

ANNUAL VARIATION IN BIRD POPULATIONS OF MIXED CONIFER-NORTHERN HARDWOOD FORESTS¹

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Abstract. We examined annual variation in breeding bird populations at sites in northwestern Wisconsin and in the Upper Peninsula of Michigan from 1986 to 1992 to determine (1) the extent to which different bird species vary in abundance over time and (2) whether or not patterns of variation differ when viewed at local and regional spatial scales. Total abundance of long-distance migrants (species that winter in the tropics) declined during the first few years in both states but subsequent increases returned abundance to levels close to those that occurred at the start of the study. Short-distance migrants (species that winter in temperate regions) showed the greatest similarity between states in the extent and direction of variation in abundance among years; abundance reached a low in both states during 1990. Unlike migrant groups, abundance of permanent residents was not correlated between states. Permanent residents declined in abundance from 1987 to 1988 in Michigan, for example, but increased in abundance in Wisconsin. Fluctuations in abundance generally were poorly correlated among groups within a state. Repeated-measures analysis of variance (one-way) revealed that abundances of 13 and 21 (62%) common, long-distance migrants, 13 of 16 (81%) short-distance migrants, and 7 of 9 (78%) permanent residents varied significantly among years in one or both states. Fluctuations in abundance likely occurred in response to events on the breeding grounds. Factors likely to have affected populations include severe drought, particularly during 1987 and 1988, as well as successional changes in habitat. It is unlikely that events on tropical wintering grounds caused population fluctuations observed in neotropical migrants. Two-way ANOVA indicated that patterns of variation differed between the two study regions (significant interaction effects) for a number of species, particularly permanent residents. Results of this study thus illustrate the importance of considering temporal variation in abundance at more than one spatial scale.

Key words: *Annual variation; bird populations; forest birds; northern hardwoods; migrants; population declines; spatial scale.*

INTRODUCTION

Fluctuations in abundance of bird populations are common (e.g., Järvinen 1979; Loiselle 1988; Wiens 1989; Droege and Sauer 1990; Blake and Loiselle 1991; Loiselle and Blake 1991, 1992; Virkkala 1991; Järvinen and Rajasärkkä 1992) and occur in response to variations in resource abundance, habitat, weather, and population processes (e.g., recruitment) (Järvinen and Väisänen 1978, Grant 1986, Holmes et al. 1986, Holmes and Sherry 1988, Hutto 1989, DeSante 1990, Arcese et al. 1992, Blake et al. 1992, Marzluff and Balda 1992, Loiselle and Blake 1993). Although fluctuations in abundance are a natural component of the population dynamics of many

species, recent concern has focused on apparent declines of many species during the past few decades. Species showing declines include primarily migratory species that breed in temperate habitats and winter in tropical habitats (Lack 1989, Robbins et al. 1989, Terborgh 1989, Askins et al. 1990, papers in Hagan and Johnston 1992) but also include many species that do not winter in tropical habitats (Droege and Sauer 1990, Finch 1991, Hagan et al. 1992, Witham and Hunter 1992).

Although declines in bird populations are evident in some areas, agreement has not been reached regarding the extent or causes of such changes (e.g., see Hagan and Johnston 1992). Differences in patterns of year-to-year variation in abundance between migratory groups have led some to suggest that declines in abundance of long-distance migrants are tied to events on the wintering grounds (e.g., Robbins et al. 1989) whereas others attribute population declines to

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breeding ground effects (e.g., Böhning-Gaese et al. 1993). Part of the disagreement may stem from the scale at which studies are conducted (Sauer and Droege 1992). Trends observed in bird populations at a single study site often differ from trends observed at larger, more regional scales (Holmes and Sherry 1988, Witham and Hunter 1992). Similarly, changes observed in one part of a species' range are not always evident in other regions, indicating that population trends are not spatially uniform (James et al. 1992).

Regional variation in population processes may have important consequences for species as a whole. Populations experiencing low reproductive success may be maintained by immigrants from other regions where reproductive success is greater ("source vs. sink"; Pulliam 1988, Temple and Cary 1988, Robinson 1992). Differences in habitat may influence reproductive success and thereby influence the extent of variation shown by a species inhabiting a particular region; apparent trends in abundance may reflect or depend on the habitat(s) studied. Various studies have addressed annual variation in bird populations in North America, but much of the northern hardwoods and southern boreal forest habitats of north-central US and adjoining Canada has received little attention (Robbins et al. 1986, Hunter 1992). Yet, this region is an important breeding area for many species, including many neotropical migrants (e.g., Parulinae) and may, consequently, serve as a source of individuals for other areas (Temple and Cary 1988). Thus, it is an important region to consider when discussing annual changes in breeding bird populations.

In this paper, we examine annual variation in abundances of birds breeding in mixed conifer-northern hardwoods forest habitats of northwestern Wisconsin and the Upper Peninsula of Michigan over a seven-year period (1986–1992). We ask the following questions. (1) What is the extent of annual variation in abundance of birds breeding in these regions? (2) Does the direction (increase or decrease) and extent of variation differ among species or groups of species defined on the basis of migratory strategy? (3) Are trends in one state similar to those observed in the other; that is, are populations affected over broad geographical scales or are they responding to more localized events?

Our study was originally designed to test for effects of the US Navy's extremely low frequency (ELF) communications systems on bird popu-

lations. We do not discuss potential effects of the antenna system here (see Hanowski et al. 1993, Helle et al. 1993 for details), but it is important to note the following. First, we have not detected any differences in bird abundances between treatment (areas adjacent to the antenna) and control (areas >10 km from the antenna) study sites that could not be attributed to inherent differences in habitat. Second, we have not detected any differences in annual trends in bird populations between treatment and control sites. Hence, observed changes in bird populations among years can not be attributed to antenna operations.

STUDY AREAS AND METHODS

STUDY AREAS

Bird abundances were sampled in northwestern Wisconsin (Chequamegon National Forest: Ashland, Bayfield, and Sawyer counties) and in the Upper Peninsula of Michigan (Copper Country and Escanaba River state forests: Dickinson and Marquette counties), at sites approximately 240 km apart. The two study regions were sufficiently far apart to be independent with respect to bird populations, local alterations in habitat, and local weather patterns. The areas were, however, characterized by similar habitats (Table 1) and affected by similar climatic patterns. Dominant tree species present on study sites included sugar maple (*Acer saccharum*), red maple (*A. rubrum*), balsam fir (*Abies balsamea*), birch (*Betula papyrifera*, *B. lutea*), black ash (*Fraxinus nigra*), aspen (*Populus tremuloides*, *P. grandidentata*), black spruce (*Picea mariana*), cedar (*Thuja occidentalis*), and red pine (*Pinus resinosa*).

We established 20, randomly selected 4.35-km transects: 10 in Michigan and 10 in Wisconsin. Detailed descriptions of selection procedures are in Hanowski et al. (1990, 1993). Transects were distributed over approximately 860 km² in Wisconsin and 1,500 km² in Michigan. By sampling a series of plots within each region we avoid scale problems associated with "chance reshufflings of territories" (Rotenberry and Wiens 1980; see also Wiens 1981, 1989). That is, patterns of variation are viewed at a large enough scale that plot effects do not predominate. Similarly, by comparing results between regions separated by over 200 km, we are better able to evaluate regional trends in populations.

Each 4.35-km transect consisted of eight 500-m

segments arrayed in a single line, with segments separated by a 50-m buffer. Throughout this paper, "sample unit" or "segment" refers to a single 500-m segment; "transect" refers to the eight contiguous segments. In an ideal experimental design, locations of each sample unit would be randomly selected. Logistically this would be impractical; too few sites could be sampled in a single day. As a compromise between statistics and field work, we grouped eight sample units (500-m segments), each separated by 50 m. Certainly, individual birds may move from one segment to an adjacent segment and could potentially be counted on more than one segment. We reduced this probability (of double-counting) by noting on field maps the position and direction of movement (if any) of all individuals. It also is possible that results (i.e., bird occurrences) from one segment might be correlated with results from adjacent segments because of similarities in habitat between adjacent segments. This problem was reduced somewhat by the fact that the study region was naturally and anthropogenically fragmented by frequent, often abrupt habitat discontinuities (e.g., bogs, clearcuts). This patchiness tended to reduce habitat similarity between adjacent segments. The 50-m buffer between segments was introduced to reduce autocorrelation (i.e., caused by movement of birds or similarities in habitat) between adjacent sample units. We used Moran's I statistic (Sokal and Oden 1978) to test spatial autocorrelation of adjacent segments with respect to bird distribution patterns. Results indicated that a 50-m buffer eliminated autocorrelation between 99% (831 of 840 tests) of adjacent segments (Hanowski et al. 1990).

BIRD COUNTS

We counted birds along each 500-m segment (80/state) twice each year during the breeding season: mid-May through early July, 1986 through 1992. (An earlier paper [Blake et al. 1992] that considered variation from 1985 through 1989 was based on a single sample per transect because all transects were sampled only once in 1985; 1985 data are not included here.) Counts started approximately one half hour before sunrise and lasted up to approximately four hours after sunrise on days with little wind (<15 km/hr) and little or no precipitation. Observers walked at a rate of 30 min/500 m segment and recorded the identity and location of all birds seen or heard within 100 m of the segment center line. Two transects were

TABLE 1. Percentage of study sites in northwestern Wisconsin and Upper Peninsula Michigan covered by different habitats. Habitats were characterized every 25 m along the center line of each transect; percentages are calculated from those data.

Habitat type	Michigan Wisconsin	
Upland, mixed conifer-deciduous	19.4	32.2
Upland, deciduous	19.9	19.5
Upland, conifer	3.2	5.0
Lowland, mixed conifer-deciduous	6.8	15.7
Lowland, deciduous	7.0	9.3
Lowland, conifer	19.4	9.3
Young clearcut	7.0	1.3
Older clearcut	11.0	2.0
Forest opening	4.6	2.2
Water, marsh, cattail	1.8	3.7

sampled simultaneously by two observers. We randomly selected observers for the first count on each transect and randomly selected the daily order in which transects (groups of eight segments) were sampled; observers switched transects for the second count so that each segment was sampled by each observer. Two observers conducted most (80%) of the counts in both states; all observers were thoroughly familiar (by sight and sound) with birds of the region.

Various factors influence the probability that individual birds will be detected during a count: observers often differ in abilities to detect certain species; species often differ in period of peak song production; species differ in spring arrival dates; and weather often affects song production and sound propagation. To account, at least partially, for these effects we combined results of the two counts from each segment by taking the higher of the two counts for each species (i.e., the maximum number of individuals recorded for each species; numbers were based on individuals recorded, not on estimated numbers of pairs) and summing across all species to arrive at total numbers of individuals and species. The higher of the two counts for each species was taken as an indication of the minimum number of individuals of that species known to occur on that segment during the breeding season. Even this is likely an underestimate as some individuals probably were not detected on either sampling date.

We used the actual number of individuals recorded for our analyses rather than attempting to calculate a density value (see Verner 1985, Hilden and Järvinen 1989). Density theoretically could be calculated with any one of a variety of

formulae (e.g., Järvinen and Väisänen 1975, Burnham et al. 1981) but there are several assumptions that must be met before these methods can be used. A critical assumption is that distances are measured accurately; such measurements are difficult or impossible to obtain when birds are heard but not seen, as is frequently true during counts in forests and other dense habitats (e.g., Scott et al. 1981, Blake 1992). Without accurate distance estimates, density estimates simply provide an index that may be no better than the original count (Wilson and Bart 1985). Here, we assumed only that number of birds recorded was related to density and probability of detection of birds in the area being sampled (Raphael 1987).

Birds were classified by migratory status (long-distance migrant: generally winters in the tropics; short-distance migrant: generally winters south of the study region, with most (but not all) individuals wintering north of the tropics; permanent resident: individuals are present in study region throughout the year) based on published information (e.g., Terres 1982, American Ornithologists' Union 1983, Ehrlich et al. 1988) and personal observations.

ANALYSES

Based on an analysis of hourly variation in bird detections (Blake et al. 1991), we eliminated the 7th and 8th segments of each transect from our analyses. Hourly declines in bird detections, when significant, generally occurred during the last hour of sampling. We also eliminated from all analyses those segments where logging affected at least 20% of the length of the segment (seven in Wisconsin; nine in Michigan), leaving sample sizes of 53 segments for Wisconsin and 51 for Michigan. For analyses of individual species, we eliminated from consideration all segments on which the species was not recorded in any year, assuming that such segments represented unsuitable habitat for those species. Thus, sample sizes (number of segments) differ among species.

We used repeated-measures analysis of variance (ANOVA) (univariate or multivariate) to examine year-to-year variation in abundance of birds. Time (year) represents a quantitative factor whose effects can be examined in a repeated-measures analysis through polynomial contrasts (Freund et al. 1986). A significant first degree (linear) polynomial would indicate a significant

linear relationship between bird abundance and year (e.g., consistent increase or decrease in abundance over time). A significant second degree (quadratic) polynomial contrast would indicate a significant curvilinear relationship (e.g., increase followed by decrease). Higher level polynomials (cubic, etc.) indicate more complex effects of time.

Annual variation in abundance of migratory groups was based on the sum of individuals within that group. We also examined annual variation after standardizing abundances of species (standardized abundance for a species in one year = [abundance in that year - mean abundance for that species]/standard deviation of abundance of that species) within each migratory group. Standardization eliminated effects of very abundant species (i.e., so that no species carried more weight in the analyses than any other). Results based on standardized data did not differ in any substantial way from unstandardized data (i.e., no change in significance) and we only report results based on the actual abundances.

Data were examined for normality (Wilk-Shapiro test) and homogeneity of variances (Bartlett's test). Transformations (logarithmic, square root, rank) were used when data did not meet assumptions. Univariate repeated measures tests assume compound symmetry; we tested this assumption with a sphericity test and used the more conservative multivariate test when that assumption was not met. We used one-way analyses to examine variation within each state separately and two-way analyses to examine regional variation in population trends. A significant interaction (state-by-year) effect indicated that annual trends in populations for that species or group differed between states.

RESULTS

TOTAL INDIVIDUALS AND SPECIES

We recorded 104 species during this study, including 99 in Michigan and 98 in Wisconsin (Appendix 1). Of these species, 53 were present in Michigan during all years of the study; 55 were recorded in Wisconsin during all years. Species varied in their occurrence among 500-m segments; 20 species in Michigan and 21 in Wisconsin were recorded on at least 75% of all segments, whereas 24 species in Michigan and 26 in Wisconsin occurred on <10% of all segments.

TABLE 2. Species showing significant differences among years in mean number of birds detected per 500-m segment (see text) based on repeated measures ANOVA. Polynomial contrast (PC; see Methods for description) showing greatest significance is indicated by number (1 to 6).

Species	Michigan			Wisconsin		
	Tr. ^a	F	PC	Tr. ^a	F	PC
Permanent residents	root	8.39***	3	ln	3.31**	2
Ruffed Grouse				ln	2.58*	3
Downy Woodpecker	rank	3.77**	1			
Blue Jay	rank	5.65***	3	rank	11.28***	1
Black-capped Chickadee	root	4.52***	1, 3	root	3.80***	1
Red-breasted Nuthatch	rank	6.45***	3	rank ^b	12.02***	2, 3
White-breasted Nuthatch	rank ^b	12.14***	4			
Cedar Waxwing				rank ^b	9.53***	1, 6
Short-distance migrants	ln ^b	4.56***	1	rank	9.64***	3
Northern Flicker	rank	3.02**	1	rank	2.62*	1
Brown Creeper	rank ^b	5.26***	3	rank	4.96***	3
Winter Wren	ln	2.54*	—	ln	4.17***	6
Golden-crowned Kinglet	ln	2.72*	4	root	3.94***	2
Ruby-crowned Kinglet				rank	2.81*	6
Hermit Thrush	root	2.46*	—	root	2.26*	—
American Robin	rank	3.26**	1	rank	5.56***	1
Common Yellowthroat	ln ^b	3.13*	6	ln ^b	3.70**	3
Chipping Sparrow	root ^b	2.85*	1	rank ^b	3.77**	1
Song Sparrow	rank	2.78*	—	root	3.41**	1, 3
Swamp Sparrow	ln ^b	6.95*	4	ln	2.83*	—
White-throated Sparrow	ln	6.74***	1	root ^b	10.48***	1, 4
Brown-headed Cowbird	rank ^b	5.00**	1			
Long-distance migrants	—	7.84***	2	— ^b	26.22***	2, 5
Yellow-bellied Flycatcher	rank	2.62*	2			
Veery	ln	2.98**	3			
Wood Thrush	rank ^b	53.87***	1	rank	8.12***	1
Red-eyed Vireo	root	7.23***	2	root ^b	7.08***	2, 6
Golden-winged Warbler	root	2.72*	4	ln ^b	15.33***	2
Nashville Warbler				root	19.67***	2
Northern Parula				ln	2.29*	5
Chestnut-sided Warbler	ln	2.53*	2			
Black-throated Green Warbler	root	3.66**	2	root	2.95**	2
Ovenbird	root	7.64***	2	root ^b	5.05***	2
Canada Warbler	rank	2.47*	6			
Rose-breasted Grosbeak	ln ^b	4.43**	5	rank	2.64*	5
Indigo Bunting				rank ^b	3.37*	3

^a Transformations used include rank, square root (root), and natural log (ln).

^b Multivariate repeated measures test used (see text).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Mean number of individuals and species present on 500-m segments varied among years in both states (Tables 2, 3).

MIGRATORY GROUPS

Long-distance migrants comprised the largest proportion of species and individuals recorded in both states, followed by short-distance migrants and permanent residents. Mean number of individuals varied among years within each state for all three groups (Fig. 1, Table 2) but patterns of variation differed among groups with-

in each state (Kendall's coefficient of concordance, Michigan: $\chi^2 = 5.32$, $W = 0.32$, $0.50 > P > 0.10$; Wisconsin: $\chi^2 = 2.2$, $W = 0.12$, $0.9 > P > 0.50$).

Long-distance migrants showed sharp declines in abundance from 1987 to 1988 in both states. Subsequent increases returned population levels approximately to levels before 1988. (Michigan had experienced a previous decline from 1985 to 1986; 1992 levels were not back to 1985 levels [see Blake et al. 1992].) This decrease and subsequent increase in abundance is reflected in the

TABLE 3. Results (F values and significance levels) of two-way repeated measures ANOVA, testing for effects of time (annual variation), state (Michigan, Wisconsin), and time by state interaction. Polynomial contrast (PC) showing greatest significance for time effect is indicated by number (1 to 6).

Species	Trs. ^a	Time	State	Time × State	PC
Permanent residents	root	5.52***	6.25*	4.17***	3
Ruffed Grouse	ln	2.36*	2.30	0.05	3
Downy Woodpecker	rank	3.53**	3.58	0.4	1
Blue Jay	root	11.11***	0.66	3.11*	1, 3
Black-capped Chickadee	ln	5.42***	14.22***	3.15**	1
Red-breasted Nuthatch	rank ^b	18.42***	2.36	6.68***	3, 2
Cedar Waxwing	rank	4.58***	4.18*	0.63	1, 4
Short-distance migrants	rank ^b	12.08***	0.0	2.11	1, 3
Yellow-bellied Sapsucker	ln	1.55	0.95	2.32*	—
Northern Flicker	ln	3.87***	5.91*	2.53*	1
Brown Creeper	rank	6.71***	1.46	2.13*	3, 1
Winter Wren	root	5.45***	0.71	1.83	6
Golden-crowned Kinglet	ln	5.13***	1.05	1.48	4
Ruby-crowned Kinglet	rank ^b	4.07**	1.09	1.35	6
Hermit Thrush	root	4.36***	11.30**	0.41	1
American Robin	rank	6.87***	7.16**	1.75	1
Yellow-rumped Warbler	root	2.78*	0.27	0.23	4, 3
Common Yellowthroat	ln ^b	4.30**	0.06	2.44*	4
Chipping Sparrow	rank ^b	6.12***	0.0	0.20	1
Song Sparrow	rank	5.04***	0.64	0.82	1, 3
Swamp Sparrow	ln	2.50*	0.87	2.09	2, 4
White-throated Sparrow	ln	14.75***	1.17	5.13***	1
Brown-headed Cowbird	ln	1.39	2.25	2.15*	2
Purple Finch	rank	3.05**	0.07	0.55	1
Long-distance migrants	— ^b	29.09***	15.24***	4.74***	2, 6
Great Crested Flycatcher	rank	2.18*	6.66*	0.36	1
Veery	ln	2.03	8.23**	1.13	3
Wood Thrush	rank ^b	35.93***	0.18	1.23	1
Solitary Vireo	ln	4.09***	1.25	0.78	1
Red-eyed Vireo	root ^b	10.04***	0.01	2.34*	2, 6
Golden-winged Warbler	ln ^b	21.99***	0.03	1.58	1, 2
Nashville Warbler	root ^b	13.03***	0.67	7.21***	2
Northern Parula	ln	2.03	10.26**	2.55*	5
Chestnut-sided Warbler	root	3.51**	3.58	0.52	1
Black-throated Green Warbler	root	5.72***	5.57*	0.85	2
Blackburnian Warbler	ln	2.08	11.08**	1.32	—
Black-and-white Warbler	root	1.63	6.72*	1.74	—
Ovenbird	root	11.21***	2.03	2.18*	2, 6
Canada Warbler	rank ^b	3.11*	3.78	0.57	6
Rose-breasted Grosbeak	rank ^b	0.52	10.14**	6.70***	—
Indigo Bunting	rank ^b	3.67**	4.42*	0.89	3

^a Transformations used include rank, square root (root), and natural log (ln).

^b Multivariate repeated measures test used (see text).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

significant second degree (quadratic) polynomial in the repeated-measures analyses of variance (ANOVA) (Table 2). Patterns of variation nonetheless differed between regions as seen by the significant interaction effect in the two-way ANOVA results (Table 3).

Short-distance migrants also varied in abundance among years in both states (Fig. 1, Table 2) but there was no difference in abundance between states and no significant interaction effect

(Table 3), indicating that patterns of variation were comparable in both areas. Declines in abundance were apparently more consistent, however, in Michigan (significant linear contrast) than in Wisconsin (significant cubic contrast). Abundances of long-distance and short-distance migrants were not well correlated in either state (Michigan, $r = 0.53$; Wisconsin, $r = 0.42$).

Trends in abundance of permanent residents (Fig. 1) differed somewhat between states (Tables

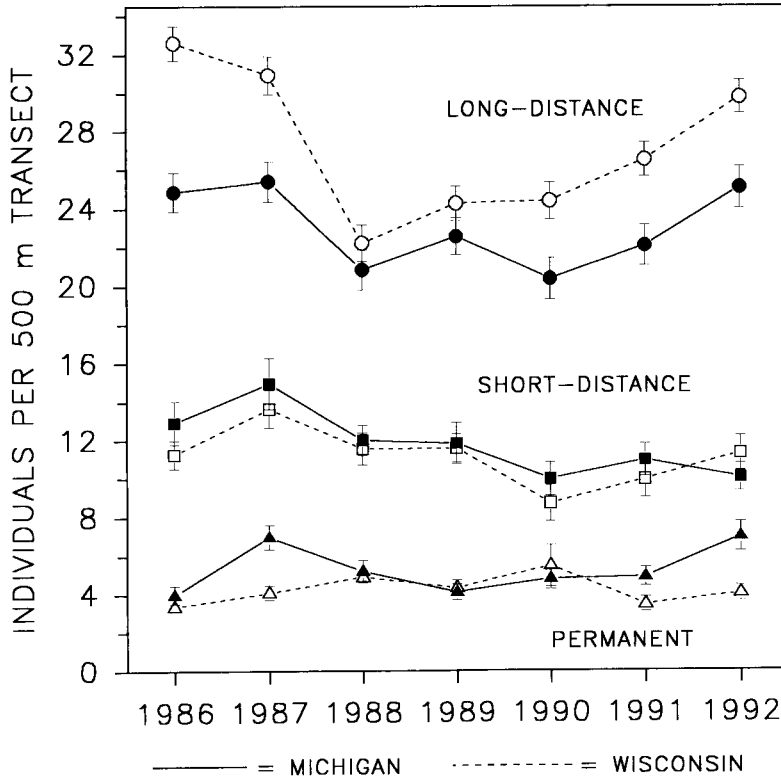


FIGURE 1. Mean (and SE) number of long-distance migrant, short-distance migrant, and permanent resident birds recorded per 500-m segment on study sites in Michigan and Wisconsin, 1986-1992.

2, 3). Permanent residents declined in abundance from 1987 to 1988 in Michigan, paralleling changes in migrant abundance, but increased in abundance in Wisconsin during the same period (Fig. 1). Abundance of permanent residents was poorly or negatively correlated with abundance of migrants (Michigan: $r = 0.48$ with long-distance and $r = 0.28$ with short-distance migrants; Wisconsin: $r = -0.74$ with long-distance and $r = -0.13$ with short-distance migrants).

INDIVIDUAL SPECIES

Ten of 21 (48%) long-distance migrants in Michigan and 9 of 20 (45%) in Wisconsin (Figs. 2, 3) varied in abundance among years (Table 2), including four that varied only in Michigan, three that varied only in Wisconsin, and six that varied in abundance among years in both states. Several species varied in similar ways among years between states (e.g., Great Crested Flycatcher, $r = 0.96$ [scientific names are in Appendix 1]) whereas others displayed very different patterns between states (e.g., Rose-breasted Grosbeak, $r =$

-0.77). Overall, trends in abundance of most species did not differ significantly between states; only Nashville Warbler and Rose-breasted Grosbeak showed highly significant interaction effects and three others showed weaker effects (Table 3). Most long-distance migrants that varied in abundance among years declined in abundance, particularly from 1987 to 1988. Species showing particularly strong declines during this period included Red-eyed Vireo, Nashville Warbler, and Ovenbird (Fig. 3). Declines in abundance were followed by increases for many species although patterns of increase varied among species and between states (e.g., compare Red-eyed Vireo and Ovenbird). In some cases, declines have not been followed by increases (e.g., Wood Thrush, Mourning Warbler, Chesnut-sided Warbler). Whereas most species declined in abundance during the middle part of this study, Golden-winged Warbler increased sharply in abundance from 1986 to 1987-1989 and then sharply declined. Overall, the complex nature of year-to-year variation is seen in the significance of higher

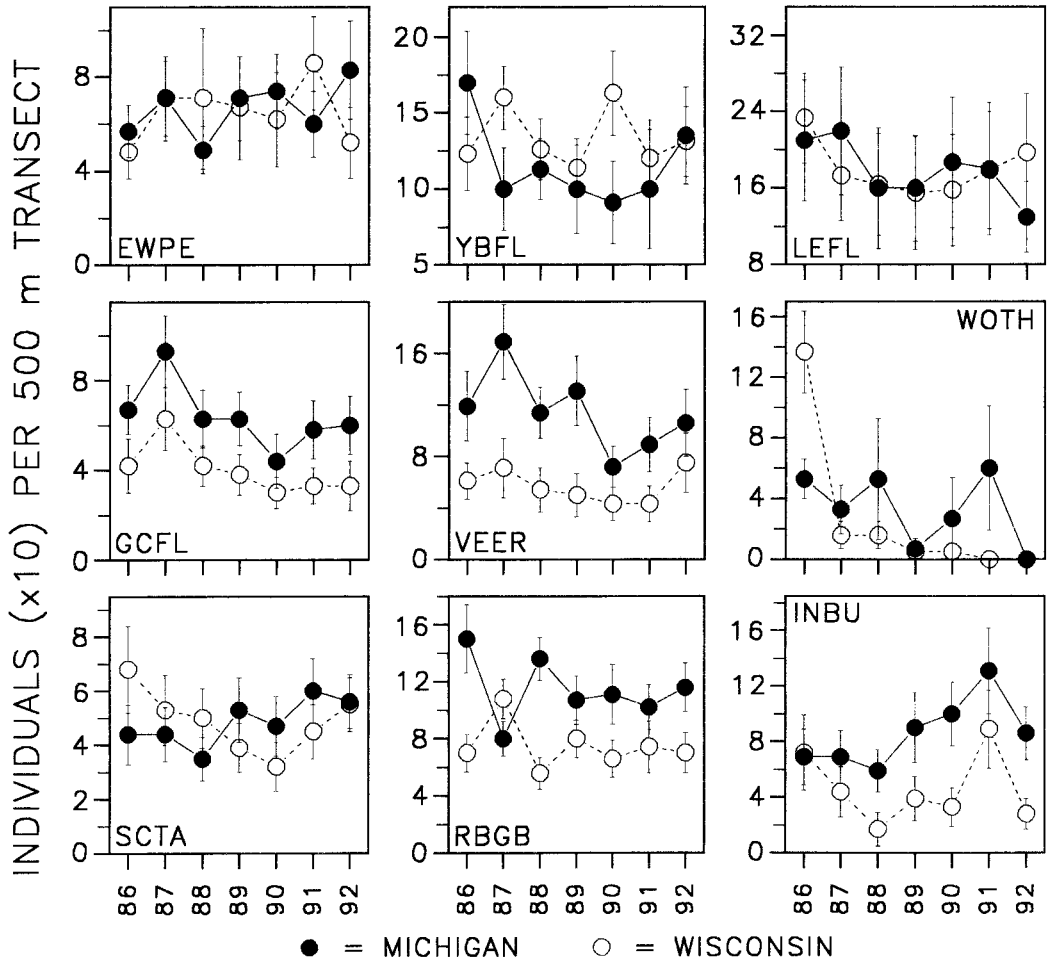


FIGURE 2. Mean (and SE) number of individuals of nine common long-distance migrants recorded on study sites in Michigan and Wisconsin, 1986–1992. EWPE = Eastern Wood-Pewee; YBFL = Yellow-bellied Flycatcher; LEFL = Least Flycatcher; GCFL = Great Crested Flycatcher; VEER = Veery; WOTH = Wood Thrush; SCTA = Scarlet Tanager; RBGB = Rose-breasted Grosbeak; INBU = Indigo Bunting.

level contrasts shown by many species (Tables 2, 3).

Of 16 short-distance migrants examined (Fig. 4), only Yellow-bellied Sapsucker, Yellow-rumped Warbler, and Purple Finch showed no significant variation in abundance from year-to-year within either state (Table 2) when states were examined separately. Patterns of variation were relatively similar between states for many species (e.g., Chipping Sparrow, $r = 0.98$) but were dissimilar for others (e.g., Ruby-crowned Kinglet, $r = -0.27$; Fig. 4). Between-state comparisons demonstrated few interaction effects, including only one strong effect (White-throated

Sparrow, Table 3) reflecting the overall similarity between states in trends in abundance of short-distance migrants. In comparison with long-distance migrants, analyses demonstrated significant linear effects for many short-distance migrants, reflecting the general decrease in abundance for these species (Fig. 1).

Nine permanent residents were examined for annual variation in abundance (Fig. 5). Five species varied significantly among years in Michigan, five varied in Wisconsin, and three species varied in abundance among years in both states (Tables 2, 3). The extent to which variation in one state paralleled that in the other differed con-

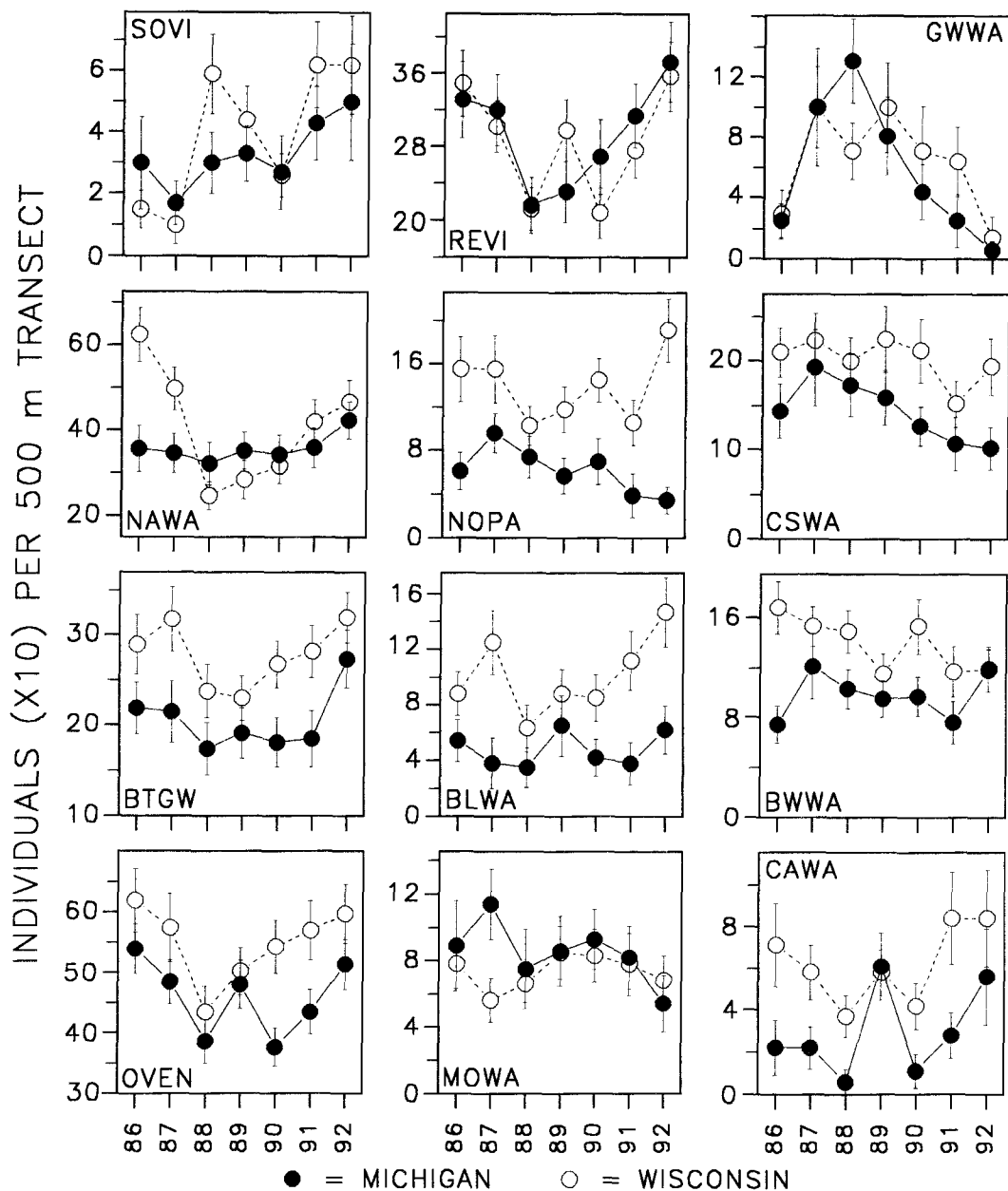


FIGURE 3. Mean (and SE) number of individuals of 12 common long-distance migrants (vireos and warblers) recorded on study sites in Michigan and Wisconsin, 1986–1992. SOVI = Solitary Vireo; REVI = Red-eyed Vireo; GWWA = Golden-winged Warbler; NAWA = Nashville Warbler; NOPA = Northern Parula; CSWA = Chestnut-sided Warbler; BTGW = Black-throated Green Warbler; BLWA = Blackburnian Warbler; BWBA = Black-and-white Warbler; OVEN = Ovenbird; MOWA = Mourning Warbler; CAWA = Canada Warbler.

siderably among species. Downy Woodpeckers, for example, showed a similar decline in abundance in both states (Fig. 5, $r = 0.84$); two-way ANOVA indicated a strong year effect but no

interaction effect (Table 3). Red-breasted Nuthatches, in contrast, showed a strong interaction effect (Table 3, Fig. 5). Overall, three of six permanent resident species showed significant inter-

actions between state and year, suggesting that patterns of annual variation often differed between the two regions. That species showed little similarity in patterns of variation helps account for the fact that permanent residents, as a group (Fig. 1), showed few consistent changes in abundance among years.

In summary, of 46 species tested in Michigan, 27 showed year-to-year variation at a probability level of $P < 0.05$, 16 species at $P < 0.01$, and 9 at $P < 0.001$. Similar numbers for the 44 species tested in Wisconsin were 26, 18, and 14. The number of significant results is significantly greater than might be expected by chance, given the number of tests performed.

DISCUSSION

Populations of many bird species breeding in northwestern Wisconsin and Upper Peninsula Michigan varied in abundance from 1986 through 1992. All groups (long-distance migrants, short-distance migrants, permanent residents) varied in abundance among years but patterns of variation often differed among groups and between states. Population trends of short-distance migrants were remarkably similar between sites in Wisconsin and Michigan but greater differences were noted between states for long-distance migrants and permanent residents. Thus, although changes in total abundance of birds were comparable between states, considerable variation in local vs. regional patterns existed when changes in abundance were viewed at migratory group or individual species levels.

The extent to which groups within and between regions differ in temporal patterns of abundance is an important consideration when attempting to understand conservation implications of observed population changes. As this and various other studies (e.g., James et al. 1992, Sauer and Droege 1992, and others in Hagan and Johnston 1992) have made clear, population fluctuations of migrant and non-migrant species often differ markedly both within and among regions. Given the current level of concern regarding pop-

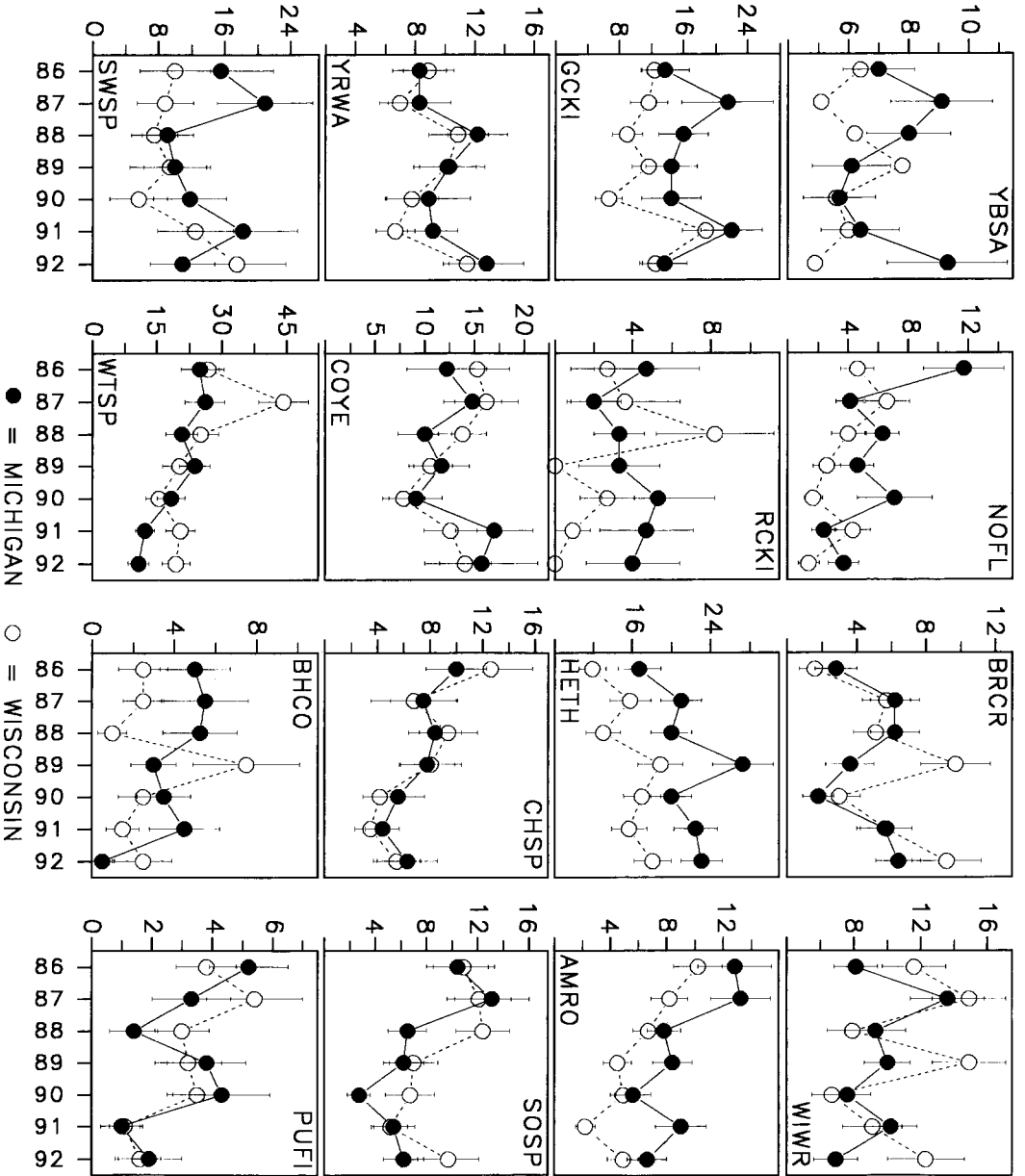
ulation declines of many species, it is important to bear in mind that our perceptions of population change depend on the scale, both temporal (number of years) and spatial, at which those fluctuations are observed. Further, differences in trends between migratory groups (i.e., combining species by migratory status) may not reflect simple breeding versus wintering ground effects. Declines in abundance of long-distance migrants that were not matched by permanent residents during the early part of this study might, for example, have suggested wintering ground effects (e.g., habitat loss in the tropics). The subsequent increase in abundance of many long-distance migrants tends to refute that possibility.

Lack of similarity among groups and between regions in patterns of annual variation reflect the fact that species differ in their response to factors (e.g., resource abundance, habitat change, weather) that influence populations. Among migrant species, some of the most dramatic fluctuations in this study were seen in numbers of Red-eyed Vireos, Nashville Warblers, and Ovenbirds. Although fluctuations in abundance in one state sometimes closely tracked that in the other state (e.g., Red-eyed Vireo from 1986 to 1988), there were substantial differences in other cases (e.g., Nashville Warbler). Permanent residents, whose numbers often are primarily affected by events and conditions during winter (e.g., Holmes et al. 1986, Sauer and Droege 1990, Arcese et al. 1992), varied in different ways between states, suggesting that conditions differed between the two study regions. Further, changes in abundance of permanent residents did not closely parallel those shown by either migratory group in either state, again suggesting that different factors influence different groups or that different groups and species respond in different ways to the same factor (see Brown and Heske 1990). In contrast, Johnston and Hagan (1992) found that population trends of permanent residents and migrants often were positively correlated; they suggested that both groups might be responding to the same factor(s). Differences in population trends ob-

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FIGURE 4. Mean (and SE) number of individuals of 16 common short-distance migrants recorded on study sites in Michigan and Wisconsin, 1986–1992. YBSA = Yellow-bellied Sapsucker; NOFL = Northern Flicker; BRGR = Brown Creeper; WIWR = Winter Wren; GCKI = Golden-crowned Kinglet; RCKI = Ruby-crowned Kinglet; HETH = Hermit Thrush; AMRO = American Robin; YRWA = Yellow-rumped Warbler; COYE = Common Yellowthroat; CHSP = Chipping Sparrow; SOSP = Song Sparrow; SWSP = Swamp Sparrow; WTSP = White-throated Sparrow; BHCO = Brown-headed Cowbird; PUF1 = Purple Finch.

INDIVIDUALS (X10) PER 500 m TRANSECT



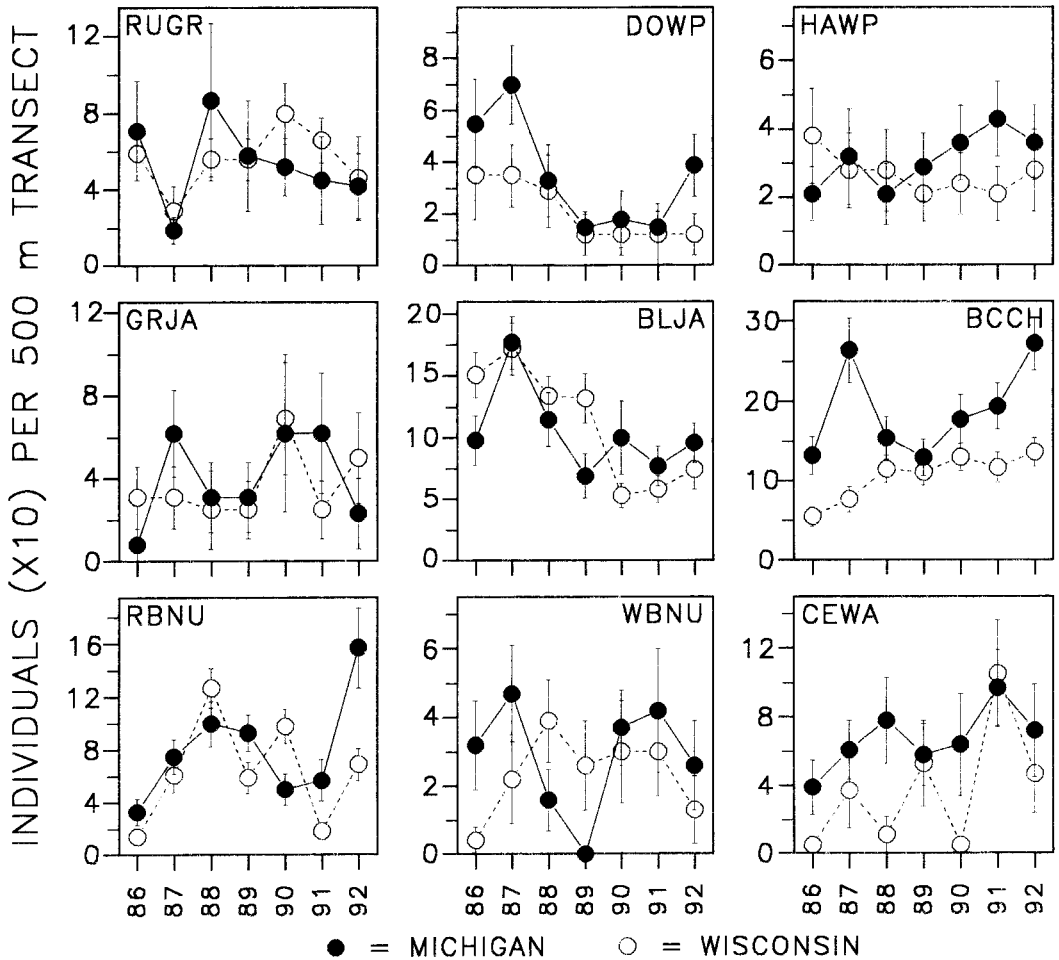


FIGURE 5. Mean (and SE) number of individuals of nine common permanent residents recorded on study sites in Michigan and Wisconsin, 1986–1992. RUGR = Ruffed Grouse; DOWP = Downy Woodpecker; HAWP = Hairy Woodpecker; GRJA = Gray Jay; BLJA = Blue Jay; BCCH = Black-capped Chickadee; RBNU = Red-breasted Nuthatch; WBNU = White-breasted Nuthatch; CEWA = Cedar Waxwing.

served in regions that support comparable habitats and that are relatively close geographically (i.e., as in this study), illustrate the spatial complexity of population variation. They further reinforce the need for comparative, concurrent studies if changes in abundance of species are to be properly evaluated. Changes occurring in one part of a species' range may not be representative of trends in other regions (James et al. 1992).

Population declines of breeding birds have been variously attributed to conditions and events that affect birds on breeding grounds, during migration, and/or on nonbreeding grounds (reviews in Askins et al. 1990, Finch 1991). Much of the

annual variation in bird abundances observed during this study likely occurred in response to altered conditions on the breeding grounds (see also Holmes and Sherry 1988, Blake et al. 1992, Robinson 1992, Sherry and Holmes 1992, Böhning-Gaese et al. 1993). Large changes in abundance occurred over the span of one to several years; such a rapid change is unlikely to be caused by alterations in tropical, wintering habitats. In contrast, changes in weather can have dramatic and rapid consequences for bird populations (Robbins et al. 1986, Holmes and Sherry 1988, Virkkala 1991, Faaborg and Arendt 1992).

Declines in abundance that occurred during

the first few years of this study likely were in response to a series of severe droughts that affected most of the upper midwest, including both regions where this study was conducted (Blake et al. 1992). Such a general response by many species, including both migratory and nonmigratory species, would not be likely to occur in response to conditions or events in tropical habitats. Abundances of many species reached low points in 1988, the year of the most severe drought. The fact that populations of many species have increased in abundance over the past few years, even reaching levels seen at the onset of this study, lends support to the argument that most species were affected by breeding ground effects, such as drought.

Although environmental conditions (e.g., drought, temperature) likely influenced population abundances, other factors, including successional changes in habitat, probably influenced abundance of several species, as has been noted by other studies (e.g., Holmes and Sherry 1988). The increase in abundance of Indigo Buntings in Michigan may have occurred, for example, in response to the clearing of the antenna right-of-way. The right-of-way was cleared in 1984 (and has been kept clear of tall vegetation since) and subsequent development of suitable breeding habitat has favored species such as the Indigo Bunting. Conversely, continued growth of early successional vegetation on previously logged areas may account for declines in abundance of several species (e.g., Song Sparrow, Chestnut-sided Warbler) associated with early regrowth. Declines in abundance of migrants that breed in brushy habitats appears, however, to be more than a local phenomenon as such changes have been noted by others as well (Hagan et al. 1992, Sauer and Droege 1992, Witham and Hunter 1992). Changes observed in our region may be a reflection of more widespread changes in populations of some species. Striking declines also were noted for the Wood Thrush, particularly in Wisconsin sites, which are near the northern limit of the Wood Thrush distribution (AOU 1983). Such fluctuations may reflect conditions elsewhere in the species range. Several studies have suggested that Wood Thrush populations may be seriously affected by loss of tropical (wintering) habitats (e.g., Rappole et al. 1992, Powell et al. 1992).

Conditions on breeding or wintering grounds receive the greatest attention when discussing causes of population variation; few studies con-

sider events during migration. Yet, migratory species also must contend with factors that influence survival during movements to and from breeding grounds (Morse 1980, Moore and Simons 1992). Various examples of large-scale mortality during migration that have occurred as a result of severe weather in spring have been noted (see Morse 1980 for examples); such disasters can severely depress breeding bird densities for several years (Zumeta and Holmes 1978). A brief period of cold, wet weather during early May 1986 in Michigan had a severe negative effect on reproductive success of Tree Swallows (Beaver et al. 1988) and could have negatively affected populations of other species in the Michigan region as well. Abundance was, overall, considerably lower in June 1986 than in June 1985 in Michigan (Blake et al. 1992). Migration is an energetically expensive period so that if food supplies or opportunities for foraging are limited (i.e., loss of suitable habitats along migration routes) survival may be affected (Loria and Moore 1990; Moore and Young 1991; see also Stiles 1988; Loiselle and Blake 1991, 1992).

Long-term changes in abundance of breeding bird populations will reflect, in most cases, events and conditions that occur during both breeding and nonbreeding seasons. Short-term fluctuations (i.e., year to year) in migratory species are, by contrast, more likely to reflect breeding ground or migratory period influences. Separating the effects of breeding and nonbreeding season conditions is, however, difficult in many cases, particularly for migrants (Finch 1991). This study was designed to explore the extent of variation present among birds breeding in northern hardwood forests. The causes of that variation were not directly investigated (i.e., there was no experimental manipulation of communities; demographics of populations were not investigated) so that our discussion of factors promoting population variation is necessarily speculative. For example, the mechanisms by which changed weather conditions might have affected populations of birds in our study regions are varied. Changes in resource (e.g., insect) abundance may affect reproductive success, altering patterns of present and future habitat use (i.e., if unsuccessful breeders do not return in subsequent years). Alternatively, changes in detection probability (i.e., rates of song production), if related to annual differences in weather patterns, might suggest variation in abundance when what is actu-

ally being detected are changes in detection probability or frequency.

Holmes et al. (1986) described two basic approaches to investigations of population variation: (1) simultaneously sample birds on many plots representing different habitats; or (2) intensively sample birds on one to several plots for many years. Clearly, intensive study of many plots over many years would be ideal but not possible under most circumstances of time and money. Our approach falls somewhere between the two approaches described above: we sampled many plots representing various habitats over a moderately long period. Thus, this study was relatively extensive, rather than intensive; the area covered in each state was considerably larger than that covered in many studies on population trends but much smaller than the statewide or geographic region approach of others (e.g., Breeding Bird Survey; Robbins et al. 1986). Intensive, single-plot studies provide detailed data on the population changes at a local scale but such changes do not necessarily reflect population changes at more regional levels (Holmes and Sherry 1988, Witham and Hunter 1992). By comparing results from two geographically distant regions but with similar habitats, one can better assess the extent or generality of observed patterns of variation (James et al. 1992). Such larger scale studies are a necessary complement to more intensive studies.

Populations of birds typically fluctuate in abundance on various temporal scales. Separating shorter-term fluctuations in abundance that are a natural component of population dynamics from longer-term trends that suggest fundamental changes in a species' abundance is of critical importance for conservation. Migratory birds are a particularly challenging group because populations are influenced by conditions in both temperate and tropical regions. Local, breeding-ground effects often cause large changes in abundance from year to year, as seen in this study. Similarly, substantial annual fluctuations in abundance may occur among populations on wintering (tropical) grounds (Blake and Loiselle 1992). Such fluctuations may mask more subtle, longer-term changes in populations. Gradual loss of breeding or nonbreeding habitat may result in chronic declines in populations that become apparent only after many years. A further problem arises because wintering sites for specific breeding populations largely are unknown. Studies are

urgently needed that link specific breeding and wintering populations if dynamics of migratory birds are to be understood.

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APPENDIX 1. Mean number individuals per 500 m segment (rounded to nearest 0.1) for species recorded on at least five segments (i.e., $\approx 10\%$ of total) in Michigan and Wisconsin, 1986–1992. Additional (rare) species are listed at the end. n = total number of separate segments the species was recorded on during at least one year. Taxonomic sequence follows American Ornithologists' Union (1983, and supplements). Letter codes are given for species mentioned in text. + = <0.05 birds/segment.

English name, code	Scientific name	Michigan (n = 51)					Wisconsin (n = 53)										
		n	86	87	88	89	90	91	92	n	86	87	88	89	90	91	92
Sharp-shinned Hawk	<i>Accipiter striatus</i>	10			0.1	0.2	0.2	0.2	0.2	0.4	2			0.5			
Broad-winged Hawk	<i>Buteo platypterus</i>	14	0.2	0.1		0.2	0.3	0.2	0.2	0.4	12	0.3	0.2	0.1	0.3	0.1	0.1
Ruffed Grouse, RUGR	<i>Bonasa umbellus</i>	31	0.7	0.2	0.9	0.6	0.5	0.5	0.4	0.4	41	0.6	0.3	0.6	0.6	0.8	0.7
American Woodcock	<i>Scolopax minor</i>	16	0.5	0.7	0.6	0.3	0.1	0.5	0.2	0.8	8		0.5	0.1	0.4	0.3	0.4
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	11	0.2	0.5	0.1	0.1		0.3		1	1				1.0		
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	7	0.3	0.3	0.4	0.1		0.1		1	1		1.0				
Barred Owl	<i>Strix varia</i>	3	0.7	0.3						7	0.2		0.2	0.2	0.1	0.1	0.3
Chimney Swift	<i>Chaetura pelagica</i>	3	0.3			0.7		0.7		7		1.7	0.3	0.3		0.1	
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	12	0.4			0.3	0.4	0.3	0.2	5		0.2		0.2	0.2		0.4
Yellow-bellied Sapsucker, YBSS	<i>Sphyrapicus varius</i>	44	0.7	0.9	0.8	0.6	0.6	0.6	0.9	46	0.6	0.5	0.6	0.8	0.6	0.6	0.5
Downy Woodpecker, DOWP	<i>Picoides pubescens</i>	33	0.6	0.7	0.3	0.2	0.2	0.2	0.4	17	0.4	0.4	0.3	0.1	0.1	0.1	0.1
Hairy Woodpecker, HAWP	<i>Picoides villosus</i>	28	0.2	0.3	0.2	0.3	0.4	0.4	0.4	29	0.4	0.3	0.3	0.2	0.2	0.2	0.3
Black-backed Woodpecker	<i>Picoides arcticus</i>	5	0.2			0.6	0.4	0.2	0.4	4			1.0	1.0			
Northern Flicker, NOFL	<i>Dryobates auratus</i>	41	1.2	0.4	0.6	0.5	0.7	0.2	0.4	35	0.5	0.7	0.4	0.3	0.2	0.4	0.1
Pileated Woodpecker	<i>Dryocopus pileatus</i>	13	0.1	0.2	0.1	0.2	0.2	0.1	0.4	16	0.3	0.1	0.1	0.1	0.1	0.1	0.3
Olive-sided Flycatcher	<i>Contopus borealis</i>	12	0.3	0.8	0.1	0.1		0.1	0.2	9	0.2	0.1	0.3	0.6			0.2
Eastern Wood-Pewee, EWPE	<i>Contopus virens</i>	35	0.6	0.7	0.5	0.7	0.7	0.6	0.8	21	0.5	0.7	0.7	0.7	0.6	0.9	0.5
Yellow-bellied Flycatcher, YBFL	<i>Empidonax flaviventris</i>	23	1.7	1.0	1.1	1.0	0.9	1.0	1.4	35	1.2	1.6	1.3	1.1	1.6	1.2	1.3
Least Flycatcher, LEFL	<i>Empidonax minimus</i>	30	2.1	2.2	1.6	1.6	1.9	1.8	1.3	33	2.3	1.7	1.6	1.6	1.6	1.8	2.0
Great Crested Flycatcher, GCFL	<i>Myiarchus crinitus</i>	43	0.7	0.9	0.6	0.6	0.6	0.6	0.6	40	0.4	0.6	0.4	0.4	0.3	0.3	0.3
Tree Swallow	<i>Tachycineta bicolor</i>	10	0.2	1.2	0.2	0.2		0.2		11		0.7	1.0	0.5	0.8	1.1	0.4
Gray Jay, GRJA	<i>Perisoreus canadensis</i>	13	0.1	0.6	0.3	0.3	0.6	0.6	0.2	16	0.3	0.3	0.3	0.3	0.7	1.3	0.5
Blue Jay, BLJA	<i>Cyanocitta cristata</i>	48	1.0	1.8	1.2	0.7	1.0	0.8	1.0	53	1.5	1.7	1.3	1.3	0.5	0.6	0.7
American Crow	<i>Corvus brachyrhynchos</i>	18	0.5	0.7	0.4	0.1		0.1		8	0.4	0.1	0.9	0.3			
Common Raven	<i>Corvus corax</i>	27	0.1	0.6	0.1	0.2	0.3	0.1	0.3	9	0.2	0.2	0.2	0.3	0.4	0.2	
Black-capped Chickadee, BCCH	<i>Parus atricapillus</i>	50	1.3	2.6	1.5	1.3	1.8	1.9	2.7	53	0.6	0.8	1.2	1.1	1.3	1.2	1.4
Boreal Chickadee	<i>Parus hudsonicus</i>	11	0.3	0.1	0.4	0.3	0.2	0.4	0.8	5	0.2	0.4	0.4		0.4		
Red-breasted Nuthatch, RBNU	<i>Sitta canadensis</i>	19	0.3	0.8	1.0	0.9	0.5	0.6	1.6	49	0.1	0.6	1.3	0.6	1.0	0.2	0.7
White-breasted Nuthatch, WBNU	<i>Sitta carolinensis</i>	40	0.3	0.5	0.2	0.4	0.4	0.4	0.3	23	+	0.2	0.4	0.3	0.3	0.3	0.1
Brown Creeper, BRCR	<i>Certhia americana</i>	39	0.3	0.6	0.6	0.4	0.2	0.6	0.6	37	0.2	0.6	0.5	1.0	0.3	0.6	0.9
Winter Wren, WTWR	<i>Troglodytes troglodytes</i>	42	0.8	1.4	0.9	1.0	0.8	1.0	0.7	43	1.2	1.5	0.8	1.5	0.7	0.9	1.2
Golden-crowned Kinglet, GCKI	<i>Regulus striata</i>	40	1.4	2.2	1.6	1.5	1.5	2.2	1.4	42	1.2	1.2	0.9	1.2	0.7	1.9	1.3
Ruby-crowned Kinglet, RCKI	<i>Regulus calendula</i>	15	0.5	0.2	0.3	0.3	0.5	0.5	0.4	11	0.3	0.4	0.8				
Eastern Bluebird	<i>Sialia sialis</i>	6	1.0	0.7	0.2			0.5		1		2.0					
Veery, VEER	<i>Catherpes fuscescens</i>	36	1.2	1.7	1.1	1.3	0.7	0.9	1.1	28	0.6	0.7	0.5	0.5	0.4	0.4	0.8

APPENDIX 1. Continued.

English name, code	Scientific name	Michigan (n = 51)					Wisconsin (n = 53)											
		n	86	87	88	89	90	91	92	n	86	87	88	89	90	91	92	
Hermit Thrush, HETH	<i>Catharus guttatus</i>	51	1.7	2.1	2.0	2.7	2.0	2.3	2.3	2.3	53	1.2	1.6	1.3	1.9	1.7	1.6	1.8
Wood Thrush, WOTH	<i>Hylocichla mustelina</i>	15	0.5	0.3	0.5	0.1	0.3	0.6			19	1.4	0.2	0.2	0.1	0.1		
American Robin, AMRO	<i>Turdus migratorius</i>	50	1.3	1.3	0.8	0.8	0.6	0.9	0.7	51	1.0	0.8	0.7	0.5	0.5	0.2	0.5	
Gray Catbird	<i>Dumetella carolinensis</i>	7	0.1	0.7		0.1	0.1			6	0.5	0.5	0.2					
Brown Thrasher	<i>Toxostoma rufum</i>	11	0.5	0.5	0.4	0.5	0.2	0.1		5	0.4		0.2	0.4				
Cedar Waxwing, CEWA	<i>Bombicilla cedrorum</i>	36	0.4	0.6	0.8	0.6	1.0	0.7		19	0.1	0.4	0.1	0.5	0.1	1.1	0.5	
European Starling	<i>Sturnus vulgaris</i>	5	0.4	1.2			0.2	0.2	0.2	1	1.0							
Solitary Vireo, SOVI	<i>Vireo solitarius</i>	30	0.3	0.2	0.3	0.3	0.3	0.4	0.5	39	0.2	0.1	0.6	0.4	0.3	0.6	0.6	
Yellow-throated Vireo	<i>Vireo flavifrons</i>	11	0.2		0.2	0.2		0.5		4	0.3	0.5	0.3		0.3		0.3	
Philadelphia Vireo	<i>Vireo philadelphicus</i>	4	0.3		0.3	0.3			0.3	5	0.2	0.2	0.2	0.2				
Red-eyed Vireo, REVI	<i>Vireo olivaceus</i>	51	3.3	3.2	2.2	2.3	2.7	3.1	3.7	51	3.5	3.0	2.1	3.0	2.1	2.8	3.6	
Golden-winged Warbler, GWWA	<i>Vermivora chrysoptera</i>	16	0.3	1.0	1.3	0.8	0.4	0.3	0.1	14	0.3	1.0	0.7	1.0	0.7	0.6	0.1	
Tennessee Warbler	<i>Vermivora peregrina</i>	8	0.3	0.6	0.6	0.3				32	1.0	0.4	0.2	0.2	0.1	0.1	+	
Nashville Warbler, NAWA	<i>Vermivora ruficapilla</i>	46	3.6	3.5	3.2	3.5	3.4	3.6	4.2	51	6.3	5.0	2.5	2.9	3.2	4.2	4.7	
Northern Parula, NOPA	<i>Parula americana</i>	23	0.6	1.0	0.7	0.6	0.7	0.4	0.4	33	1.6	1.6	1.0	1.2	1.5	1.1	1.9	
Yellow Warbler	<i>Dendroica petechia</i>	5	0.8	0.4	0.2			1.0		10	0.4	0.8	0.5	0.7	0.5	0.6	0.2	
Chestnut-sided Warbler, CSWA	<i>Dendroica pensylvanica</i>	41	1.4	1.9	1.7	1.6	1.3	1.1	1.0	48	2.1	2.2	2.0	2.3	2.1	1.5	1.9	
Magnolia Warbler	<i>Dendroica magna</i>	11	0.3		0.2	0.3	0.2	0.4	0.5	24	0.3	0.2	+	0.3	0.4	0.3	0.5	
Cape May Warbler	<i>Dendroica tigrina</i>	14	0.4	0.5	0.1		0.1		0.4	17	0.9	0.5	0.1		0.1	0.1		
Yellow-rumped Warbler, YRWA	<i>Dendroica coronata</i>	36	0.8	0.8	1.2	1.0	0.9	0.9	1.3	46	0.9	0.7	1.1	1.0	0.8	0.7	1.2	
Black-throated Green Warbler, BTGW	<i>Dendroica virens</i>	47	2.2	2.2	1.7	1.9	1.8	1.9	2.7	50	2.9	3.2	2.4	2.3	2.7	2.8	3.2	
Blackburnian Warbler, BLWA	<i>Dendroica fusca</i>	26	0.5	0.4	0.4	0.7	0.4	0.4	0.6	40	0.9	1.3	0.6	0.9	0.9	1.1	1.5	
Pine Warbler	<i>Dendroica pinus</i>	7	0.7	0.4	0.1				0.1	10	0.5	0.5	0.3		0.2	0.4		
Palm Warbler	<i>Dendroica palmarum</i>	3	0.3					1.3		8	1.0	1.1	0.5	0.4	0.1	0.3	0.3	
Bay-breasted Warbler	<i>Dendroica castanea</i>	2	1.0						0.5	6	0.8		0.2					
Black-and-white Warbler, BWWA	<i>Mniotilta varia</i>	38	0.7	1.2	1.0	1.0	1.0	0.8	1.2	47	1.7	1.5	1.5	1.2	1.5	1.2	1.2	
American Redstart	<i>Setophaga ruticilla</i>	10	0.2	0.2	0.3	0.1	0.1		0.3	16	0.2	0.3	0.2	0.2	0.2	0.2	0.1	
Ovenbird, OVEN	<i>Seiurus aurocapillus</i>	51	5.4	4.8	3.9	4.8	3.8	4.4	5.1	53	6.2	5.7	4.3	5.0	5.4	5.7	6.0	

APPENDIX 1. Continued.

English name, code	Scientific name	Michigan (n = 51)					Wisconsin (n = 53)											
		n	86	87	88	89	90	91	92	n	86	87	88	89	90	91	92	
Northern Waterthrush	<i>Seiurus noveboracensis</i>	8	0.1	0.4	0.3	1.0	0.3	0.1			18	0.3	0.3	0.2	0.3	0.4	0.6	0.8
Connecticut Warbler	<i>Oporornis agilis</i>	6	0.8	1.0	0.7	0.3	0.3			14	0.4	0.4	0.4	0.1	0.5	0.2		
Mourning Warbler, MOWA	<i>Oporornis philadelphia</i>	28	0.9	1.1	0.8	0.9	0.9	0.8	0.5	41	0.8	0.6	0.7	0.9	0.8	0.8	0.7	
Common Yellowthroat, COYE	<i>Geothlypis trichas</i>	23	1.2	1.5	1.0	1.2	0.9	1.7	1.6	34	1.5	1.6	1.4	1.1	0.8	1.3	1.4	
Canada Warbler, CAWA	<i>Wilsonia canadensis</i>	18	0.2	0.2	0.1	0.6	0.1	0.3	0.6	38	0.7	0.6	0.4	0.6	0.4	0.8	0.8	
Scarlet Tanager, SCTA	<i>Piranga olivacea</i>	43	0.4	0.4	0.4	0.5	0.5	0.6	0.6	38	0.7	0.5	0.5	0.4	0.3	0.5	0.6	
Rose-breasted Grosbeak, RBGB	<i>Pheucticus ludovicianus</i>	44	1.5	0.8	1.4	1.1	1.1	1.0	1.2	50	0.7	1.1	0.6	0.8	0.7	0.7	0.7	
Indigo Bunting, INBU	<i>Passerina cyanea</i>	29	0.7	0.7	0.6	0.9	1.0	1.3	0.9	18	0.7	0.4	0.2	0.4	0.3	0.9	0.3	
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	14	1.0	0.4	0.6	0.6	0.3	0.4	0.5	2								
Chipping Sparrow, CHSP	<i>Spizella passerina</i>	32	1.0	0.8	0.8	0.8	0.6	0.4	0.6	31	1.1	1.2	1.2	0.7	0.7	0.5	1.0	
Song Sparrow, SOSP	<i>Melospiza melodia</i>	26	1.0	1.3	0.7	0.6	0.3	0.5	0.6	33	1.1	1.2	1.2	0.7	0.7	0.5	1.0	
Lincoln's Sparrow	<i>Melospiza lincolni</i>	2	1.0							8	0.3	1.0	0.1	0.1		0.1	0.9	
Swamp Sparrow, SWSP	<i>Melospiza georgiana</i>	11	1.6	2.1	0.9	1.0	1.2	1.8	1.1	16	1.0	0.9	0.8	0.9	0.6	1.3	1.8	
White-throated Sparrow, WTSP	<i>Zonotrichia albicollis</i>	41	2.5	2.6	2.1	2.4	1.8	1.2	1.1	47	2.7	4.4	2.5	2.0	1.6	2.0	1.9	
Dark-eyed Junco	<i>Junco hyemalis</i>	6	0.3	0.5	1.7	0.3	0.7	0.3	0.2	9	0.6	0.3	0.8	0.2	0.4	0.2		
Common Grackle	<i>Quiscalus quiscula</i>	11	1.2	1.8	0.4	0.6	0.5	0.9	0.4	8	0.8	1.4	2.4	0.8	0.5	1.4	1.1	
Brown-headed Cowbird, BHCO	<i>Molothrus ater</i>	20	0.5	0.6	0.6	0.3	0.4	0.5	0.1	20	0.3	0.3	0.1	0.8	0.3	0.2	0.3	
Northern Oriole	<i>Icterus galbula</i>	8	0.3	0.1	0.1	0.3	0.1	0.5	0.4	5	0.2	0.4	0.4		0.2	0.6	0.2	
Purple Finch, PUF1	<i>Carpodacus purpureus</i>	21	0.5	0.3	0.1	0.4	0.4	0.1	0.2	37	0.4	0.5	0.3	0.3	0.4	0.1	0.2	
White-winged Crossbill	<i>Loxia leucoptera</i>	5					0.8			2								
Pine Siskin	<i>Carduelis pinus</i>									10			0.1	0.2	0.1	3.6		
American Goldfinch	<i>Carduelis tristis</i>	23	0.2	0.5	0.1	0.2	0.5	0.1	0.3	30	0.1	0.2	0.5	0.5	0.3	0.2	0.3	
Evening Grosbeak	<i>Coccothraustes vespertina</i>	10		0.4	0.4	0.4		0.1	0.1	8	0.5	0.8		0.4		0.9	1.5	
Total species*	104	99	79	82	81	79	76	73	76	98	75	83	82	77	75	71	71	

* Includes rare species: Great Blue Heron, *Ardea herodias*; Wood Duck, *Aix sponsa*; Hooded Merganser, *Lophodytes cucullatus*; Red-breasted Merganser, *Mergus serrator*; Cooper's Hawk, *Accipiter cooperii*; Northern Goshawk, *Accipiter gentilis*; Red-tailed Hawk, *Buteo jamaicensis*; American Kestrel, *Falco sparverius*; Mourning Dove, *Zenaidura macroura*; White-poor-will, *Caprimulgus vociferus*; Red-bellied Woodpecker, *Melanerpes carolinus*; Eastern Phoebe, *Sayornis phoebe*; House Wren, *Troglodytes aedon*; Gray-cheeked Thrush, *Callanus rutinus*; Swainson's Thrush, *Callanus ustulatus*; Warbling Vireo, *Vireo gilvus*; Black-throated Blue Warbler, *Dendroica caerulescens*; Blackpoll Warbler, *Dendroica striata*.