Common name	Scientific name	2006	2007	2008
Acadian flycatcher	*Empidonax virescens*	165	550	562
American crow	*Corvus brachyrhynchos*	261	276	176
American goldfinch	*Spinus tristis*	2	3	0
American redstart	*Setophaga ruticilla*	4	5	4
American robin	*Turdus migratorius*	5	1	3
Barred owl	*Strix varia*	7	0	0
Black-and-white warbler	*Mniotilta varia*	11	1	165
Blackpoll warbler	*Setophaga striata*	0	0	33
Black-throated green warbler	*Setophaga virens*	5	13	16
Blue jay	*Cyanocitta cristata*	155	271	161
Blue-gray gnatcatcher	*Polioptila caerulea*	42	130	229
Blue-headed vireo	*Vireo solitarius*	0	0	1
Blue-winged warbler	*Vermivora cyanoptera*	1	0	0
Broad-winged hawk	*Buteo platypterus*	0	5	6
Brown-headed cowbird	*Molothrus ater*	81	305	256
Canada goose	*Branta canadensis*	0	8	8
Carolina chickadee	*Poecile carolinensis*	102	60	89
Carolina wren	*Thryothorus ludovicianus*	4	5	14
Cedar waxwing	*Bombycilla cedrorum*	37	18	36
Cerulean warbler	*Setophaga cerulea*	15	55	141
Chestnut-sided warbler	*Setophaga pensylvanica*	3	2	0
Chimney swift	*Chaetura pelagica*	0	4	11
Chipping sparrow[a]	*Spizella passerina*	0	0	0
Common grackle	*Quiscalus quiscula*	1	0	0
Common yellowthroat	*Geothlypis trichas*	2	0	0
Cooper’s hawk	*Accipiter cooperii*	0	0	1
Downy woodpecker	*Picoides pubescens*	37	41	17
Eastern phoebe	*Sayornis phoebe*	6	9	2
Eastern screech-owl	*Megascops asio*	0	0	1
Eastern towhee	*Pipilo erythrophthalmus*	0	44	33
Eastern wood-pewee	*Contopus virens*	440	412	413
Field sparrow	*Spizella pusilla*	0	0	1
Gray catbird	*Dumetella carolinensis*	8	8	6
Great crested flycatcher	*Myiarchus crinitus*	28	42	11
Great horned owl	*Bubo virginianus*	1	0	1
Hairy woodpecker	*Picoides villosus*	0	1	12
Hooded warbler	*Setophaga citrina*	232	243	273
Indigo bunting	*Passerina cyanea*	27	13	29
Kentucky warbler	*Geothlypis formosa*	20	41	102
Louisiana waterthrush	*Parkesia motacilla*	41	30	22
Magnolia warbler	*Setophaga magnolia*	1	0	2
Mourning dove	*Zenaida macroura*	4	24	4
Northern cardinal	*Cardinalis cardinalis*	256	184	112
Northern flicker	*Colaptes auritus*	10	19	47
Northern mockingbird	*Mimus polyglottos*	1	0	0
Northern parula	*Setophaga americana*	105	34	33
Northern waterthrush	*Parkesia noveboracensis*	1	0	3
Ovenbird	*Seiurus aurocapilla*	298	376	413
Pileated woodpecker	*Dryocopus pileatus*	60	97	82
Pine warbler	*Setophaga pinus*	12	16	12
Red-bellied woodpecker	*Melanerpes carolinus*	258	136	172
Red-eyed vireo	*Vireo olivaceus*	622	797	821
Red-headed woodpecker	*Melanerpes erythrocephalus*	30	3	5
Red-shouldered hawk	*Buteo lineatus*	0	2	0
Red-tailed hawk	*Buteo jamaicensis*	4	4	4

(Table 3 continued on next page)

Table 3 (continued).—Total detections for all HEE survey points during each pre-treatment sampling year.

Common name	Scientific name	2006	2007	2008
Rose-breasted grosbeak	*Pheucticus ludovicianus*	0	2	3
Ruby-throated hummingbird	*Archilochus colibris*	12	34	3
Scarlet tanager	*Piranga olivacea*	79	260	380
Summer tanager	*Piranga rubra*	2	5	12
Swainson's thrush	*Catharus ustulatus*	0	2	15
Tennessee warbler	*Oreothlypis peregrina*	3	50	176
Tree swallow	*Tachycineta bicolor*	2	0	0
Tufted titmouse	*Baeolophus bicolor*	110	296	451
Warbling vireo	*Vireo gilvus*	0	4	0
Whip-poor-will	*Caprimulgus vociferus*	0	0	4
White-breasted nuthatch	*Sitta carolinensis*	335	96	157
White-eyed vireo	*Vireo griseus*	1	6	0
Wild turkey	*Meleagris gallopavo*	21	6	16
Wood thrush	*Hylocichla mustelina*	272	242	339
Worm-eating warbler[a]	*Helmitheros vermivorum*	419	506	402
Yellow warbler	*Setophaga petechia*	0	137	3
Yellow-billed cuckoo	*Coccyzus americanus*	1	187	29
Yellow-throated vireo	*Vireo flavifrons*	163	88	101
Yellow-throated warbler	*Setophaga dominica*	8	31	97
Total		4,833	6,240	6,733

[a] Chipping Sparrow and Worm-eating Warbler have been combined and placed under Worm-eating Warbler. See Materials and Methods section for explanation.

Many of our species of interest exhibited an increase in detections throughout the study period (Table 4). Notable changes from 2006 to 2007 included a substantial increase in detections of acadian flycatcher, brown-headed cowbird, scarlet tanager, cerulean warbler, and eastern towhee. Besides another marked increase in scarlet tanager, wood thrush, and cerulean warbler, most of these species exhibited minor fluctuations from 2007 to 2008.

Table 4.—Unadjusted detections and relative abundances for focal species at all HEE survey points.

	Detections (relative abundance)			
Species	2006	2007	2008	Total
Red-eyed vireo	622 (0.13)	797 (0.13)	821 (0.13)	2,240 (0.13)
Worm-eating warbler[a]	419 (0.09)	506 (0.08)	402 (0.06)	1,327 (0.08)
Acadian flycatcher	165 (0.03)	550 (0.09)	562 (0.09)	1,277 (0.07)
Ovenbird	298 (0.06)	376 (0.06)	413 (0.06)	1,087 (0.06)
Wood thrush	272 (0.06)	242 (0.04)	339 (0.05)	853 (0.05)
Hooded warbler	232 (0.05)	243 (0.04)	273 (0.04)	748 (0.04)
Scarlet tanager	79 (0.02)	260 (0.04)	380 (0.06)	719 (0.04)
Brown-headed cowbird	81 (0.02)	305 (0.05)	256 (0.04)	642 (0.04)
Cerulean warbler	15 (0.00)	55 (0.01)	141 (0.02)	211 (0.01)
Eastern towhee	0 (0.00)	44 (0.01)	33 (0.01)	77 (0.00)
Indigo bunting	27 (0.01)	13 (0.00)	29 (0.00)	69 (0.00)
Carolina wren	4 (0.00)	5 (0.00)	14 (0.00)	23 (0.00)
Total breeding bird detections	4,823	6,037	6,480	17,340

[a] Chipping sparrow and worm-eating warbler have been combined and placed under worm-eating warbler. See Methods section for explanation.

We estimated the mean detections per point for each proposed management type using the maximum number of individuals detected over the two point visits (Table 5). Individual species showed little variation in abundance among the management types.

Detection Models

The covariates that affected detectability and their associated weights differed for each species (Table 2). Across all species, the binary time of day was the covariate that was most consistently included in the best models. Even when the time of day was not present in the best model, it was usually contained in the next-best model. Year was contained in the best model for some species (e.g., acadian flycatcher and red-eyed vireo), but for other species (e.g., eastern towhee and worm-eating warbler) it did not appear within the best 90 percent of models. Harvest type was usually found within the top 80 percent of models. Observer rank had a relatively small impact on detectability, and management unit was contained only once within the models contributing over 99 percent of the parameter weights.

A model-averaged covariate significantly contributed to detectability estimates if its 95-percent confidence interval did not include zero. Significant covariates within the red-eyed vireo models were the years 2007 and 2008, and observer rank 3 (see Methods: Data Analysis for definitions of observer rank). Worm-eating warbler models contained observer rank 1 as a significant covariate (Table 2). Most of the covariate values were very small and/or had large standard errors. Overall, the individual coefficients had a minimal effect on the estimates of detection probability.

Our method of model averaging yielded a unique probability of detection ($\hat{p}$) for each combination of covariates. Most of these values were close to 1.0 due to the small covariate estimates, thus resulting in relatively small changes in relative abundance (Table 6). The average detection probabilities for individual species ranged from 0.67 to 0.96. In general, detectability was positively correlated with abundance estimates. Most species showed a relative abundance change of less than 0.5 percent. The exception was Brown-headed Cowbird, whose relative abundance increased by 1.56 percent (mean $\hat{p}$ = 0.67) when adjusted for detectability, which is still a small change.

Table 5.—Mean maximum abundance (of the two visits) estimated for focal species after being adjusted for differences in detectability. Values represent the expected maximum abundance/point (with standard deviation) over the complete survey period.

	Proposed management type		
Species	Control	Even-aged	Uneven-aged
Red-eyed vireo	2.20 (0.33)	2.22 (0.41)	2.22 (0.63)
Worm-eating warbler	1.34 (0.24)	1.40 (0.18)	1.36 (0.22)
Acadian flycatcher	1.22 (0.46)	1.20 (0.43)	1.36 (0.57)
Brown-headed cowbird	1.19 (0.76)	1.26 (0.64)	0.99 (0.57)
Ovenbird	0.92 (0.52)	1.13 (0.55)	1.37 (0.38)
Scarlet tanager	0.94 (0.46)	0.93 (0.49)	0.90 (0.60)
Wood thrush	0.78 (0.18)	1.10 (0.66)	0.87 (0.39)
Hooded warbler	0.79 (0.28)	0.87 (0.28)	0.99 (0.15)
Cerulean warbler	0.23 (0.21)	0.27 (0.22)	0.27 (0.48)
Eastern towhee	0.13 (0.16)	0.11 (0.14)	0.12 (0.14)
Indigo bunting	0.08 (0.06)	0.11 (0.07)	0.12 (0.13)
Carolina wren	0.01 (0.02)	0.05 (0.05)	0.06 (0.10)

Table 6.—Changes in count totals and relative abundances (R.A.) of focal species between raw detections and detections adjusted for variations in detectability. Probability of detection values = mean (minimum, maximum).

	Pre-adjustment			Post-adjustment		
Species	Total	R.A. (%)	Probability of detection	Total	R.A. (%)	Change in R.A.
Red-eyed vireo	2,240	12.92	0.95 (0.83, 1.00)	2,353.11	12.92	0.00
Worm-eating warbler	1,327	7.65	0.96 (0.88, 0.99)	1,382.34	7.59	-0.06
Acadian flycatcher	1,277	7.36	0.96 (0.87, 0.98)	1,335.67	7.33	-0.03
Ovenbird	1,087	6.27	0.96 (0.95, 0.97)	1,135.59	6.23	-0.04
Wood thrush	853	4.92	0.95 (0.94, 0.97)	895.10	4.91	-0.01
Hooded warbler	748	4.31	0.92 (0.89, 0.93)	816.75	4.48	0.17
Scarlet tanager	719	4.15	0.86 (0.79, 0.93)	837.18	4.60	0.45
Brown-headed cowbird	642	3.70	0.67 (0.60, 0.72)	957.93	5.26	1.56
Cerulean warbler	211	1.22	0.91 (0.89, 0.96)	231.22	1.27	0.05
Eastern towhee	77	0.44	0.85 (0.79, 0.95)	90.90	0.50	0.05
Indigo bunting	69	0.40	0.83 (0.76, 0.89)	83.20	0.46	0.06
Carolina wren	23	0.13	0.75 (0.67, 0.86)	31.04	0.17	0.04
Total breeding bird detections	17,340			18,217		

HEE and HNF Comparisons

The HEE and HNF surveys resulted in similar species lists and abundance rankings in the comparison period of 2006-08 (Table 7). We examined the abundance rankings of the 10 most common species in the HEE database, plus the brown-headed cowbird, which is of particular management interest and was ranked in the HEE database as the 11th most common species. Though not in identical order, the most numerous 11 species in the HEE during 2006-08 matched the most numerous species in HNF with two exceptions: brown-headed cowbird and hooded warbler ranked 15th and 16th in abundance in HNF, rather than within the top 11 (Table 7). These top 11 species differed in relative abundance between the two study areas by less than 2 percent except for red-eyed vireo and worm-eating warbler, which were higher in HEE by a difference of 6.1 percent and 4.0 percent, respectively.

We saw an increase in total detections in the HEE database each year with a substantial increase from 2006 to 2007, and a smaller increase from 2007 to

Table 7.—Comparative rankings of most abundant species in the HEE and HNF database, 2006-08. Order of species is given in column 1 based on rank order of HEE species across all 3 years.

	HEE				HNF			
Species	Total	2006	2007	2008	Total	2006	2007	2008
Red-eyed vireo	1	1	1	1	3	5	7	1
Worm-eating warbler	2	3	3	6	10	9	9	16
Acadian flycatcher	3	11	2	2	4	10	2	4
Eastern wood-pewee	4	2	4	4	6	2	4	6
Ovenbird	5	5	5	5	1	1	5	2
Tufted titmouse	6	14	7	3	7	6	12	7
Wood thrush	7	6	12	8	2	3	3	3
Hooded warbler	8	10	11	9	16	18	17	10
Scarlet tanager	9	18	10	7	9	11	10	9
American crow	10	7	8	12	5	4	1	8
Brown-headed cowbird	11	17	6	10	15	19	18	5

2008 (Table 1). The increase between the first 2 years was reflected in the HNF survey as well. Total detections per point (summarizing both visits and comparing 2006 to 2007) increased from 20.1 to 26.0 and from 20.8 to 26.1 for the HEE and HNF, respectively. The small increase in detections from 26.0 to 28.1 in the HEE database during the final 2 years (2007 compared to 2008) was not matched in the HNF database, in which total detections decreased slightly to 26.1 in 2008.

DISCUSSION

The increase in total detections each year in the HEE database is somewhat puzzling as there were no weather-related or logistic issues that could account for the increase. Field technicians were trained in the same way across years, and the increased numbers were not associated with the records of particular individuals. It was therefore of interest to find the same increase in total detections in the HNF database, especially from 2006-07. The HNF data were collected by different observers trained with the same overall techniques.

Because we employed full model averaging, all covariates contributed something to the adjusted detection probability. The amount that the covariate contributes to the average shrinks toward zero by the degree to which it is uninformative. Models that do not contain the covariates of interest simply contribute zero to the average. It is not surprising that the binary time of day was the largest contributor because most birds sing more frequently in the early morning, making them easier to detect during the earlier period.

Considering that our data were collected prior to any harvests, it is noteworthy that the proposed harvest type had an effect on detectability. Saunders and Arseneault (this publication) found differences in forest structure within the study area, so we will examine the possibility of those effects in future analyses. Management unit appeared to have no substantial effect on detectability. We were expecting the observer rank to have more of an effect on detectability than the results showed. However, it is encouraging that observer differences only marginally affected detections, because the HEE will have a great variety of observers in the future.

Adjustments for detectability were minor due to a combination of small β values for covariate coefficients and the resulting large detection probabilities. Red-eyed vireo and worm-eating warbler were the only species whose models contained covariates that significantly affected detection probabilities. The largest change in relative abundance occurred in brown-headed cowbird, which is reasonable since its calls are challenging to some technicians.

It is encouraging to discover that the HEE sites support substantial populations of Indiana species of concern, and this finding stresses the importance of the study area as habitat for these species. Hooded warbler and worm-eating warbler had higher relative abundances in the HEE than in the HNF sites (Table 7). The highest record in the 2006-08 study period for cerulean warbler was 141 detections (2.2 percent relative abundance), whereas the highest record in HNF was 16 detections (0.3 percent relative abundance).

We also detected some rarer species within the HEE sites that could be breeding in our research area. These species included American redstart with 4-5 detections per year, and black-throated green warbler with 5-16 detections per year. We detected black-and-white warbler 11 times in 2006 and once in 2007, but saw an increase to 165 detections in 2008. There was a higher frequency of black-and-white warbler detections during the beginning of the field season, which can implicate them as migrants, but a strong presence until the end of the season supports the theory that some stayed to breed in the area. The high numbers of black-and-white warblers in the region in 2008 were consistent with anecdotal observations in the area that summer.[4] Broad-winged hawk (five detections in 2007, six in 2008) and Cooper's hawk (one detection in 2008) were also rare species to find in a mature forest.

We had a few data sets that caused problems when fitting appropriate models. Maximum likelihood estimation would fail to converge, or convergence was successful but with parameter estimates that were unrealistic. These results occurred with Carolina wren, indigo bunting, and eastern towhee, which are early-successional species with relatively sparse observations. In each case, there were still some valid results, so we used those models to calculate the averages.

CONCLUSION

The similarities between the HEE and HNF results give us confidence that our surveys during the pre-treatment years of the HEE project adequately quantified the bird species common in mature Indiana forests and present on the HEE sites. Individual management units and proposed harvest type were not found to be significant predictors of detectability. Observer rank and year were significant predictors for two species. There was few differences among pre-treatment management types based on the mean detections/point for each species. We are therefore confident that the HEE pre-treatment data will be a suitable basis for comparison with those of post-harvest years.

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[4] Personal communication with J.K. Riegel, Purdue University

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