ASSESSING POPULATION TRENDS OF NEW HAMPSHIRE FOREST BIRDS: LOCAL VS. REGIONAL PATTERNS

RICHARD T. HOLMES AND THOMAS W. SHERRY

Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA

ABSTRACT.—We examined the changes in abundance between 1969 and 1986 of 19 forest-dwelling, mostly migratory bird species breeding in New Hampshire at 2 different scales: one local (an intensively studied 10-ha plot in unfragmented forest) and the other regional (Breeding Bird Surveys statewide). Twelve of the 19 species exhibited similar trends at both scales. Eight neither increased nor decreased, and 4 (Least Flycatcher, Winter Wren, Wood Thrush, and Swainson's Thrush) declined significantly. Others increased, decreased, or remained steady at one or the other scale. Overall, more species declined than increased both locally (8 vs. 1) and regionally (5 vs. 1). Comparisons of these patterns, combined with results of intensive studies at the local level, suggest that changes in food abundance and in vegetation structure related to forest succession on the breeding grounds, along with other processes that influence bird reproductive success and survivorship, are the most plausible explanations for most of the observed trends. Winter mortality was also identified as affecting breeding abundances, but only in short-distance migrant and permanently resident species. We have no evidence to indicate that the numbers of long-distance migrants were affected by events in their Neotropical wintering areas, although this possibility is difficult to assess from breeding-ground data. We urge caution in attributing declines of breeding forest migrant birds to tropical deforestation or similar causes until we either can eliminate alternate explanations that involve breeding-season events or have available critically needed demographic information on migrant populations in their wintering areas. *Received 18 March 1988, accepted 27 May 1988.*

SEVERAL studies have reported declining populations of songbirds in eastern North America (Aldrich and Robbins 1970, Temple and Temple 1976, Robbins 1979, Morse 1980, Ambuel and Temple 1982, Hall 1984, Holmes et al. 1986, Askins and Philbrick 1987, Johnston and Winings 1987). From analyses of breeding bird censuses, Morse (1980) noted that the species most affected seemed to be those that migrate to, and winter in, the Neotropics. These observations have led, largely inferentially, to the suggestion that events in tropical winter areas (such as forest destruction and other habitat alterations) may be of major importance in causing these population changes (Terborgh 1980, Lovejoy 1983, Rappole et al. 1983, Steinhart 1984, Leahy 1985, Wallace 1986, Marshall 1988).

As logical and provocative as this idea might be, there are major questions to be resolved. First, are North American songbirds actually declining, and if so which species are involved? Contrary to the citations above, analyses of Breeding Bird Surveys (BBS) conducted between 1966 and 1979 across North America indicate that most migratory bird species had either relatively stable population trends or actually increased. Only a few declined (Robbins et al. 1986). More recent BBS data suggest an apparent downward trend in some species since the late 1970s (C. S. Robbins and S. Droege pers. comm.). Such differing assessments may be due to species increasing in one area and decreasing in another; or to trends on small census plots not being representative of trends at larger, regional scales. It is important to consider what scale(s) should be used for examining population trends and what constitutes an adequate sampling unit (Wilcove and Terborgh 1984).

Assuming trends in abundance can be identified, a second question concerns the causes of these changes. There is little agreement on the factors that regulate songbird populations, especially the relative importance of seasonal events that affect species that migrate to tropical wintering areas (Greenberg 1980, 1986; Cox 1985). Theoretical arguments (Fretwell 1972, Alerstam and Hogstedt 1982) suggest that migratory bird species may be limited principally by events that affect overwintering survivorship. This is supported largely by circumstantial evidence for a few species, such as the Greater Whitethroat, *Sylvia communis* (Winstanley et al. 1974) and the Dickcissel, *Spiza americana* (Fretwell 1986), and by some investigations of bird community patterns that indicate little or at least infrequent resource limitation for birds during the breeding season at temperate latitudes (e.g. Wiens 1977, Wiens and Rotenberry 1980).

In contrast, other authors consider events on the breeding grounds to be equally or more important factors (e.g. Probst 1986, Holmes et al. 1986, Martin 1987). Fragmentation of forest habitats in eastern North America has been strongly implicated as one cause of lowered breeding densities of some songbird species (Robbins 1979, Whitcomb et al. 1981, Ambuel and Temple 1983, Wilcove and Whitcomb 1983, Lynch and Whigham 1984). Reduction of undisturbed forest interior breeding habitat, increased nest predation, or nest parasitism along forest edges are invoked (Mayfield 1978, Brittingham and Temple 1983, Wilcove 1985, Wilcove et al. 1986, Andren and Angelstam 1988). Moreover, natural changes in habitat characteristics that occur with succession, fluctuations in food availability and the occurrence of extreme weather events affect long-term densities of breeding birds in temperate forests (Holmes et al. 1986). Finally, Rappole and Warner (1980) and Cox (1985) have argued that migratory birds have probably long been limited by events in both the wintering and breeding areas.

To help resolve the question of whether songbirds in northeastern North America are in fact declining and, if so, what the probable causes might be, we compared 18 years of bird abundance data from a small (10-ha) study plot in New Hampshire with data for the same species and time period from Breeding Bird Surveys (BBS) throughout the state. We believe the study at Hubbard Brook, with its more intensive and consistent methodology, allows for greater precision in estimating bird densities, and uses intensive observational and experimental methods to determine potential limiting factors. In contrast, the broader scale data from the BBS, even with their inherent biases (see Discussion), help to establish perspective and generality concerning regional population trends.

Methods

Density Determinations

Local bird densities at Hubbard Brook.—Bird populations were censused during the breeding period, late May through early July, 1969–1986, in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. The study site consisted of a 10-ha gridded sector of a large unfragmented, second-growth northern hardwoods forest, dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). Censuses consisted of a modified spot-map procedure, supplemented by more detailed territory mapping, mist-net captures, observations of individually marked birds, and locations of nests. From these records, we estimated the number of adult individuals (males + females) of each species that occupied the 10-ha site during each year's breeding period. Detailed descriptions of the study site and of the census methods are given by Holmes and Sturges (1975) and Holmes et al. (1986).

Regional bird population trends in New Hampshire.—Breeding Bird Surveys (BBS) are coordinated by the U.S. Fish and Wildlife Service. In New Hampshire, these surveys were conducted each year along 19–23 routes. The starting points and directions of travel of each route were selected randomly from secondary roads within the state, given the limitation of the road system (C. S. Robbins pers. comm.). Each route was censused annually by a volunteer observer in June or early July at the peak of avian reproductive activity. Routes were 39.4 km in length; observers began the counts 0.5 h before sunrise, and stopped for 3 min at 0.8 km intervals, during which all birds seen or heard within 400 m were recorded (Robbins et al. 1986). These surveys were conducted on the same routes each year at approximately the same part of the breeding season, often but not always by the same observer. Routes were widely distributed throughout the state, and thus included deciduous and boreal forest, as well as forest edge, old fields, wetlands, and other successional habitats.

Data Analysis

Trends in bird abundance from New Hampshire BBS routes were determined from data collected between 1969 and 1986, using the "Route Regression" method (Geissler and Noon 1981, Geissler 1984). This procedure yielded bootstrap estimates for each species of the median "trend," from which the average % annual change was calculated, along with an estimate of variance of these trends among routes for each species. Statistical significance was determined with z-tests. Analyses of the BBS data were performed by U.S. Fish and Wildlife Service personnel, courtesy of C. S. Robbins and S. Droege.

Population trends for each species at Hubbard Brook between 1969 and 1986 were calculated differently, because only one estimate of abundance was available each year per species. Specifically, we calculated a simple linear regression model for the changing abundance of each species over time: $\log_e(\text{count}_i + 0.5) = \text{year}_i(\log_e[B]) + \log_e(A)$, where count_i is the abundance of birds/10 ha in year_i; 0.5 is an arbitrary constant added because the logarithm of zero is un-

TABLE 1. Population trends of forest birds at Hubbard Brook and in New Hampshire, 1969–1986, based on regression technique.

Bird species	Hubbard Brook			BBS
	Abundance[a] (mean ± SD)	Regression slope[b]	% annual change[c]	% annual change[d]
North temperate residents				
Downy Woodpecker (*Picoides pubescens*)	2.42 ± 1.40	−0.07 ± 0.03	−6.603*	+1.62 ± 0.43
Hairy Woodpecker (*Picoides villosus*)	1.83 ± 0.73	+0.00 ± 0.02	+0.087	+1.02 ± 0.21
White-breasted Nuthatch (*Sitta carolinensis*)	2.19 ± 1.58	−0.02 ± 0.02	−2.000	+3.66 ± 0.26*
Short-distance migrants				
Winter Wren (*Troglodytes troglodytes*)	1.22 ± 1.77	−0.10 ± 0.03	−9.560**	−5.23 ± 0.49*
Hermit Thrush (*Catharus guttatus*)	3.69 ± 2.51	−0.08 ± 0.03	−7.635*	−0.96 ± 0.47
Dark-eyed Junco (*Junco hyemalis*)	2.73 ± 3.15	−0.19 ± 0.03	−17.671***	−2.29 ± 0.46
Neotropical migrants				
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	3.31 ± 1.38	+0.00 ± 0.02	+0.013	−1.12 ± 0.43
Least Flycatcher (*Empidonax minimus*)	21.21 ± 18.9	−0.31 ± 0.05	−26.583***	−3.35 ± 0.21**
Veery (*C. fuscescens*)	2.47 ± 1.17	+0.02 ± 0.02	+1.490	−1.18 ± 0.18
Swainson's Thrush (*C. ustulatus*)	5.61 ± 3.31	−0.10 ± 0.02	−9.888***	−3.89 ± 0.35**
Wood Thrush (*Hylocichla mustelina*)	4.64 ± 2.83	−0.10 ± 0.02	−9.897***	−3.60 ± 0.15**
Red-eyed Vireo (*Vireo olivaceus*)	22.91 ± 4.52	−0.01 ± 0.01	−1.098	−0.35 ± 0.16
Black-throated Blue Warbler (*Dendroica caerulescens*)	10.58 ± 2.51	+0.02 ± 0.01	+2.115	−0.48 ± 0.43
Black-throated Green Warbler (*D. virens*)	8.75 ± 2.28	+0.00 ± 0.01	+0.294	−2.31 ± 0.43
Blackburnian Warbler (*D. fusca*)	3.17 ± 1.99	−0.07 ± 0.02	−6.318*	−1.33 ± 0.44
Ovenbird (*Seiurus aurocapillus*)	11.28 ± 3.48	+0.03 ± 0.01	+2.729*	−0.60 ± 0.12
American Redstart (*Setophaga ruticilla*)	28.67 ± 8.84	+0.00 ± 0.02	+0.013	−4.60 ± 0.24**
Scarlet Tanager (*Piranga olivacea*)	4.25 ± 1.96	−0.02 ± 0.02	−1.707	−0.58 ± 0.16
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	5.89 ± 1.95	−0.03 ± 0.01	−2.479	+2.87 ± 0.33

[a] Mean number of individual adult birds (males + females) per 10 ha in June (mid-breeding period).
[b] Least-squares regression slope of bird abundance against time (±SE of regression slope estimate—see text).
[c] Percentage annual change on 10-ha Hubbard Brook census plot (see text): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
[d] Percentage annual change (median ± SE, n = 19–23 BBS routes in New Hampshire); same significance levels as in footnote [c].

fined; $year_i$ is a number from 1–18 corresponding with the 18 yr of censuses, 1969–1986; $\log_e(A)$ and $\log_e(B)$ are fitted constants for the y-intercept and slope, respectively. The trend in original (non-log-transformed) units of abundance was calculated by taking the antilog of the slope in the above regression:

$$\text{trend} = e^{(\log_e[B] - 0.5[\text{variance}])},$$

where variance is the square of the standard error (SE) of the estimate of slope in the above regression. The variance term corrects for the asymmetry of the log-normal distribution (Geissler 1984). Finally, we transformed population changes to units of average % annual change: $(t - 1)(100)$, where t = trend. Trends in the Hubbard Brook bird abundances were considered statistically significant when the linear regressions had slopes that were statistically different from zero ($P < 0.05$), based on standard F-tests. We used the simple linear regression model because preliminary analyses showed that more complicated regression models (e.g. inclusion of a second-order polynomial term or the previous year's abundance as additional independent variables) rarely explained more variance in the log-transformed population abundances than did the simple model.

To compare year-to-year changes in bird abundance at the 2 scales, we calculated correlation coefficients (r) between the abundances of each species at Hubbard Brook and in New Hampshire (1969–1986). We used these as indicators of the degree of congruence in population changes within species. These correlations were considered statistically significant when $r > 0.47$, the critical value ($P < 0.05$) for 16 df.

RESULTS

Nineteen bird species occurred commonly (mean 18-yr density of ≥ 1 individual/10 ha) on the census plot at Hubbard Brook (Table 1). Taken together, their cumulative abundance increased in the first years of this study, reached a peak in 1971–1972, and then declined steadily to about one-third of peak abundance by 1986 (Fig. 1). A similar pattern held for the combined abundance of the same 19 species on the BBS routes (Fig. 1). The year-to-year patterns in cumulative abundance of these 19 species at Hubbard Brook and on the BBS routes were significantly correlated over the 18-year period (r = 0.79, $P < 0.01$).

The patterns imply a major decline in bird abundance at both Hubbard Brook and in New Hampshire among these 19 species. To understand this overall decline, however, one must look further at trends among individual species. For this purpose we categorized the species (Table 1) by the location of their wintering ranges (Holmes et al. 1986): north temperate residents, species that remain on the study area and in New Hampshire year-round (Fig. 2); short-distance migrants, that winter primarily in the mid-Atlantic states or southeastern U.S. (Fig. 2); and Neotropical migrants that migrate to the Caribbean basin (Fig. 3), Central America (Fig. 4), or South America (Fig. 5).

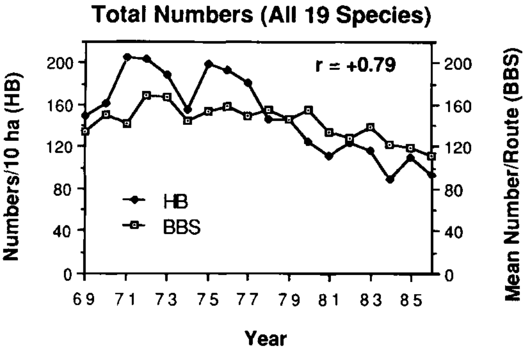

Fig. 1. Combined abundances of 19 selected species of forest-dwelling birds on the 10-ha study plot at Hubbard Brook (HB) and on the Breeding Bird Surveys (BBS) routes in New Hampshire, 1969–1986.

Linear Regression Analyses of Population Trends of New Hampshire Forest Birds

Local trends at Hubbard Brook.—Of the 19 species that occurred regularly on the Hubbard Brook study area, 8 populations declined significantly between 1969 and 1986, and 1 (Ovenbird) increased significantly (Table 1). The declining species included one permanent resident (Downy Woodpecker), all 3 short-distance migrants (Winter Wren, Hermit Thrush, and Dark-eyed Junco), and four Neotropical migrants (Least Flycatcher, Swainson's Thrush, Wood Thrush, and Blackburnian Warbler). The remaining 10 species fluctuated in abundance, but none exhibited a significant upward or downward trend.

Statewide trends in New Hampshire.—Based on data from all BBS routes in New Hampshire, 5 of the 19 species declined significantly in abundance (Winter Wren, Least Flycatcher, Swainson's and Wood thrushes, American Redstart), 1 increased (White-breasted Nuthatch), and 13 remained relatively stable between 1969 and 1985 (Table 1).

Comparisons between the local (Hubbard Brook) and regional (New Hampshire) trends for each species show a complex pattern (Table 1; see Table 2 for summary). Four species exhibited significant declines at both scales (Winter Wren, Least Flycatcher, Swainson's and Wood thrushes). Five declined at Hubbard Brook and showed no change in New Hampshire generally (Downy Woodpecker, Hermit Thrush, Blackburnian Warbler, and Dark-eyed Junco). One declined in New Hampshire with no upward or downward trend at Hubbard Brook (American Redstart), while 1 other (Ovenbird) increased significantly at Hubbard Brook but remained steady on the BBS counts. The White-breasted Nuthatch increased significantly on the BBS statewide, but remained stable at Hubbard Brook (Table 1).

When trends were examined by general location of wintering areas (Table 2), the only obvious pattern was for short-distance migrants, which all declined at both scales (Table 1).

Another way of considering the overall pattern of trends is to determine if either more or fewer species declined, relative to the null hypothesis of an equal number of increases and declines. Considering only individual population increases or decreases that were statistically significant (Table 1), 5 of the 19 declined and 1 increased on the BBS routes, while 8 species declined and 1 species increased at Hubbard Brook. Only the pattern at Hubbard Brook was statistically different ($\chi^2 = 5.4$, 1 df, $P < 0.05$). Overall, 9 species declined and 2 increased at 1 or both scales of investigation, which differs significantly from the null hypothesis of equal distribution ($\chi^2 = 4.5$, 1 df, $P < 0.05$). Although the number of species considered was small, we interpret these results to indicate that more

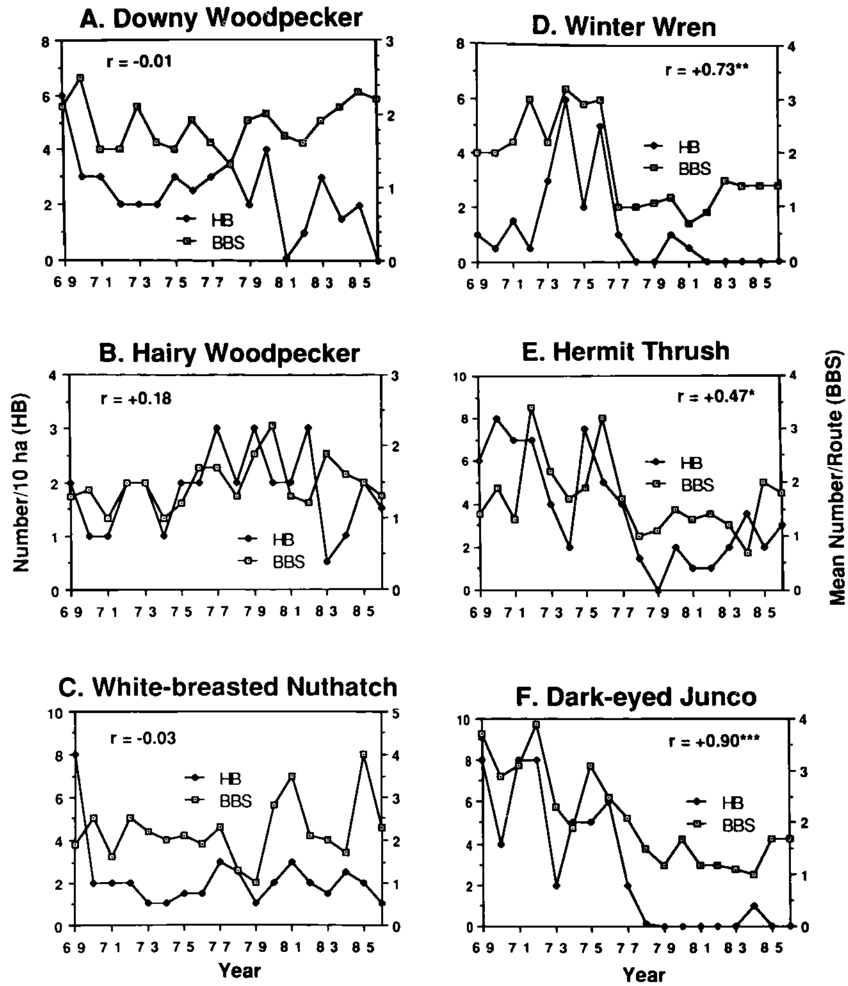

Fig. 2. Abundances of permanently resident (A–C) and short-distance migrant (D–F) bird species at Hubbard Brook (HB) and in New Hampshire (BBS), 1969–1986. Asterisks in Figs. 2–5 refer to those species that exhibited statistically significant correlations. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

species declined than increased when compared with the null hypothesis.

Correlational Analyses of Year-to-year Patterns in Abundances of New Hampshire Forest Birds (1969–1986)

The abundance patterns of forest birds at Hubbard Brook and in New Hampshire as a whole exhibited marked year-to-year variability which was often masked in the linear trends. American Redstarts, for example, showed no significant linear change at Hubbard Brook (Table 1), although they clearly increased from 1969 to ca. 1977. They gradually decreased thereafter (see Fig. 3D). If the regression analysis had been performed on just the data since 1977, a significant decline would probably result. Similarly, Yellow-bellied Sapsuckers at Hubbard Brook appear to have declined since the mid-1970s (Fig. 3A), as have Red-eyed Vireos at the New Hampshire level (Fig. 5C), yet the regression results indicate no significant change. These observations confirm that simple regression methods are often not appropriate for species with complex long-term abundance patterns (Geissler and Noon 1981), and illustrate the need for other analyses that consider year-to-year patterns in abundances. Consequently, we compared the correlations between population

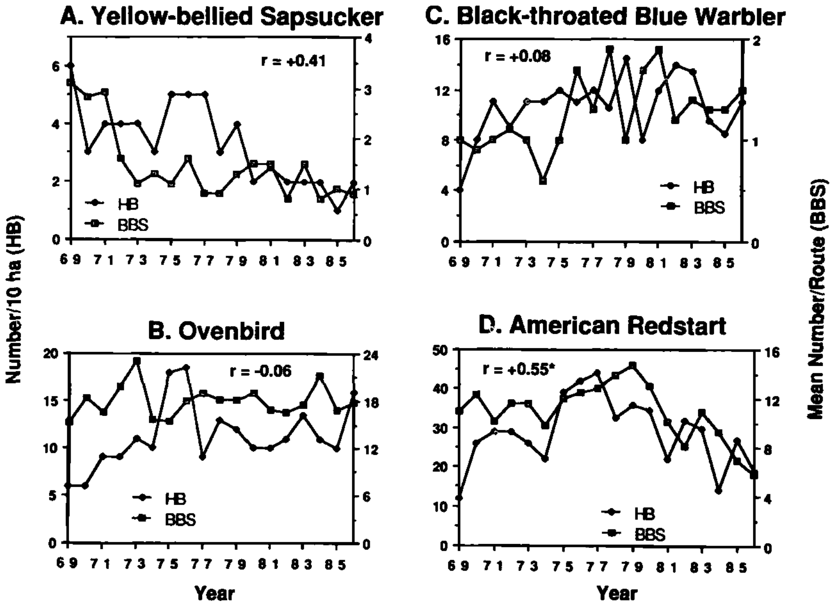

Fig. 3. Abundances of long-distance migrant, Caribbean-wintering bird species at Hubbard Brook (HB) and in New Hampshire (BBS), 1969–1986.

trends on the local scale at Hubbard Brook with those statewide on the BBS. The species again were grouped by major wintering areas.

North temperate residents.—Abundances of permanently resident species were low throughout the study period (Fig. 2A–2C), making assessments of their population changes difficult. Nevertheless, the numbers of all 3 species

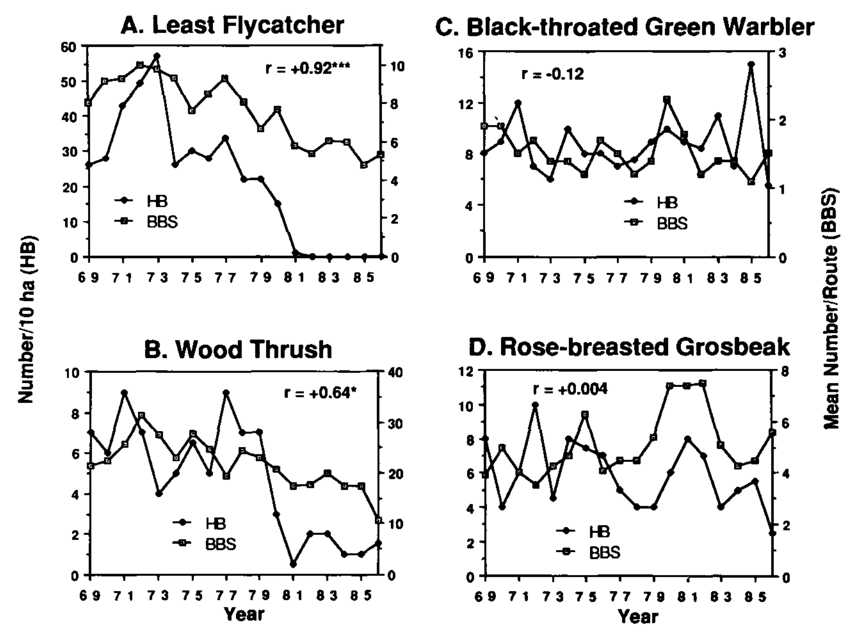

Fig. 4. Abundances of long distance migrant, Central American-wintering bird species at Hubbard Brook (HB) and in New Hampshire (BBS), 1969–1986.

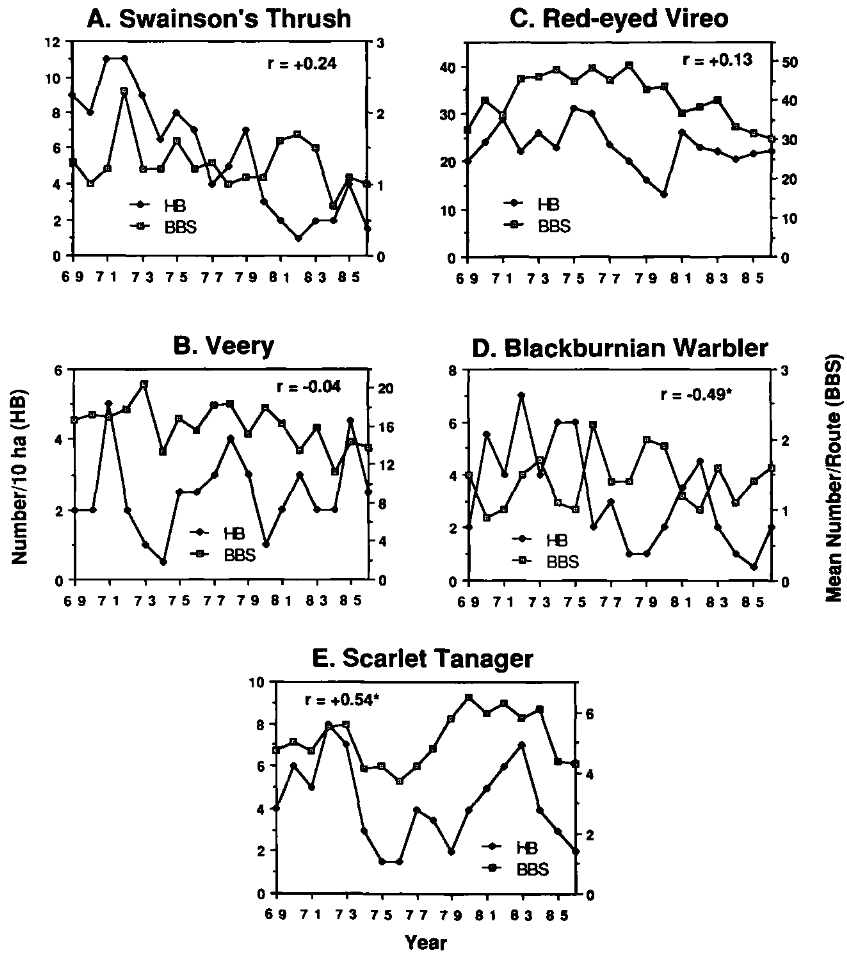

Fig. 5. Abundances of long distance migrant, South American-wintering bird species at Hubbard Brook (HB) and in New Hampshire (BBS), 1969-1986.

declined between the summers of 1969 and 1970 at Hubbard Brook but not statewide. After 1971, all 3 fluctuated in abundance, often asynchronously, at both scales. Year-to-year changes at Hubbard Brook were not significantly correlated with those from the BBS for any 1 of these species (Fig. 2).

Short-distance migrants.—The year-to-year abundances of each of the 3 short-distance migrants were positively and significantly correlated at the local (HB) and statewide (BBS) levels (Fig. 2D-2F). Trends for Hermit Thrush and Dark-eyed Junco were largely synchronous, with that of the Winter Wren showing similar declines at both scales in some years (e.g. 1977, Fig. 2).

Neotropical migrants.—Because Neotropical migrants were of particular interest, we consider the 13 species in this category by Neotropical subregions that represent the presumed center of their wintering ranges: Caribbean basin, Central America, and South America (Holmes et al. 1986).

Four of the 13 Neotropical migrants winter primarily in the Caribbean basin, which includes the Greater Antilles and the Caribbean lowlands of Mexico, Central America and northern South America. Of these 4, only the relationship for the redstart was statistically significant (Fig. 3). Redstart numbers increased at both sampling scales from the late 1960s through the late 1970s, and then gradually declined through 1986. No correlations were found between the abundance patterns at Hubbard Brook and New Hampshire for either Ovenbirds or Black-throated Blue Warblers (Fig. 3). Ovenbirds exhibited nearly stable abundances on the BBS routes throughout the 18-year period, while there was an increasing trend at Hubbard Brook prior to the mid-1970s (Fig. 3, see Table 1). Numbers of Black-throated Blue Warblers recorded on the BBS were low (Fig. 3), but this species tends to occur in forest interior away from roadsides.

Four of the 13 species winter primarily in Central America from Mexico to northern South America. The population trends of 2, the Least Flycatcher and Wood Thrush, showed significant positive intraspecific correlations between Hubbard Brook and the statewide BBS (Fig. 4). Both species declined through the 18-year period at both Hubbard Brook and in New Hampshire (Fig. 4). Abundances of the other 2 species in this group, the Rose-breasted Grosbeak and the Black-throated Green Warbler, were not closely correlated at the 2 scales (Fig. 4).

Of the 5 species that winter primarily in South America, only Scarlet Tanager abundances were significantly positively correlated at the 2 sampling scales (Fig. 5). Tanagers exhibited almost a cyclic pattern, with peak numbers in 1972, 1973, and again in 1980–1983; the pattern was more pronounced at Hubbard Brook (Fig. 5). Changes in the Blackburnian Warbler populations at Hubbard Brook and statewide were significantly negatively correlated, which implies that very different factors were affecting these populations at the 2 scales (Fig. 5). However, as with other species in our sample, the numbers of Blackburnian Warblers in the samples were low. Swainson's Thrush declined significantly at both scales (Table 1), but they were not significantly correlated at the 2 sampling scales (Fig. 5).

Populations of these species often fluctuated similarly at both local and regional scales, with statistically significant positive correlations for 7 of the 19 species (Figs. 2–5), and 1 significant negative correlation (Blackburnian Warbler, Fig. 5D). Of the winter-area groups, the short-distance migrants seemed to exhibit the most similar patterns of fluctuation from year to year (Fig. 2D–2F).

TABLE 2. Summary of the abundance trends of 19 forest bird species at Hubbard Brook (HB) and on Breeding Bird Surveys (BBS) in New Hampshire from 1969–1986 (see Table 1) and their major wintering areas (Holmes et al. 1986).

	Main winter area
HB steady, BBS steady[a]	
Hairy Woodpecker	North Temperate
Yellow-bellied Sapsucker	Caribbean
Veery	South America
Red-eyed Vireo	South America
Black-throated Blue Warbler	Caribbean
Black-throated Green Warbler	Central America
Scarlet Tanager*[b]	South America
Rose-breasted Grosbeak	Central America
HB decline, BBS steady	
Downy Woodpecker	North Temperate
Hermit Thrush*	South Temperate
Blackburnian Warbler*	South America
Dark-eyed Junco***	South Temperate
HB increase, BBS steady	
Ovenbird	Caribbean
HB steady, BBS decline	
American Redstart*	Caribbean
HB steady, BBS increase	
White-breasted Nuthatch	North Temperate
HB decline, BBS decline	
Least Flycatcher***	Central America
Winter Wren**	South Temperate
Swainson's Thrush	South America
Wood Thrush*	Central America

[a] Trends based on linear analyses (see Table 1).

[b] Asterisks refer to those species that exhibited statistically significant correlations between abundances at Hubbard Brook and in New Hampshire (BBS routes), 1969–1986 (see Figs. 2–5).

DISCUSSION

Forest birds in New Hampshire have declined at least among the subset of species we considered. Between 1969 and 1986, the combined abundance of the 19 bird species on the Hubbard Brook census plot and on the BBS routes in New Hampshire declined sharply. Among the individual species, more exhibited significant declines than increases at both the local (8 vs. 1) and regional (5 vs. 1) scales (Table 1); 4 species (Winter Wren, Least Flycatcher, Swainson's and Wood thrushes) declined significantly at both scales. Furthermore, visual examinations of the data imply that population declines for some species (e.g. sapsucker and redstart, Fig. 3; Least Flycatcher and Wood Thrush, Fig. 4; Swainson's Thrush and Red-eyed Vireo, Fig. 5) have become more pronounced since the early 1980s, a trend consistent with recent analyses of BBS data for eastern North America (C. S. Robbins and S. Droege pers. comm.). On the other hand, some species increased on at least 1 scale of analysis, and nearly all species fluctuated widely in abundance (Figs. 2-5). Thus, although some bird populations have declined, the patterns are complex and vary among species.

An overall decline in bird abundances coupled with the fact that the most common species considered winter in the Neotropics (see Table 1) make it easy to infer that events in these Neotropical wintering areas may be causing the declines. This line of argument has led to the popular idea that tropical deforestation is currently having an effect on the breeding populations of some songbirds. However logical this may be, it is difficult to prove, at least from the data at hand. Indeed, considerations of the most probable causes for population changes in the Neotropical-migrant species in New Hampshire birds illustrate the problems involved, and lead to a number of equally plausible alternate hypotheses that involve events on the breeding grounds. Our arguments follow.

Analyses of numerical trends alone tell little if anything about what factors may be causing the population trends. Information from the long-term and intensive studies of birds at Hubbard Brook suggests that many factors affect the numbers of breeding birds. These include changes in food abundance, gradual changes in forest structure as a result of secondary succession, weather on breeding grounds, and events that occur away from the breeding area (Holmes et al. 1986). Similar factors were identified as important in affecting the numbers of Kirtland's Warblers (*Dendroica kirtlandii*) in Michigan (Probst 1986) plus cowbird (*Molothrus ater*) brood parasitism, which has not yet been recorded at Hubbard Brook (R. T. Holmes pers. observ.).

Effects of food abundance.—Increased abundance of most warblers, thrushes, the Scarlet Tanager, Least Flycatcher, and Red-eyed Vireo at Hubbard Brook during the first 2-3 yr of this study coincided with the irruption of a defoliating caterpillar (Holmes and Sturges 1975). During the years of the outbreak, food was abundant in midsummer during and just after fledging of young. This was correlated with high survivorship and high returns of birds in subsequent years (Holmes et al. 1986). Similar increases in abundance in the early 1970s occurred on the BBS in only a few species, e.g. Wood Thrush and Least Flycatcher (Fig. 4A, 4B), Swainson's Thrush (Fig. 5A), and American Redstart (Fig. 3D). This suggests little regional effect of that particular insect outbreak. It appears that most irruptions of defoliating caterpillars in northern hardwoods forests are erratic in space and time, common in one location one year, and somewhere else the next. As a result, the probability that any particular forest stand will experience an outbreak in a given year is quite low (Holmes in press). Subsequently, no major outbreak has occurred at Hubbard Brook since the one in the early 1970s, even though some have occurred in other parts of the state (Holmes in press). This "boom and bust" nature of a major component of the food supply probably accounts, at least in part, for the peak in bird numbers at Hubbard Brook in the early 1970s and the gradual decline thereafter (Fig. 1).

The possibility that summer food may regularly limit temperate forest birds is supported further by recent studies of food availability and bird demography at Hubbard Brook (Rodenhouse 1986, Holmes in press). These demonstrate that abundance and availability of food, particularly Lepidoptera larvae, significantly affect the frequency of renesting, second-brood attempts, nestling starvation, growth rates, fledging and hatching success, and to some extent clutch size of breeding passerines (Rodenhouse 1986 and in prep.). In a recent review, Martin (1987) similarly concluded that food is often limiting for birds in temperate habitats.

Habitat change.—Although the numbers and abundances of bird species, especially Neotropical migrants, have decreased with increased fragmentation of their breeding habitat, this does not account for the patterns of population change at Hubbard Brook, which is in an unfragmented forest. It is also probably not now a major factor over most of New Hampshire, where forests predominate and where urban development is only beginning to affect the landscape.

Nevertheless, habitat change on a more local scale can affect species distributions and abundances. Species with particular habitat associations may change in abundance locally as that habitat (especially, the physical structure of the vegetation) changes over time, i.e. as the vegetation undergoes natural succession (Johnston and Odum 1956). Holmes et al. (1986) hypothesized this as the major cause of the decline in Least Flycatchers at Hubbard Brook. This species tends to settle in forests with relatively open subcanopies beneath a dense upper canopy (Sherry 1979), a condition that occurs during intermediate successional stages in northern hardwoods (Aber 1979). Bond (1957) also reported that Least Flycatchers occurred in mid-stages of forest succession in Wisconsin. The loss of this once abundant species from the Hubbard Brook study area accounts for a large part of the decline in overall bird numbers there since the early 1970s (Fig. 1). Its decline on New Hampshire BBSs may also reflect gradual maturing of forests and woodlands around the state as they recover from the extensive clearing of the late nineteenth and early twentieth centuries (Irland 1982). The 20-year trends for Least Flycatchers on BBS routes in other New England states are variable (decreasing in Massachusetts and Connecticut, but only statistically significant in the former; increasing in Vermont and Maine, significant only in Vermont [Droege and Sauer 1987]). This suggests that regional land-use patterns may be very important in affecting habitat suitability for this species. These differences among adjacent states and the fact that the 20-year continental trend of Least Flycatchers on all BBS routes across North America showed no significant change (Droege and Sauer 1987) seem to rule out events in winter or on migration as likely causes for the declines in New Hampshire.

Other species that might be affected by changing structure of the habitat include American Redstarts and Wood Thrushes, which also reach maximal densities in mid-successional forests (Bond 1957). Changes in the abundances of Swainson's Thrushes might be similarly related to vegetation changes, although little is known about its habitat associations and preferences.

Climatic events in the breeding areas.—Inclement weather can affect bird survival and nesting success. In late May 1974, a week of cold wet weather in New Hampshire resulted in the death of many birds, mostly from starvation (Zumeta and Holmes 1978). Those most affected were species, such as swallows and kingbirds, that feed on large flying insects in more open habitats. At Hubbard Brook, adult Scarlet Tanagers, particularly males, were found dead on the study plot. Their numbers in that year and several subsequent ones were markedly reduced (Fig. 5). Moreover, tanager numbers dropped notably in 1974 on the BBS counts, demonstrating the regional effect of this storm.

Climatic events in the wintering areas.—Hermit Thrush, Dark-eyed Junco and to some extent Winter Wren, all short-distance migrants, exhibited synchronous trends in abundance at both Hubbard Brook and overall in New Hampshire. The sharp declines in breeding densities in 1973, 1977, and 1978 coincided with the occurrence of severe weather in the southeastern United States during the preceding winters (Holmes et al. 1986). This is another example (Winstanley et al. 1974, Fretwell 1986) of circumstantial evidence for winter mortality influencing the numbers of breeding birds over a relatively large part of their breeding ranges. Furthermore, the Winter Wren and Dark-eyed Junco subsequently remained at low population levels both at Hubbard Brook and statewide. Presumably such winters can depress population sizes and many years may be required for the populations to recover.

Another set of species affected by winter conditions are the permanent residents, 2 woodpeckers and a nuthatch, all of which are bark-foragers. Their drop in numbers at Hubbard Brook between 1969 and 1970 was correlated with a severe late-winter ice storm (Holmes and Sturges 1975), which either resulted in direct mortality of overwintering birds or had indirect effects through reducing food availability (Holmes et al. 1986). The importance of winter weather in the regulation of species permanently resident in the temperate zone is generally accepted (e.g. Fretwell 1972, Graber and Graber 1983, Nilsson 1987).

Winter events in the Neotropics.—For the Neotropical migrants, there was no clear relationship between population declines or fluctuations and wintering locations (Table 2). Of the 13 such species we considered, 3 (Least Flycatcher, Swainson's Thrush, and Wood Thrush) declined significantly at both scales in New Hampshire. The decline of all 3 at Hubbard Brook and perhaps elsewhere in New Hampshire may be related to changes in the successional status of the forest vegetation during the last 20 yr, as discussed above. BBS data indicate that Least Flycatcher, Wood Thrush, and Swainson's Thrush abundances neither increased nor decreased from 1966 to 1979 in the eastern half of the U.S. (Robbins et al. 1986). This suggests that events in the winter grounds did not have long-term or large-scale effects on these species. It also implies that the habitat change explanation postulated above is pertinent mainly to

New Hampshire and not to all parts of the breeding ranges of these 3 species. A Swainson's Thrush decline in a local area of the Sierra Nevada in California, was interpreted (Marshall 1988) as most likely due to events in the winter grounds.

The other 10 Neotropical species either declined at Hubbard Brook, declined statewide, or remained steady. We believe that large scale effects in winter areas were either not important or were not detectable from our data. This raises an important point. It is very difficult to detect the effects of events during a species' migration or winter season on subsequent numbers of breeders (Wilcove and Terborgh 1984, Svensson 1985). For instance, if only a portion of a species population was affected by some event in winter (e.g. habitat destruction, a hurricane, or drought), this may not be apparent on a single or even a large number of breeding-bird censuses in North America, especially if there was considerable mixing of birds from different parts of the breeding range in any one particular winter area (Ramos and Warner 1980, Wilcove and Terborgh 1984). Although Neotropical migrants are known to return to very specific sites in winter (e.g. Loftin 1977, Faaborg and Arendt 1984, Kricher and Davis 1986) and in the breeding season (Welty 1982), there is little information on how close together individuals from the same breeding area might be in the winter and vice versa. If mixing is high, then local events in the Tropics, including deforestation, will be hard to detect subsequently in the species' breeding grounds. If there is little or no mixing, a local scale event on the winter grounds might affect numbers on some breeding plots but not on others. In any event, such effects would be difficult to detect.

To understand the rôle of events in the nonbreeding season, demographic and population studies of migrants in their wintering areas, especially mortality rates, sources of mortality, site return capacities, possible limiting factors, etc., are required (Greenberg 1980). Ultimately, data will also be needed on events during migration. Because such information is currently unavailable for any Neotropical migrant species, we urge caution in attributing breeding-season declines in bird populations, especially those of the Neotropical migrants, to what might be happening in the winter areas.

Local vs. regional analyses of bird population trends.—Bird population trends at the regional and larger scales, such as those from the Breeding Bird Surveys, reflect the integrated results of numerous factors that affect bird abundances, and by themselves do not provide evidence or insight on the causes of the observed changes, including events on the wintering areas. This is particularly true as we know almost nothing about where particular breeding populations of these species winter, and vice versa. Also, it must be remembered that BBS data are based on a series of roadside counts, each of which is made only once per year; sometimes by the same observer, sometimes not. The routes are widely scattered, cover a diverse set of habitats, and therefore include counts of birds in a mix of pastures, old fields, wetlands, and forest edge, always along roadsides. This makes it difficult to separate patterns that may occur within particular habitat types or to assess the effects of density-dependent habitat selection (Rosenzweig 1985) as populations decline or increase. Nonetheless, the relatively high agreement and correlations we found between bird population trends from BBS and Hubbard Brook data (12/19 species, Table 2, Figs. 2-5) suggest that the BBS results may, despite their biases, be useful for identifying large scale trends in bird abundance and for providing perspective about the generality of those trends.

Studies at the local scale, such as Hubbard Brook, provide a measure of population trends, but perhaps more importantly, a basis for understanding causes of the observed changes. The finding that regional trends in abundances in New Hampshire are often closely mirrored on the Hubbard Brook plot means that local censuses may be useful in monitoring the abundances of some species. Finally, given current technology and financial limitations, it is probably only at the local level that alternate hypotheses about the effects of habitat selection, food abundance, and various sources of mortality on bird populations can be tested, experiments performed, and where resources and demography and demographic processes can be quantified. At the present time, it is premature to attribute observed population trends in North American songbirds to any one causal factor. Many processes are undoubtedly involved and each species must be considered separately. Tropical deforestation may be affecting populations of some migratory songbird species, but alternate explanations that involve breeding season events must be eliminated before we can conclude that it is the only, or even a major, factor of importance.

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