# CHANGES IN THE AVIFAUNA OF THE GREAT SMOKY MOUNTAINS: 1947–1983

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ABSTRACT. – In 1982–1983, I repeated ten breeding bird censuses made by B. Fawver in 1947–1948 in the Great Smoky Mountains National Park, Tennessee and North Carolina. Populations of neotropical migrants did not show significant changes. In contrast, during this period, many of the same species of neotropical migrants had declined in small woodlots and urban parks throughout the eastern United States. These findings support the hypothesis that declines in woodlots result from the fragmentation of breeding habitat and demonstrate the importance of large parks such as the Great Smoky Mountains National Park for the preservation of neotropical migrants.

Among the permanent residents and short-distance migrants, the Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), and Dark-eyed Junco (*Junco hyemalis*) showed substantial population increases during this period. All three species probably have benefited from human activity outside the park boundaries. *Received 16 June 1987, accepted 8 Dec. 1987.* 

Investigators recently have called attention to long-term changes in bird communities in small forest fragments and urban parks throughout the eastern United States (Briggs and Criswell 1979, Robbins 1979, Butcher et al. 1981, Ambuel and Temple 1982). In most areas, breeding populations of forest-dwelling neotropical migrants have declined, while populations of permanent residents and short-distance migrants have either increased or remained stable (Whitcomb et al. 1981). Without comparable data from extensive, undisturbed forest tracts, it is difficult to judge whether the avifaunal changes in the small woodlots are a consequence of the small size and isolated nature of the fragments themselves, the loss of winter habitat for the migratory species, or some other factor (see Morse 1980).

Since 1947, observers in West Virginia have been monitoring bird populations within an extensive red spruce-northern hardwood forest. These censuses reveal a steady decline in the diversity and numbers of neotropical migrants (Hall 1984). However, this study covers only one type of forest (red spruce [*Picea rubens*]—northern hardwoods), and only 6.1 ha of forest are censused. More studies are needed to fully understand what is happening to bird populations in large forest tracts.

In 1982–1983 I repeated ten breeding bird censuses made by B. Fawver in 1947–1948 in Great Smoky Mountains National Park, Tennessee and

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Locality	Elevation (m)	Area (ha) censused <sup>a</sup>	Census method <sup>b</sup>	Years censused
Cove forests				
Lower Ramsey Creek	660-780	12.8	С	1948, 1982
Middle Ramsey Creek	910-1,040	5.6	S	1947, 1982, 1983
Lower Porter Creek	730-800	6.8	S	1948, 1982
Hemlock-deciduous forests				
Spruce Flats	900-910	4.2	S	1948, 1982, 1983
Brushy Mountain	1,220-1,370	9.0	S	1948, 1982
Roaring Fork	1,000-1,130	7.8	С	1948, 1982, 1983
Chestnut oak forests				
Bullhead Trail	860-1,000	4.8	S	1947, 1982
Greenbrier Pinnacle	1,080-1,090	11.0	S	1948, 1982, 1983
Red oak forests				
Greenbrier Pinnacle	1,250-1,300	7.5	С	1948, 1982
Beech gap forests				
Double Spring Gap	1,660–1,680	7.0	S	1947, 1982

TABLE 1
ELEVATION, PLOT SIZE, CENSUS METHOD, AND CENSUS YEARS FOR THE
Study Areas in the Great Smoky Mountains National Park

\* Refers to the actual count area censused by Wilcove in 1982-1983.

<sup>b</sup> Cruising count (C) or spot-mapping (S). See text for details.

North Carolina (see Fawver 1950, Kendeigh and Fawver 1981). These ten censuses covered five distinct forest types within one of the largest and least disturbed forest tracts in the eastern United States. My objective was to determine whether significant changes had occurred in the avifauna of the Great Smoky Mountains, and, if so, to compare these changes with what has happened in small woodlots and urban parks.

### METHODS

Study sites.—In 1982 I relocated most of Fawver's field sites using directions in his thesis, old maps from the park library, and information provided by Fawver and long-time residents of the area. I rejected tracts showing obvious successional changes and tracts altered by road construction. Ultimately, I censused birds at 10 localities representing five types of mature forest (Table 1). In 1983, I returned to four of these sites to replicate the counts.

Fawver (1950) obtained detailed botanical descriptions of most of his study sites. These were qualitatively updated in 1982–1983. Brief descriptions of the study sites are presented below. The classification of forest types follows Whittaker (1956), and includes:

(1) Cove forests (three sites). Found in moist stream valleys and north-facing slopes, cove forests are characterized by a high, mostly deciduous canopy consisting of large, widely spaced trees of many species. *Rhododendron* forms dense thickets along streams. Two of

the sites (Lower Porter Creek, Middle Ramsey Creek) are virgin tracts. Lower Ramsey Creek was logged sometime in the 19th century, but by 1947 was a closed canopy forest (Fawver 1950). By 1982, the trees were larger, the canopy more closed, and the understory reduced as compared to 1947.

(2) Hemlock-deciduous forests (three sites). Eastern hemlock (*Tsuga canadensis*) is the dominant tree species. At Spruce Flats, American beech (*Fagus grandifolia*) is a prominent component of the understory and canopy, while at Roaring Fork and Brushy Mountain, the understory largely consists of sweet and yellow birches (*Betula lenta* and *B. alleghaniensis*). Extensive *Rhododendron* thickets border the streams. All three sites are virgin tracts that have changed little since 1947–1948, judging from Fawver's descriptions.

(3) Chestnut oak forests (two sites). This forest type is characterized by relatively small trees 6–18 m in height. The principal species include chestnut oak (*Quercus prinus*), northern red oak (*Q. rubra*), and pitch pine (*Pinus rigida*). Ericaceous shrubs form a dense, often impenetrable understory. Both sites had standing, dead American chestnut (*Castanea dentata*) trees in 1947–1948, which were gone by 1982. At the Greenbrier site, chestnuts comprised less than 5% of the trees (Fawver 1950), and their loss probably had insignificant effects on the forest structure. At the Bullhead site almost 30% of the trunks in 1947–1948 were standing dead chestnuts. They created a very open canopy, permitting an extensive understory of tree saplings and mountain laurel (*Kalmia latifolia*) to grow up (B. Fawver, pers. comm.). By 1982, the canopy had filled in with various oaks, and the understory was much reduced (pers. obs.; see also Woods and Shanks 1959, Mackey and Sivec 1973).

(4) Northern red oak forests (one site). In oak forests at higher elevations, northern red oak replaces chestnut oak as the dominant species, although the forests are otherwise similar (Whittaker 1956). At the study site, standing dead chestnuts accounted for less than 5% of the trees in 1947. Their subsequent loss probably had little effect on the forest structure.

(5) Beech forests (one site). In this unique forest type, American beech comprises over 90% of the trees. The trees are small (8-12 m tall) and widely spaced. Grasses and herbs cover the forest floor. The study plot is a virgin tract.

*Census techniques.* – Fawver used two census techniques: spot-mapping of singing males (Kendeigh 1944, Robbins 1970) and cruising counts. In a cruising count, the observer counts all singing males within a predetermined distance on either side of a transect line. Several such counts are made, and the largest number of each species observed on any one count is assumed to be the population of that species. Fawver censused birds during June and July 1947 and from May through July 1948. I censused birds from 19 May to 27 June 1982 and from 31 May to 14 June 1983. At each site, I repeated the census method used by Fawver (Table 1). Spot-map sites were visited at least four times in 1947–1948 and 7–10 times in 1982–1983. In 1947–1948, the three cruising count sites were visited two, three, and five times, respectively; in 1982–1983, they were visited five, six, and six times, respectively. By increasing the number of visits to each site, I was potentially biasing the data in favor of recording larger populations (see Dickson 1978). However, studies of bird census techniques now recommend a minimum of 8 visits per spot-mapping site (Robbins 1970). Because I wanted the 1982–1983 data to be as accurate as possible for future replication, I increased the census effort.

Statistical tests. -- Three statistical tests were used to compare populations in different years: (1) the sign test was used to evaluate the direction of change (increase, decrease) of each species over all study sites; (2) the chi-square one-sample test (two-tailed) was used to evaluate overall population changes of major groups (e.g., neotropical migrants, residents, and short-distance migrants) in the individual study sites or across all study sites; and (3) the binomial test (two-tailed) was used in place of the chi-square test when sample sizes were too small (Siegel 1956). No attempt was made to assess the significance of population

changes of individual species within each study site, due to the small sample sizes typically involved. All statistical tests were performed on the actual census counts, and not the density (pairs/10 ha) values. The actual counts can be calculated from the density values using the plot sizes from Table 1. It should be noted that the increased census effort in 1982–1983 compared to 1947–1948 decreased the likelihood of recording statistically significant population declines.

## RESULTS

Census results are presented as density estimates: pairs/10 ha (Tables 2-4). If only a small fraction of a species' territory extended onto the study plot, or if that species was recorded less than three times on the plot, it was not included in the population tallies.

Neotropical migrants: overall numbers. – In 9 of the 10 study sites, the total number of breeding pairs of neotropical migrants did not change significantly between 1947–1948 and 1982 (Table 5). At the tenth site, Greenbrier Pinnacle red oak forest, neotropical migrants declined by 48% ( $\chi^2 = 5.46$ , df = 1, P < 0.05). This was largely due to the local disappearance of the Wood Thrush (*Hylocichla mustelina*) and Red-eyed Vireo (*Vireo olivaceus*), both formerly common breeders at this site. One locality (Roaring Fork hemlock-deciduous forest) experienced a significant decline in total pairs of neotropical migrants between 1982 and 1983 ( $\chi^2 = 5.73$ , df = 1, P < 0.05). Intervear population changes at the three other sites censused in both 1982 and 1983 were not significant (Table 5).

Neotropical migrants: individual species. - Only one species, Blackthroated Green Warbler (Dendroica virens), showed a significant, widespread increase between 1947 and 1982 (P = 0.032, two-tailed sign test). However, it declined sharply between 1982 and 1983; in the four areas censused in consecutive years, the population declined by 50%, from 28 to 14 pairs. Two species (Northern Parula [Parula americana] and Indigo Bunting [Passerina cyanea]) not found in the study sites in 1947-1948 were recorded in 1982-1983. Northern Parula was recorded in three localities, and Indigo Bunting appeared in two localities. A number of species (e.g., Acadian Flycatcher [Empidonax virescens], Blackburnian Warbler [Dendroica fusca], Worm-eating Warbler [Helmitheros vermivorus], Kentucky Warbler [Oporornis formosus]) were either so uncommon or so localized that little can be said of their population status. Between 1947 and 1982, Solitary Vireos (Vireo solitarius) increased at one site (Middle Ramsey Creek cove forest), disappeared from a stronghold (Spruce Flats hemlock-deciduous forest), and appeared in two new localities (Bullhead Trail chestnut oak forest, Greenbrier Pinnacle red oak forest). Between 1982 and 1983, the species declined at Middle Ramsey Creek, returned to Spruce Flats in large numbers, and appeared for the

TABLE 2	BIRD POPULATION DATA FOR COVE FOREST STUDY SITES. NUMBERS REPRESENT BREEDING	PAIRS PER 10 HA. NEOTROPICAL MIGRANTS ARE DENOTED BY AN ASTERISK		
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	Lower Rai	Lower Ramsey Creek	Mid	Middle Ramsey Creek	reek	Lower Pol	Lower Porter Creek
	1948	1982	1947	1982	1983	1948	1982
Ruffed Grouse (Bonasa umbellus)		0.8	1.2			1.2	
Ruby-throated Hummingbird* (Archilochus colubris)	0.8						
Downy Woodpecker (Picoides pubescens)	0.8	0.8					
Hairy Woodpecker (P. villosus)	0.8	0.8	1.2			1.5	1.5
Northern Flicker (Colaptes auratus)	0.8						
Pileated Woodpecker (Dryocopus pileatus)	0.8	0.8					1.5
Acadian Flycatcher* (Empidonax virescens)	0.8	0.8					
Great Crested Flycatcher* (Myiarchus crinitus)	0.8						
Blue Jay (Cyanocitta cristata)		0.8					1.5
American Crow (Corvus brachyrhynchos)		0.8					
Black-capped Chickadee (Parus atricapillus)		1.6	1.2	1.8		1.5	1.5
Tufted Titmouse (P. bicolor)	0.8	0.8					
Carolina Wren (Thryothorus ludovicianus)	0.8	0.8				1.5	
Winter Wren (Troglodytes troglodytes)			1.2	3.6	3.6		4.4
Veery* (Catharus fuscescens)					1.8		2.2
Wood Thrush* (Hylocichla mustelina)	9.2	1.6	4.2	8.9	1.8	7.0	7.4
Solitary Vireo (Vireo solitarius)	3.2	3.1	4.2	10.7	7.1	12.5	10.3
Red-eyed Vireo* (V. olivaceus)	9.2	10.9		5.4	1.8	4.2	5.9
Northern Parula* (Parula americana)				1.8	1.8		
Black-throated Blue Warbler* (Dendroica caerulescens)	6.2	8.2	26.5	14.3	14.3	29.0	23.5
Black-throated Green Warbler* (D. virens)	1.5	5.5		8.9		5.5	5.1
Blackburnian Warbler* (D. fusca)						1.5	

Lower Ramsey Creek   1948 1982   1948 1982   Black-and-white Warbler* (Mniotilla varia) 1.5 3.9   Worm-eating Warbler* (Helmitheros vermivorus) 0.8 1.6   Ovenbicd* (Seiurus aurocapillus) 5.5 4.7	amsey Creek					
1948 Ita varia) 1.5 ros vermivorus) 0.8 5.5		Mid	Middle Ramsey Creek	eek	Lower Porter Creek	er Creek
Black-and-white Warbler* (Mniotilta varia) 1.5 Worm-eating Warbler* (Helmitheros vermivorus) 0.8 Ovenbird* (Seiurus aurocapillus) 5.5	1982	1947	1982	1983	1948	1982
Worm-eating Warbler* (Helmitheros vermivorus) 0.8 Ovenbird* (Seiurus aurocapillus) 5.5	3.9			1.8		1.5
Ovenbird* (Seiurus aurocapillus) 5.5	1.6					
	4.7	1.2			4.2	1.5
Louisiana Waterthrush* (S. motacilla)				1.8		
Kentucky Warbler* (Oporornis formosus) 0.8						
Hooded Warbler* (Wilsonia citrina) 1.5	1.6					
Canada Warbler* (W. canadensis)		1.2	5.4			
Scarlet Tanager* (Piranga olivacea) 2.5	3.1	1.2		1.8	2.8	3.7
Rose-breasted Grosbeak* (Pheucticus ludovicianus)	1.6					
Dark-eyed Junco (Junco hyemalis)		1.2	7.1	7.1	1.5	2.9

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BIRD POPULATION DATA FOR HEMLOCK-DECIDUOUS FOREST STUDY SITES. NUMBERS REPRESENT BREEDING Pairs per  $10~\mathrm{Ha}.$  Neotropical Migrants Are Denoted by an Asterisk

		Spruce Flats			Roaring Fork		Brushy N	Brushy Mountain
	1948	1982	1983	1948	1982	1983	1948	1982
Barred Owl (Strix varia)		2.4						
Downy Woodpecker (Picoides pubescens)			1.2					
Hairy Woodpecker (P. villosus)			1.2	1.2	1.3	1.3	0.8	
Northern Flicker (Colaptes auratus)							0.8	
Pileated Woodpecker (Dryocopus pileatus)	1.0		1.2	1.2		1.3		1.1
Acadian Flycatcher* (Empidonax virescens)	5.0	6.0	7.1		1.3			
Blue Jay (Cyanocitta cristata)					1.3			2.2
American Crow (Corvus brachyrhynchos)		2.4	2.4		1.3	1.3		
Black-capped Chickadee (Parus atricapillus)	2.0			1.2	1.3	3.8	1.8	1.1
Tufted Titmouse (P. bicolor)		2.4	2.4		1.3			
Red-breasted Nuthatch (Sitta canadensis)				3.8	2.6	1.3	4.2	3.9
White-breasted Nuthatch (S. carolinensis)						1.3		
Brown Creeper (Certhia americana)							1.5	1.1
Winter Wren (Troglodytes troglodytes)			2.4	2.5	2.6	2.6	2.5	5.0
Golden-crowned Kinglet (Regulus satrapa)					1.3	2.6	2.5	5.6
Veery* (Catharus fuscescens)				1.2	2.6	1.3	3.2	6.1
Wood Thrush* (Hylocichla mustelina)	8.0	2.4	2.4	6.2		1.3	1.5	
American Robin (Turdus migratorius)				2.5				
Cedar Waxwing (Bombycilla cedrorum)					1.3			
Solitary Vireo (Vireo solitarius)	18.0		9.5	5.0	6.4	6.4	85	61

		Spruce Flats			Roaring Fork	,	Brushy Mountain	Iountain
	1948	1982	1983	1948	1982	1983	1948	1982
Red-eyed Vireo* (V. olivaceus)	1.0	3.6	6.0		7.7	2.6		
Northern Parula* (Parula americana)					2.6	2.6		
Black-throated Blue Warbler* (Dendroica caerulescens)	11.0	11.9	11.9	18.8	23.1	12.8	22.0	17.8
Black-throated Green Warbler* (D. virens)	14.0	21.4	7.1	17.5	17.9	14.1	10.2	28.9
Blackburnian Warbler* (D. fusca)	15.0	9.5	8.3	10.0	5.1	5.1	3.2	3.3
Ovenbird* (Seiurus aurocapillus)	27.0	23.8	16.7	8.8	14.1	5.1		
Hooded Warbler* (Wilsonia citrina)		2.4						
Canada Warbler* (W. canadensis)	0.5			8.8	7.7	7.7	12.8	6.7
Scarlet Tanager (Piranga olivacea)	1.0			2.5	2.6	1.3	0.8	11
Rose-breasted Grosbeak* (Pheucticus ludovicianus)					1.3			
Dark-eyed Junco (Junco hyemalis)	4.0	10.7	8.3	10.0	11.5	9.0	5.0	8.3

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# BIRD POPULATION DATA FOR OAK AND BEECH FOREST STUDY SITES. NUMBERS REPRESENT BREEDING Pairs per 10 ha. Neotropical Migrants Are Denoted by an Asterisk

1947	Chestnut Oak	Jak	Greenbri	Greenbrier Chestnut Oak	ut Oak	Red Oak	Dak	Double Spring Gap	ing Gap
		1982	1948	1982	1983	1948	1982	1947	1982
Kulled Orouse (Bonasa umbelins)						1.2		1.2	1.4
Ruby-throated Hummingbird* (Archilochus colubris)		2.1		0.9					
Downy Woodpecker (Picoides pubescens)					0.9				
Hairy Woodpecker (P. villosus)		2.1	1.0	0.9		1.2	1.3		
Northern Flicker (Colaptes auratus) 1.2	1.2		1.0						
Pileated Woodpecker (Dryocopus pileatus)				0.9			1.3		
Eastern Wood-Pewee* (Contopus virens)						1.2			
Great Crested Flycatcher* (Myiarchus crinitus) 5.2	5.2				1.8	1.2			
Blue Jay (Cyanocitta cristata)		4.2	1.0	1.4	0.9		2.0		
Black-capped Chickadee (Parus atricapillus) 1.2	1.2				0.9	1.2			4.3
Carolina Chickadee (P. carolinensis)			2.2						
Tufted Titmouse (P. bicolor)					1.8				
Red-breasted Nuthatch (Sitta canadensis)		2.1					2.7		
Golden-crowned Kinglet (Regulus satrapa)									1.4
Veery* (Catharus fuscescens)								5.0	
Wood Thrush* (Hylocichla mustelina) 1.2	1.2			0.9		6.5			
American Robin (Turdus migratorius)								1.2	1.4
White-eyed Vireo* (Vireo griseus) 1.2	1.2								
Solitary Vireo (V. solitarius)		5.2			1.8		5.3	6.2	8.6
Red-eyed Vireo* (V. olivaceus) 11.8	8.1	8.3	5.5 2.7	2.7	2.7	10.5			

	Bullhead Chestnut Oak	nead ut Oak	Greenbr	Greenbrier Chestnut Oak	nut Oak	Greenbrier Red Oak	ıbrier Oak	Double S <sub>1</sub>	Double Spring Gap
	1947	1982	1948	1982	1983	1948	1982	1947	1982
Northern Parula* (Parula americana)							1.3		
Chestnut-sided Warbler* (Dendroica pensylvanica)						2.5		12.8	
Black-throated Blue Warbler* (D. caerulescens)	1.2	18.7	7.5	4.1	5.0	6.5	5.3		
Black-throated Green Warbler* (D. virens)	1.2	7.3							
Black-and-white Warbler* (Mniotilta varia)	1.2	4.2	3.2	3.2	3.2	1.2	4.0		
Worm-eating Warbler* (Helmitheros vermivorus)	2.8	2.1	2.2	0.9	1.8				
Ovenbird* (Seiurus aurocapillus)	6.5	7.3	7.5	7.7	5.4	10.5	6.7		
Kentucky Warbler* (Oporornis formosus)	2.8								
Hooded Warbler* (Wilsonia citrina)	9.0	6.2	8.5	5.0	5.0	2.5	1.3		
Canada Warbler* ( <i>W. canadensis</i> )		1.0					1.3	1.2	
Yellow-breasted Chat* (Icteria virens)	1.2								
Scarlet Tanager* ( <i>Piranga olivacea</i> )	5.2	2.1	2.2	2.3	1.8	2.5	4.0		
Northern Cardinal (Cardinalis cardinalis)	1.2								
Rose-breasted Grosbeak* (Pheucticus ludovicianus)		7.3							
Indigo Bunting* (Passerina cyanea)		2.1							10.0
Rufous-sided Towhee (Pipilo erythropthalmus)	10.5	5.2	8.5	1.8	1.8	2.5	5.3		
Dark-eyed Junco (Junco hyemalis)		8.3		1.8	1.8		18.7	14.0	12.1

# Populations of Neotropical Migrants and Other Birds (Permanent Residents and Short Distance Migrants) at Each of the Study Sites in the Great Smoky Mountains National Park. Numbers Refer to the Total Number of Breeding Pairs at Each Locality. Underlined Values Represent Significant (P < 0.05) Population Changes

	Nec	tropical migr	ants		Other birds	
Locality	1947/48	1982	1983	1947/48	1982	1983
Lower Ramsey Creek	53	54.5	_	10	14	
Middle Ramsey Creek	19	25	15	5	13	10
Lower Porter Creek	36.5	34.5	_	13.5	16	
Spruce Flats	35	34	25	10.5	7.5	12
Roaring Fork	58	67	42	22	25	24
Brushy Mountain	48.5	57.5	_	25	32	_
Bullhead Trail						
(Chestnut Oak Forest)	24	33	_	6.5	13	_
Greenbrier Pinnacle						
(Chestnut Oak Forest)	41	30.5	29.5	15	7.5	11
Greenbrier Pinnacle						
(Red Oak Forest)	35	18	_	5	27.5	_
Double Spring Gap	13.5	7	_	16.5	20.5	_

first time at the Greenbrier Pinnacle chestnut oak forest. Between 1947 and 1982, the Red-eyed Vireo appeared in two new localities (Middle Ramsey Creek cove forest, Roaring Fork hemlock-deciduous forest) and disappeared from a stronghold (Greenbrier Pinnacle red oak forest). Between 1982 and 1983, it declined sharply at Roaring Fork, but did not change appreciably elsewhere. No correlation between the population changes of the two vireo species was apparent.

Residents and short-distance migrants: overall numbers.—At nine localities, the total number of permanent residents and short-distance migrants did not change significantly between 1947–1948 and 1982 (Table 5). At the tenth, Greenbrier Pinnacle red oak forest, residents and shortdistance migrants increased by 450% ( $\chi^2 = 15.58$ , df = 1, P < 0.001). This overall increase was almost entirely due to an increase in Dark-eyed Junco (Junco hyemalis) populations (see below). Breeding populations in 1983 did not differ significantly from 1982 values at any of the four sites that were censused in consecutive years.

Residents and short-distance migrants: individual species. — The Blue Jay (Cyanocitta cristata), American Crow (Corvus brachyrhynchos), and

# TABLE 5

Dark-eyed Junco have increased dramatically since 1947–1948. In 1947–1948 Fawver found breeding jays at one of 10 study sites (a chestnut oak forest). In 1982–1983, I found breeding jays at seven localities, including cove forests, hemlock-deciduous forests, and oak forests. This increase was significant (P = 0.016, two-tailed sign test).

Of the American Crow, Fawver (1950) noted "[it] was seen only in areas of cutover and farm lands at lowest elevations in and around the park. None was found in census areas." In 1982–1983, I found crows at three sites. At Spruce Flats, I observed two adults and two fledglings, evidence of successful breeding. Elsewhere in the park, I saw crows almost daily along the roadside, especially at dawn.

Perhaps the greatest change in the avifauna was the increase of the Dark-eyed Junco. Fawver recorded it at six of the 10 study sites, where it was common only in the high elevation hemlock-deciduous and beech forests. In 1982, I found breeding juncos at nine of the study sites. The population increase was statistically significant (P = 0.04, two-tailed sign test). Today the Dark-eyed Junco may be the most common bird in the park after the Black-throated Blue Warbler (*Dendroica caerulescens*).

The absence of the Brown-headed Cowbird (*Molothrus ater*) is noteworthy. In over 9 weeks of field work, I never saw a cowbird inside the park, although they were common in cleared areas along park borders. Fawver did not record cowbirds at any of his study sites in 1947–1948.

### DISCUSSION

Discussion of these data must begin with the caveat that they cover only two or three points in time over a period of 36 years. Populations of small passerines may show such tremendous short-term variability that significant changes are apparent only with much more extensive data. Also, by conducting more counts per study site, I may have biased the data in favor of recording larger populations in 1982–1983 versus 1947– 1948. Therefore, conclusions from this study are at best preliminary.

Status of neotropical migrants. — There was no evidence of a widespread decline in neotropical migrants in the Great Smoky Mountains. As noted earlier, this is not the case for many small woodlots where populations of neotropical migrants have declined dramatically. Some of the species declining in small woodlots have not declined in the Great Smoky Mountains (e.g., Black-and-white Warbler [*Mniotilta varia*], Northern Parula, Ovenbird [*Seiurus aurocapillus*]). This suggests that declines in forest fragments may be due principally to the fragmentation process itself and not the loss of winter habitat. This idea is further supported by two additional lines of evidence. First, neotropical migrants in some fragments were declining as early as the late 1940s before Latin American defor-

estation was a critical problem (Wilcove 1985a). Second, until quite recently, deforestation was far more extensive in North America than in countries to the south. The settling of eastern North America during the 19th century saw the loss of perhaps half the original habitat available to forest-dwelling birds. In Latin America, extensive deforestation began with the post-World War II population boom. Recent estimates indicate that the amount of forest in Central America and the West Indies has been reduced by about 50% (Myers 1980), so that the amounts of breeding and wintering habitat may be roughly in balance. If so, the loss of winter habitat may not yet be a major factor in the decline of migratory passerines, although this will certainly change as more of the tropical forests are destroyed (see Wilcove and Terborgh 1984).

However, three factors make it impossible to interpret the present data as unambiguous evidence that tropical deforestation has not affected these birds.

First, any event that reduces the overall population of a species without destroying its breeding habitat will permit a reassortment of breeding pairs. Such a reassortment can take several forms, depending on the behavior of the birds and the quality of the breeding habitat (see Morse 1976). If tropical deforestation has reduced populations of these birds, the survivors may have moved into vacancies within large tracts such as the Great Smoky Mountains. Such behavior would greatly complicate any attempts to disentangle the relative contributions of tropical deforestation.

Second, it is conceivable that neotropical migrants in the Great Smoky Mountains winter in regions of the tropics that have been less heavily affected by tropical deforestation. While it is not possible to eliminate this hypothesis, at least one study indicates that most breeding populations of neotropical migrants scatter widely within the wintering range of the species (Ramos and Warner 1980; see also Wilcove and Terborgh 1984). Thus, it is unlikely that the birds in the Great Smoky Mountains all happen to winter in parts of Latin America that have been spared from deforestation.

Third, the accumulation of small biases in my sampling methods might obscure a relatively small decline. I began censusing birds earlier in the breeding season than did Fawver, and I conducted more counts per study site. All other things being equal, both factors would tend to increase my population tallies compared with Fawver's. However, in 1982, only three individual birds were sighted that unambiguously could be categorized as transients: one Northern Oriole (*Icterus galbula*) on May 20, and two Swainson's Thrushes (*Catharus ustulatus*) on May 23. Neither species breeds in the park (Stupka 1963). Other typically late migrants such as the Blackpoll Warbler (*Dendroica striata*) were not observed. Also, longterm census data from forest fragments show declines in breeding populations of neotropical migrants as great as 70% (Wilcove 1985a). Declines of this magnitude in the Great Smoky Mountains would probably be apparent despite the biases noted above.

Some of the trends involving individual species have interesting precedents elsewhere. Population fluctuations among vireos, similar to those noted in the Great Smoky Mountains, have been recorded in New Hampshire (Robinson 1981). The sharp decline in Black-throated Green Warblers between 1982 and 1983 matches observations by Hall (1984) in West Virginia, where this species shows pronounced population fluctuations based on censuses done at 5-year intervals.

Residents and short-distance migrants. - The increase in Blue Jays, Darkeyed Juncos, and American Crows within the park may be due to human activities in the surrounding areas. Bock and Lepthien (1976) report that the North American Blue Jay population increased by about 30% between 1962 and 1971. They attribute this increase to the growing popularity of winter feeding stations. The increase in the Great Smoky Mountains may represent a spillover from the burgeoning jay populations in more settled areas. The junco subspecies in the Great Smoky Mountains, Junco hyemalis carolinensis, is an altitudinal migrant (Stupka 1963); birds summering in the mountains descend to lower elevations during the winter. If the number of feeders around the park has increased since 1947, the juncos may be faring better during the winter, thus boosting their population. Since 1966, the U.S. Fish and Wildlife Service Breeding Bird Survey has recorded significant increases in crow populations in eastern North America (Robbins et al. 1986). Crows have probably benefited from forest fragmentation (Whitcomb et al. 1981) and waste corn left in fields after harvesting by machines (J. Terborgh, pers. comm.). Within the park, increased motor traffic has probably resulted in more road-kills, providing food for crows. The overall increase in nest predators such as the Blue Jay and American Crow in the Great Smoky Mountains is of concern, as nest predation has been linked to the decline of neotropical migrants in forest fragments (Wilcove 1985b).

Conservation implications. — The Great Smoky Mountains National Park has clearly been more successful at preserving populations of neotropical migrants than most small woodlots and urban parks. The results of this study suggest that any conservation plan for migratory birds should include at least some very large forest preserves (see also Askins et al. 1987). Within a large tract, such as the Great Smoky Mountains National Park, there is less chance of a shortage of food resources (Blake 1983) or a lack of critical microhabitats (Lynch and Whigham 1984), both of which are potential problems in small woodlots. Rates of nest predation and brood parasitism are also lower in larger tracts (Wilcove 1985b). Moreover, the larger populations of birds in extensive forest tracts are less vulnerable to stochastic extinction factors (Whitcomb et al. 1981). Yet even a preserve the size of the Great Smoky Mountains National Park is not immune to the effects of human activity and land development in surrounding areas, as shown by the increase in jays, crows, and juncos (see also Janzen 1986). Suburban communities will continue to grow at the expense of forested lands. As a result, our national parks and national forests may become increasingly important for the preservation of breeding populations of neotropical migrants. This study was possible only because of the fortuitous availability of older census data. It is crucial to the development of conservation plans for these birds that regular censuses be established within large national parks and forests. These censuses would provide an invaluable baseline for long-term studies of nongame birds.

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# LITERATURE CITED

- AMBUEL, B. AND S. A. TEMPLE. 1982. Songbird populations in southern Wisconsin forests: 1954 and 1979. J. Field Ornithol. 53:149–158.
- ASKINS, R. A., M. J. PHILBRICK, AND D. S. SUGENO. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. Biol. Conserv. 39:129–152.
- BLAKE, J. G. 1983. Trophic structure of bird communities in forest patches in east-central Illinois. Wilson Bull. 95:416–430.
- BOCK, C. E. AND L. W. LEPTHIEN. 1976. Changing winter distribution and abundance of the Blue Jay, 1962–1971. Am. Midl. Nat. 96:232–236.
- BRIGGS, S. A. AND J. H. CRISWELL. 1979. Gradual silencing of spring in Washington. Atlantic Natur. 32:19–26.
- BUTCHER, G. S., W. A. NIERING, W. J. BARRY, AND R. H. GOODWIN. 1981. Equilibrium biogeography and the size of nature reserves: an avian case study. Oecologia 49:29–37.
- DICKSON, J. G. 1978. Comparison of breeding bird census techniques. Amer. Birds 32: 10-13.
- FAWVER, B. J. 1950. An analysis of the ecological distribution of breeding bird populations in eastern North America. Ph.D. diss., Univ. Illinois, Champaign, Illinois.
- HALL, G. A. 1984. Population decline of neotropical migrants in an Appalachian forest. Amer. Birds 38:14–18.

- JANZEN, D. H. 1986. The eternal external threat. Pp. 286–303 in Conservation biology: the science of scarcity and diversity (M. Soulé, ed.). Sinauer Associates, Sunderland, Massachusetts.
- KENDEIGH, S. C. 1944. Measurement of bird populations. Ecol. Monogr. 14:67-106.
  - ------ AND B. J. FAWVER. 1981. Breeding bird populations in the Great Smoky Mountains, Tennessee and North Carolina. Wilson Bull. 93:218–242.
- LYNCH, J. F. AND D. F. WHIGHAM. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biol. Conserv. 28:287–324.
- MACKEY, H. E., JR. AND N. SIVEC. 1973. The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. Ecology 54:915–919.
- MORSE, D. H. 1976. Variables affecting the density and territory size of breeding sprucewoods warblers. Ecology 57:290–301.
  - 1980. Population limitation: breeding or wintering grounds? Pp. 505–516 in Migrant birds in the Neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- MYERS, N. 1980. Conversion of tropical moist forests. National Academy of Sciences, Washington, D.C.
- RAMOS, M. A. AND D. W. WARNER. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pp. 173-180 in Migrant birds in the neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithsonian Institution Press, Washington, D.C.
- ROBBINS, C. S. 1970. Recommendations for an international standard for a mapping method in bird census work by the International Bird Census Committee with explanatory notes. Aud. Field Notes 24:723-726.
  - 1979. Effect of forest fragmentation on bird populations. Pp. 198–212 in Workshop proceedings: management of north central and northeastern forests for nongame birds (R. M. DeGraaf, coord.). USDA Forest Serv. Gen. Tech. Rep. NC-51.
- ——, D. BYSTRAK, AND P. H. GEISSLER. 1986. The breeding bird survey: its first fifteen years, 1965–1979. USDI Fish and Wildlife Service Resource Publication 157.
- ROBINSON, S. K. 1981. Ecological relations and social interactions of Philadelphia and Red-eyed vireos. Condor 83:16–26.
- SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York.
- STUPKA, A. 1963. Notes on the birds of Great Smoky Mountains National Park. Knoxville, Univ. Tennessee Press, Knoxville, Tennessee.
- WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pp. 125–205 *in* Forest island dynamics in man-dominated landscapes (R. L. Burgess and D. M. Sharpe, eds.). Springer-Verlag, New York.
- WHITTAKER, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 22: 1–44.
- WILCOVE, D. S. 1985a. Forest fragmentation and the decline of migratory songbirds. Ph.D. diss., Princeton Univ., Princeton, New Jersey.
- ----- AND J. W. TERBORGH. 1984. Patterns of population decline in birds. Amer. Birds 38:10–13.
- WOODS, F. W. AND R. E. SHANKS. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology 40:349–361.