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SONGBIRD POPULATIONS IN SOUTHERN WISCONSIN FORESTS: 1954 AND 1979

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Recent studies of breeding songbirds in the eastern deciduous forest of North America have shown that populations of certain bird species are declining in this biome (e.g., Temple and Temple 1976, Robbins 1979). The declining species are primarily birds specialized for breeding in forest environments and migrating long distances to winter in neotropical biomes (Whitcomb et al. 1981). These species include many warblers, vireos, flycatchers, and other insectivores.

We studied bird populations in upland forests of south-central Wisconsin during the summer of 1979 and have a unique opportunity to compare our results with those of Richard Bond who studied bird populations in the same region and habitat from 1952 to 1954 (Bond 1956). By comparing populations of forest songbirds at these 2 points in time, we seek to answer one question: Have populations of forest-dwelling, long-distance migrants declined in southern Wisconsin? In answering this question, we will address 3 issues. First, how comparable are the methods and study areas used in the 1954 and 1979 studies? Next, do we have good evidence for changes in bird populations in southern Wisconsin? Finally, based upon our results and previous studies, what conclusions can be drawn about populations of forest birds in eastern North America?

STUDY AREA

Bond (1956) studied birds in forests throughout southern Wisconsin; in 1979 we studied bird communities in only 7 counties of south-central Wisconsin (Sauk, Fond du Lac, Dodge, Dane, Jefferson, Green, and Rock counties). Plant communities of this region have been described in detail by Curtis (1959), Braun (1974), and Peet and Loucks (1977). At the time of settlement, oak savanna, oak-hickory forest, and maple-basswood forest were the major forest associations; however, with exclusion of fire, oak forest associations replaced uncultivated savanna (Peet and Loucks 1977). Modern forests are predominantly small, second-growth, forest islands in an agricultural and urban landscape. Detailed descriptions of the vegetation in Bond's study areas and our study areas appear in Bond (1956) and Ambuel and Temple (in press).

METHODS

Selection of study sites.—Criteria for selecting study sites were similar for the 2 studies: upland forest; no standing or running water during the breeding season; no recent, extensive cutting, grazing, storm damage, or other disturbance; no buildings; no conifers; a compact shape with minimum edge; and a range of vegetation types representing major upland forest types of the region. From samples of forests used in our research and Bond's study, we further restricted our choice of forest areas for this comparison so that: (1) all sites were greater than 12 ha in size; (2) forests from the 2 time periods had a similar geographic distribution, and (3) the 2 samples of forest represented a comparable mixture of oak-hickory and maple-basswood forest types. Using these criteria, we selected 19 of Bond's study sites and 14 of ours. Two study sites occur in both the 1954 and the 1979 samples of forest. These 33 study sites were the only ones that met all of the above selection criteria. Tree composition in these forests can be summarized as a single value using the continuum index (Curtis 1959) which is a weighted average of the relative dominance, density, and frequency of tree species (Table 1). The index has a potential range of 0 to 3000; the lower third of the continuum, representing xeric forest, is not represented in either sample.

Census methods.—Bond used a walk-and-stand census method in which he recorded all birds detected during 50 min of observation in a forest. The 50 min were subdivided into 5 successive 10-min periods of observation, and each 10-min period was further divided so that the observer remained stationary for 5 min and walked slowly for 5. Each census began 50 yards from the forest edge. Every forest was censused twice, and the largest number of individuals of a species observed on the 2 visits was used as the best index of abundance for that species. All censusing occurred between 20 May and 4 July from dawn to 08:00. Bond did not record species that in his judgement were migrants.

Our 1979 study was designed with several objectives in addition to comparing our results with Bond's, thus we did not precisely duplicate his method. We censused birds using a line-transect method in which we walked slowly along transects which traversed our study areas (Ambuel and Temple, in press). Each census began and ended at the forest edge. Each forest was sampled twice, and the largest number of individuals of a species observed on the 2 visits was used as the best index of abundance of the species. All censusing occurred between 4 June and 4 July from sunrise until 10:00. Researchers in 1954 and 1979 estimated the area of each census. The areas censused by Bond ranged from 4 to 8 ha with a mean of 6 ha, while the areas we censused ranged from 4 to 45 ha with a mean of 16 ha.

The 2 census methods differ in several ways which could bias comparisons: Bond used a walk-and-stand census while we used a line transect; Bond excluded forest edge while we included a small amount of edge in each census; and, Bond covered smaller areas per census. We compared the line-transect method with the walk-and-stand method during 1979 by using both methods on the same mornings during 2 different visits to 11 study sites, yielding 22 paired comparisons. The paired *t*-test (Box et al. 1978) was used to test differences between the methods in total number of species detected per census, and in density per census for the following groups: all birds; Red-eyed Vireo; Eastern Wood Pewee; Great Crested Flycatcher; Indigo Bunting; Gray Catbird;

TABLE 1. Continuum indices (C.I.) and area of contiguous forest for study areas.

	Characteristics of study areas[1]			
	1953–1954		1979	
Vegetation group	C.I.	Hectares	C.I.	Hectares
Xeric-Mesic	916	32	1038	132
	1006	100	1152	13
	1109	40	1194	275
	1192	22	1308	67
	1278	32	1341	36
	1336	28		
Mesic-Xeric	1536	80	1347	13
	1540	26	1518	67
	1633	160	1548	72
	1881	23	1629	17
	1897	36	1923	44
	2048	22		
Mesic	2104	25	2034	2397
	2119	200	2214	28
	2252	30	2226	50
	2344	30	2319	25
	2352	28		
	2375	120		
	2568	16		

[1] Study averaged 55 ha in 1954 and 231 ha in 1979. Median values were 30 ha and 47 ha, respectively.

Black-capped Chickadee; White-breasted Nuthatch; Northern Oriole; Scarlet Tanager; Cardinal; Rose-breasted Grosbeak; American Robin; Wood Thrush; uncommon ground feeders (Veery and Ovenbird); uncommon, cryptic, foliage feeders (Cerulean Warbler, American Redstart, Hooded Warbler, Chestnut-sided Warbler, and Blue-gray Gnatcatcher); and, other uncommon foliage feeders (Acadian Flycatcher, Least Flycatcher, Tufted Titmouse, and Yellow-throated Vireo). Only the numbers of White-breasted Nuthatches differed significantly between the methods ($P < .05$), and there was no consistent pattern in the directions of the mean differences for the other groups. These results give us some confidence in comparing species lists and relative densities among forests sampled by the 2 methods.

Some of the 1954 censuses began as early as 20 May, two weeks before the 1979 censuses began and at a time when some species would still be migrating. Bond (1956) made adjustments in his early censuses by excluding birds which in his judgement were nonresident migrants. Still, we would have preferred to use only woodlots from Bond's study which were censused after 4 June. Unfortunately Bond's original field notes have been lost, and only fragmentary information remains on census dates (Bond pers. comm.). Nonetheless, using notes provided by Richard Bond and information from his 1956 paper, we were able to determine the earliest census dates for 7 of the 19 study areas. Comparing the species lists for the 4 forests censused prior to 5 June with the 3 censused after 9 June, we found no important differences for the 8 species listed in Table 2 as declining in population. In fact, these 8 species occurred 24 out of 32 possible times in the 3 forests censused earlier (4 forests $\times$ 8 species = 32 possible occurrences), and 23 out of a possible 24 times in the 3 forests censused later. This comparison shows no evidence of a temporal bias in these 6 censuses for the 8 species which we later argue are declining.

The 1979 censuses included some forest edge while the 1954 censuses did not. We discuss potential bias from this difference in the results section.

The 1979 censuses covered a greater area within each forest than the 1954 censuses. Any bias from this difference will be conservative, making it harder for us to show declines from 1954 to 1979. Many of the forest-dwelling, long-distance migrants that may be declining are now uncommon in southern Wisconsin, therefore the larger 1979 censuses have a higher probability of including these uncommon species. This lowers the probability of our demonstrating differences between 1954 and 1979 in the species richness of forests or in a species' frequency of occurrence.

Methods of comparison.—We would ideally compare absolute densities of birds between 1954 and 1979. However, this is difficult in a comparison across observers, methods, study-areas, and time. Therefore, we rely principally upon presence-absence data to determine if species have increased or decreased in frequency of occurrence among samples of upland forest from 1954 and 1979. This approach is conservative and should minimize observer and method bias, but it has one disadvantage. Population changes in species which are either common or rare in both 1954 and 1979 will go undetected, because the frequency of occurrence of these species will not change. Hence, we are able to make meaningful comparisons for 12 of the 31 species present in the forests.

We first wished to know if there were fewer species in forests today than in 1954, and if there were fewer forest-dwelling, long-distance migrants. We tested for such differences with a nested analysis of variance (Box et al. 1978). The dependent variable, either the total number of species or the number of species of forest-dwelling, long-distance migrants, was compared between 1954 and 1979 nested within the 3 forest types shown in Table 1.

We used contingency tables to test the significance of changes in the frequency of occurrence of species on 14 study areas from 1979 and 19 study areas from 1954. Because the sample sizes were small, we used the Fisher exact probability test (Siegel 1956).

In a final analysis, we compared the relative abundance of birds in 2 woods censused in both 1954 and 1979. These woods are mature forests with large trees, a tall canopy, and foliage distributed through all layers

TABLE 2. The frequency of occurrence of bird species in forests of southern Wisconsin in 1954 and 1979.

Trends and species[1]		Frequency of occurrence[2] 1954	1979	Level of significance[3]
Increasing				
Common Grackle	(*Quiscalus quiscula*)	0/19	7/14	<0.001
American Robin	(*Turdus migratorius*)	0/19	8/14	<0.001
House Wren	(*Troglodytes aedon*)	1/19	9/14	0.001
Red-winged Blackbird	(*Agelaius phoeniceus*)	0/19	5/14	0.019
Decreasing				
*Ovenbird	(*Seiurus aurocapillus*)	18/19	4/14	<0.001
*Yellow-throated Vireo	(*Vireo flavifrons*)	15/19	3/14	0.003
*Cerulean Warbler	(*Dendroica cerulea*)	10/19	2/14	0.014
*American Redstart	(*Setophaga ruticilla*)	10/19	2/14	0.048
*Scarlet Tanager	(*Piranga olivacea*)	19/19	9/14	0.074
*Least Flycatcher	(*Empidonax minimus*)	10/19	3/14	0.079
*Blue-gray Gnatcatcher	(*Polioptila caerulea*)	16/19	7/14	0.084
*Northern Oriole	(*Icterus galbula galbula*)	11/19	5/14	0.087
Undetermined[4]				
*Wood Thrush	(*Hylocichla mustelina*)	7/19	2/14	0.422
*Acadian Flycatcher	(*Empidonax virescens*)	6/19	2/14	0.468
*Red-eyed Vireo	(*Vireo olivaceus*)	19/19	12/14	0.767
*Indigo Bunting	(*Passerina cyanea*)	13/19	11/14	0.810
*Chestnut-sided Warbler	(*Dendroica pensylvanica*)	0/19	1/14	0.848
*Mourning Warbler	(*Oporonis philadelphia*)	0/19	1/14	0.848
*Great Crested Flycatcher	(*Myiarchus crinitus*)	15/19	12/14	0.980
*Rose-breasted Grosbeak	(*Pheuticus ludovicianus*)	11/19	10/14	0.995
*Eastern Wood Pewee	(*Contopus virens*)	19/19	14/14	—
*Veery	(*Catharus fuscescens*)	4/19	2/14	0.980
Brown-headed Cowbird	(*Molothrus ater*)	19/19	10/14	0.133
Starling	(*Sturnus vulgaris*)	0/19	3/14	0.156
Gray Catbird	(*Dumetella carolinensis*)	5/19	7/14	0.303
Blue Jay	(*Cyanocitta cristata*)	16/19	14/14	0.355
Cedar Waxwing	(*Bombycilla cedrorum*)	1/19	3/14	0.387
White-breasted Nuthatch	(*Sitta carolinensis*)	17/19	14/14	0.648
Tufted Titmouse	(*Parus bicolor*)	6/19	3/14	0.810
Black-capped Chickadee	(*Parus atricapillus*)	11/19	9/14	0.994
Cardinal	(*Cardinalis cardinalis*)	6/19	4/14	0.995

[1] Forest-dwelling, long-distance migrants, as determined from life histories and distributional data (A.O.U. 1957), are indicated with asterisks.

[2] Number of forests where species was present/number of forests sampled.

[3] Probabilities are from Fisher's exact test. A significant increase or decrease was assumed when P values were $\leqslant .10$. P-values for the Oriole, Grackle, Red-wing, Starling, and Cardinal were calculated from xeric-mesic and mesic-xeric woods because these species were absent from the mesic woods in both years.

[4] Although our results indicate that the frequency of occurrence of these species did not change between 1954 and 1979, this does not rule out change in the densities of these species, which our methods would not detect.

from herb layer to canopy. Forests of this type change slowly in composition and structure (Curtis 1959); however, both forests have been affected by dutch elm disease and oak wilt in the years since Bond's study. Forest A, a diverse forest of sugar maple (*Acer saccharum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*), and American elm (*Ulmus americana*), has become more xeric since 1954 as reflected in a change in continuum index (CI) from 2252 to 1923. This change may reflect a loss of elm trees. Forest B, a red oak (*Quercus borealis*), basswood, and white oak (*Quercus alba*) forest, has changed little in composition since 1954. The CI was 1540 in 1954, and 1518 in 1979.

RESULTS

The hypothesis.—We are not testing a simple null hypothesis of "no change between 1954 and 1979." Because of vagaries of sampling we expected to find differences between samples of the bird communities from 1954 and 1979, regardless of any actual changes in population. Demonstrating a single difference, or a series of differences with no clear pattern, would be a trivial result. To support our hypothesis that forest-dwelling, long-distance migrants have declined, we required evidence that many of these species had declined, and that few, if any, had increased.

Changes in species richness.—The result of the nested analysis of variance provides no strong evidence of a change between 1954 and 1979 in the mean number of species present per forest (13.2 vs. 11.7; $P < .10$). However, the mean number of species of forest-dwelling, long-distance migrants per forest clearly declined between 1954 and 1979 (9.8 vs. 6.9; $P < .01$).

Changes in the frequency of occurrence of species.—Some species were either too common or too rare in both years to draw conclusions regarding an increase or decline (Table 2). Nonetheless, the American Redstart, Cerulean Warbler, Ovenbird, Least Flycatcher, Northern Oriole, Scarlet Tanager, Blue-gray Gnatcatcher, and Yellow-throated Vireo all declined in frequency of occurrence, whereas the Red-winged Blackbird, Common Grackle, House Wren, and American Robin all increased in frequency of occurrence ($P < .10$). These trends (Table 2) are consistent with previous studies of upland forest: forest-dwelling, long-distance migrants have declined, while certain species that migrate short distances and inhabit forest edge and agricultural habitat have increased.

Changes in 2 forests.—Further evidence of declines in forest-dwelling, long-distance migrants comes from the comparisons of the 2 forests censused in both 1954 and 1979 (Table 3). In 1954, 81% of the individuals and 7 of 11 species in Forest A were forest-dwelling, long-distance migrants. In 1979 only 43% of the individuals and 3 of 9 species were members of this ecological group. Forest B shows a similar change. In 1954, 72% of the individuals and 11 of 18 species were forest-dwell-

TABLE 3. A comparison of bird populations in two forests in 1954 and 1979.

Forest and species	Relative abundance (% of all birds detected) 1954	1979
Forest A: Sugar Maple, Basswood, and White Ash		
Red-eyed Vireo	40	13
Eastern Wood Pewee	16	10
Ovenbird	9	0
Great Crested Flycatcher	7	20
Indigo Bunting	7	0
White-breasted Nuthatch	7	10
Blue-gray Gnatcatcher	5	0
Scarlet Tanager	2	0
Yellow-throated Vireo	2	0
Blue Jay	2	13
Brown-headed Cowbird	2	0
House Wren	0	13
American Robin	0	10
Starling	0	7
Gray Catbird	0	3
Forest B: Red Oak, Basswood, and White Oak		
Red-eyed Vireo	17	5
Eastern Wood Pewee	13	8
Great Crested Flycatcher	6	3
Ovenbird	6	3
Scarlet Tanager	6	11
Yellow-throated Vireo	6	0
American Redstart	6	0
Tufted Titmouse	6	0
Blue Jay	6	8
Wood Thrush	4	3
White-breasted Nuthatch	4	3
Blue-gray Gnatcatcher	4	3
Northern Oriole	2	8
Cardinal	2	0
Rose-breasted Grosbeak	2	5
Black-capped Chickadee	2	0
House Wren	2	5
Brown-headed Cowbird	2	5
Indigo Bunting	0	18
American Robin	0	13

ing, long-distance migrants; whereas in 1979, they accounted for 50% of the individuals and 8 of 15 species.

DISCUSSION

We have observed bird populations at 2 moments in time, separated by a span of 25 years. Interpreting results of this type of comparison is difficult, and there are 4 major sources of variation that should be considered. First, our experimental design may bias comparisons between 1979 and 1954. As discussed in the methods, we have attempted to minimize this bias. Although it is possible the increases in frequency of occurrence of Red-winged Blackbirds and Common Grackles merely reflect inclusion of more edge habitat in the 1979 census, we do not think so. Both species occurred almost exclusively in xeric-mesic forests where they were found in forest interior as well as at forest edge. These species, which nest in open country or forest edge, often forage deep within forests where they move in small groups or in large flocks. One-third of our detections of these species were of large flocks (10 or more birds) found far from the forest edge. Thus, these 2 edge species have become important, if not consistant, members of the deep forest bird communities in xeric-mesic forest. The Chestnut-sided and Mourning warblers are also edge species and may still be migrating in early June. However, we detected these species throughout the month of June in small, shrubby forest openings some distance from forest edge. Three other sources of variation result from real changes in bird populations: (1) population changes caused by local, stochastic events causing temporary fluctuations in populations over a limited geographic area; (2) catastrophic, but stochastic, events causing regional fluctuations around relatively stable mean population levels; and, (3) a sustained increase or decrease in mean population levels. We are interested in distinguishing changes of type 3 from changes of type 1 and 2.

By comparing bird populations over an extensive area of south-central Wisconsin we have reduced the chance of emphasizing highly localized changes in populations. That our results corroborate the results of previous studies from other regions of the eastern United States (Temple and Temple 1976, Robbins 1979, Whitcomb et al. 1981) also indicates that the changes are regional rather than local.

Population changes in Wisconsin may represent normal fluctuations around stable means, or sustained changes in mean population levels. Evidence of simultaneous population changes in different localities, sustained over time, and for a variety of species, would indicate sustained changes in populations. Other studies provide exactly this evidence. For example, Temple and Temple (1976) show a decline in populations of the Yellow-throated Vireo in central New York State. Their annual census results span 37 successive years, during which time the magnitude of species' declines far exceeded annual variations. Robbins (1979) compared bird populations in 6 forest areas censused originally in the 1940's and 1950's, then again between 1975 and 1978. His results show a clear decline in populations of many forest-dwelling, long-distance migrants; he interprets these changes as indicative of regional changes throughout eastern North America. Evidence from these studies, in different locations, using different methods, and covering different time periods, supports the hypothesis that populations of forest-dwelling, long-distance migrants have declined.

What are the potential causes of this decline? Robbins (1979) and

Whitcomb et al. (1981) have identified destruction and fragmentation of forests within the breeding range as a probable cause. In their model, forest fragmentation leads to increased competition from edge species, increased brood parasitism from cowbirds, and changes in habitat that, in turn, result in low reproductive success for the forest-dwelling specialists.

Our results suggest that there may be additional causes for the decline. Because of our selection criteria, all of the study areas from both years were relatively extensive, undisturbed forests (Table 1), indicating that populations have changed even in reasonably high quality forest habitat. In comparison with these larger forests, smaller forests of southern Wisconsin censused in 1977, 1978, and 1979 have fewer species and a lower percentage of individuals that are forest-dwelling, long-distance migrants (Ambuel and Temple in press, Howe and Jones 1978).

Perhaps changes beyond the breeding range of these species have contributed to the decline. The migration and wintering ecology of these declining species is poorly understood. On their wintering ranges, we do know that many of these species occupy specific habitats and that some species occupy territories to which they show site fidelity from year to year (e.g., Schwartz 1964, Lack 1974, Ramos 1978, Keast and Morton 1980). Even with this sketchy knowledge of life histories, we can predict that destruction of important habitat and other environmental changes along migration routes or on wintering ranges could contribute to declines of long-distance migrants in forests of eastern North America. Such changes should also affect species of long-distance migrants which breed in other biomes of North America.

There is an urgent need for research on the ecology of forest-dwelling, long-distance migrants during migration and on their wintering range. Without such data we are in a poor position to identify ultimate factors responsible for these population declines. Nevertheless, forest-dwelling long-distance migrants have declined, and we should begin to carefully monitor their populations.

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LITERATURE CITED

AMBUEL, B., AND S. A. TEMPLE. 1982. Area dependent changes in bird communities and vegetation of southern Wisconsin forests. Ecology (in press).

AMERICAN ORNITHOLOGISTS' UNION. 1957. Checklist of North American birds. American Ornithologists' Union, Baltimore.
BOND, R. R. 1956. Ecological distribution of breeding birds in the upland forest communities of southern Wisconsin. Ecol. Monogr. 27:351–384.
BOX, G. E. P., W. G. HUNTER, AND J. S. HUNTER. 1978. Statistics for experimenters. John Wiley and Sons, New York.
BRAUN, E. L. 1950. Deciduous forests of eastern North America. The Free Press, Macmillan Publishing Co., Inc., New York.
CURTIS, J. T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison.
HOWE, R. W., AND G. JONES. 1977. Avain utilization of small woodlots in Dane County, Wisconsin. Passenger Pigeon 39:313–319.
KEAST, A., AND E. S. MORTON (eds.). 1980. Migrant birds in the neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution, Washington, D.C.
LACK, D. 1974. Island biology illustrated by the land birds of Jamaica. University of California Press, Berkeley.
PEET, R. K., AND O. L. LOUCKS. 1977. A gradient analysis of southern Wisconsin forests. Ecology 58:485–499.
RAMOS, M. A. 1978. Are migrant birds aliens in tropical wintering areas? Abstracts of presented papers, 96th meeting of the American Ornithologists' Union, Madison, Wisconsin.
ROBBINS, C. S. 1979. Effects of forest fragmentation on bird populations. Pp. 198–212, *in* R. M. DeGraaf and K. E. Evans (eds.), Management of north central and northeastern forests for nongame birds. U.S.D.A., Forest Service General Technical Report NC-51. North Central Forest Experiment Station, Saint Paul, Minnesota.
SCHWARTZ, P. 1964. The Northern Waterthrush in Venezuela. Living Bird 3:168–184.
SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Co., New York.
TEMPLE, S. A., AND B. L. TEMPLE. 1976. Avian population trends in central New York state, 1935–1972. Bird-Banding 47:238–257.
WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. *In* R. L. Burgess and D. M. Sharpe (eds.), Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

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