THIRTY-YEAR BIRD POPULATION TRENDS IN AN UNFRAGMENTED TEMPERATE DECIDUOUS FOREST: IMPORTANCE OF HABITAT CHANGE

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ABSTRACT.—Abundances of forest birds in an unfragmented, undisturbed, and relatively mature temperate deciduous forest at the Hubbard Brook Experimental Forest, New Hampshire, changed markedly between 1969 and 1998. Total numbers of birds (all species combined) declined from 210–220 individuals/10 ha in the early 1970s to 70–90/10 ha in the 1990s. Of the 24 regularly occurring species, 12 decreased significantly (four to local extinction), three increased significantly, and nine remained relatively constant in abundance. Nine of the 12 declining species were Neotropical migrants. Most species exhibited similar trends on Breeding Bird Survey (BBS) routes in New Hampshire during the same 30 year period and on three replicate study sites in nearby sections of the White Mountains from 1986–1998. Probable causes of trends were diverse and differed among species. Most could be accounted for by individual species' responses to events occurring primarily in the local breeding area. The most important local factor affecting bird abundance was temporal change in forest vegetation structure, resulting from natural forest succession and local disturbances. Four species that declined markedly and in some cases disappeared completely from the study plot (Least Flycatcher, *Empidonax minimus*; Wood Thrush, *Hylocichla mustelina*; Philadelphia Vireo, *Vireo philadelphicus*; and American Redstart, *Setophaga ruticilla*) appear to attain peak abundance in early or mid successional forests. Species preferring more mature forests, such as Black-throated Green Warbler (*Dendroica virens*) and Ovenbird (*Seiurus aurocapillus*), increased significantly in abundance over the 30 year study. Other important factors influencing bird abundances were food availability and events in the migratory and winter periods. Nest-predation rates, although varying among years, showed no long-term pattern that would account for population declines, and brood parasites were absent from this forest. Findings from this study demonstrate that major changes in bird abundances occur over time even in undisturbed and relatively mature forests, and illustrate the need for considering habitat requirements of individual species and how habitat suitability changes over time when trying to assess the causes of their long-term population trends. The results also imply that any conclusions about the effects of other factors affecting forest bird abundances, such as increased nest predation or brood parasitism associated with habitat fragmentation, must also account for successional changes that may be affecting habitat suitability. *Received 28 July 2000, accepted 28 February 2001.*

MANY SPECIES AND POPULATIONS of North American birds have undergone declines in abundance in recent decades, especially migratory songbirds. Some species have declined throughout their breeding range (Robbins et al. 1989, Peterjohn et al. 1995), whereas others have declined in some regions but remained stable or even increased in others (James et al. 1996). The extent and causes of such changes in abundance are much debated (Askins et al. 1990, Hagan and Johnston 1992, Rappole and McDonald 1994, 1998; Sherry and Holmes 1995, 1996; Martin and Finch 1995, Latta and Baltz 1997, Askins 2000). Some explanations have focused on the effects of deforestation and other changes in the tropical habitats where many of these species winter, whereas others emphasize habitat degradation and events in the north temperate breeding grounds. For the latter, extensive fragmentation of large tracts of forest land, with associated increases in nest predation and in brood parasitism by Brown-headed Cowbirds (*Molothrus ater*), is perhaps the most frequently cited factor affecting the abundances of breeding songbirds in North America (Brittingham and Temple 1983, Wilcove and Robinson 1990, Askins et al. 1990, Böhning-

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Gaese et al. 1993, Donovan et al. 1995, Robinson et al. 1995a,b; Fauth 2000).

As a result of those reported declines, research on bird populations, especially long-distance migrants, has expanded greatly in recent years. Many studies have considered effects of habitat fragmentation, forest edges, and other human-mediated changes at both local and landscape scales in breeding and wintering areas as well as along migratory routes (see Keast and Morton 1980, Hagan and Johnston 1992, Martin and Finch 1995, Schmidt and Whelan 1999, Askins 2000). However, relatively few data exist on the degree to which bird populations are changing, or have changed, in undisturbed or unfragmented habitats. Several studies have compared bird abundances at one site over long (e.g. 20–50 year) time intervals (e.g. Ambuel and Temple 1982, Marshall 1988, Wilcove 1988, Kirk et al. 1997), whereas others have tracked populations on a year-to-year basis at single localities (Kendeigh 1982, Leck et al. 1988). In the latter two investigations, in particular, the areas surrounding the study areas had changed in the intervening years, due to human development and increased isolation from other similar habitat, providing interesting but confounded conditions for assessing population trends. Similarly, the continent-wide Breeding Bird Survey (BBS) provides long-term abundance data on bird populations, but those are derived from roadside counts where nearby habitats are subject to encroaching fragmentation and other human-mediated change (e.g. Peterjohn et al. 1995, 1997). Long-term quantitative data on bird populations in undisturbed habitats are rare (see Holmes et al. 1986, Enemar et al. 1994, Wesolowski and Tomialojc 1997 as examples), yet information from such sites can be useful for understanding what factors determine bird abundances locally and for providing a control against which to compare population changes occurring in more human-influenced habitats.

In this paper, we document changes in bird populations within an unfragmented, relatively mature northern hardwood forest in the White Mountain National Forest, New Hampshire. We present data from the Hubbard Brook Experimental Forest for a continuous 30 year period (1969–1998), updating the long-term record on bird-population trends for that site (Holmes and Sturges 1975, Holmes et al. 1986, Holmes and Sherry 1988). We also provide comparative data on abundances of the same bird species on three replicate forest plots in nearby sections of the White Mountain National Forest from 1986–1998 and on BBS routes across the state of New Hampshire from 1969–1998. These data sets provide a regional perspective to population trends recorded at Hubbard Brook. We interpret causes of observed trends on the basis of available information about requirements of each species, taking advantage of our own intensive ecological and demographic studies of selected species in that same forest and, in some cases, in their winter quarters. We also take into account possible vegetation changes in this forest site that may have influenced the abundances of bird species occurring there. Results demonstrate that bird abundances change, sometimes drastically, even within relatively undisturbed forest habitats, and provide a long-term baseline for population changes of New England forest birds.

STUDY SITES

This study was conducted in the Hubbard Brook Experimental Forest, West Thornton and Woodstock, New Hampshire and in surrounding sections of the White Mountain National Forest. In the mid 1960s, forest within the Hubbard Brook valley was described as ''mature second growth'' (Bormann et al. 1970:377), ''representative of the climax'' (Whittaker et al. 1974:233), although still accumulating biomass (Bormann and Likens 1979). Recent evidence suggests that tree biomass accumulation began leveling off in the 1980s (T. G. Siccama unpubl. data) due to approaching steady-state conditions and perhaps to cation-leaching effects of acid precipitation reducing forest productivity (Likens et al. 1996).

Birds were censused from 1969 to 1998 on a 10 ha gridded plot, located within continuous, northern hardwood forest (see Holmes and Sturges 1975, Holmes et al. 1986, and Holmes 1990). From 1986 to 1998, we also censused birds on three additional 10 ha plots in nearby parts of the White Mountain National Forest, which were at the same elevation and aspect and had similar cutting history and vegetation characteristics as Hubbard Brook. Those replicate plots were located (1) on the southeast slope of Mount Moosilauke, 8 km north of Hubbard Brook, in Woodstock, New Hampshire, (2) on Stinson Mountain, 13 km to the southwest, in Rumney, New Hampshire, and (3) near Russell Pond, 11 km to the northeast, in Thornton, New Hampshire. All were situated within large tracts of continuous forest but on different mountain systems separated by inter-

TABLE 1. Tree species composition of the Hubbard Brook study area (1987) and of the three replicate study sites (1986) in the White Mountain National Forest, New Hampshire, as measured by the point quarter method (Cottam and Curtis 1956). See text for scientific names for plant species.

Size class/tree species	Importance value[a]			
	Hubbard Brook	Moosilauke	Russell Pond	Stinson Mountain
2–10 cm DBH[b]				
Sugar maple	32.8	40.3	43.5	44.0
American beech	50.4	30.5	41.4	35.6
Yellow birch	1.4	7.3	3.0	4.2
White ash	0.0	0.0	2.4	1.4
Striped maple	11.0	16.4	4.5	6.5
Red spruce	2.4	2.2	0.0	2.1
Other species	2.0	3.3	5.2	6.2
10.1–20 cm DBH				
Sugar maple	43.0	49.6	43.8	29.9
American beech	40.1	19.6	38.1	32.0
Yellow birch	9.2	16.4	7.1	10.4
White ash	0.6	2.1	4.1	14.1
Striped maple	1.7	6.1	1.2	9.2
Red spruce	0.8	1.0	0.0	0.7
Other species	4.6	5.2	5.7	3.8
>20 cm DBH				
Sugar maple	39.7	27.1	40.0	39.7
American beech	25.6	33.6	28.8	31.6
Yellow birch	22.5	23.0	14.7	9.6
White ash	10.4	9.2	13.0	17.0
Others	1.8	7.0	3.5	2.1

[a] Importance value = 100 (relative basal area + relative density + relative frequency)/3.

[b] DBH = diameter at breast height.

vening valleys containing roads, agricultural lands, and human habitations. All were on south-southeast facing slopes and at elevations of 500–600 m above sea level, and all contained at least one permanent stream, along with additional intermittent water courses. Each plot was situated within forest tracts that had been selectively logged in the early 1900s, but had remained free of any direct human disturbance since that time. Influences of natural disturbances such as a major hurricane in 1938, fungal pathogens, and sporadic ice and wind storms (Merrens and Peart 1992, Leak and Smith 1996) appear to have been similar across those sites, although an ice storm in 1998 was most severe at Stinson Mountain.

Inventories of forest trees made in 1986–1987 showed that vegetation on those replicate plots was similar to that on the long-term census plot at Hubbard Brook (Table 1, see below). All four plots were dominated by American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), with occasional white ash (*Fraxinus americanus*) and red spruce (*Picea rubens*), and forest canopies averaged 20–25 m in height. The shrub layer on each plot consisted primarily of hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and seedlings and saplings of the dominant tree species (except yellow birch and white ash, which were essentially absent from the shrub layer). Some vegetational differences did occur among plots: the Moosilauke site had relatively fewer large sugar maples than the other three sites, whereas Russell and Stinson had relatively more white ash and less yellow birch (Table 1). In the mid 1980s, the shrub and sapling layers at Hubbard Brook and Moosilauke were thicker, contained more striped maple (Table 1) and hobblebush, and were more heterogeneous than at the other two sites (see Holmes et al. 1996).

METHODS

Birds were censused annually from late May through early July, using methods described by Holmes and Sturges (1975). Those methods, which we used consistently throughout the study on all plots, consisted of timed censuses along transects and extensive territory mapping, supplemented by information on nest locations, mist net capture data, and other observations. Timed censuses were conducted at least once per week on each plot starting between 0500 and 0600 EST, and lasting 1 h. Those consisted of two observers walking at a fixed rate (50 m/6 min) on parallel lines 100 m apart and recording all birds seen or heard within 50 m on either side of the 500 m transect line. Number of individuals (separating males and females when possible) of each species within the boundaries of the 10 ha plot were determined from those data. Following the timed census, the two observers moved systematically about the study plot, recording presence of singing and especially simultaneously singing individuals, presence and activities of mates, locations of nests, and other evidence of breeding activity. Mist-netting was conducted at weekly or biweekly intervals during the breeding season in some years and locations (1969–1985 and 1989–1992 at Hubbard Brook, and 1989–1995 at Moosilauke). Number of net-captures of each species helped to confirm the visual census and territory mapping data (Holmes and Sturges 1975), but contributed little new information, so large-scale mist-netting was discontinued in later years. Some species under intensive study (especially American Redstart and Black-throated Blue Warbler, see Table 2 for scientific names) were captured and given unique combinations of color bands, which facilitated identification of individuals and hence census determinations.

All positional data (e.g. locations of singing males, simultaneous singing by neighboring conspecifics, females, nests, and mist-net captures when available) from the census period were plotted on overlay maps for each species on each plot. Numbers of ter-

TABLE 2. Frequency of occurrence, median (range), mean density, and variability in abundance of 24 bird species breeding on 10 ha study plot at Hubbard Brook Experimental Forest, New Hampshire, 1969–1998.

Bird species	Frequency[a]	Median (range)[b]	Mean density ± SD (CV)[c]
North temperate residents			
Downy Woodpecker (*Picoides pubescens*)	29	2 (0–6)	1.9 ± 1.4 (74)
Hairy Woodpecker (*Picoides villosus*)	30	2 (>1–3)	1.6 ± 0.7 (43)
White-breasted Nuthatch (*Sitta carolinensis*)	30	2 (>1–8)	1.9 ± 1.4 (71)
Black-capped Chickadee (*Poecile atricapillus*)	28	1 (0–4)	1.1 ± 1.0 (90)
Short distance migrants			
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	30	3 (1–6)	2.8 ± 1.3 (46)
Brown Creeper (*Certhia americana*)	15	>1 (0–2)	0.6 ± 0.8 (140)
Winter Wren (*Troglodytes troglodytes*)	22	1 (0–6)	1.3 ± 1.5 (123)
Hermit Thrush (*Catharus guttatus*)	29	3 (0–8)	3.5 ± 2.1 (61)
Blue-headed Vireo (*Vireo solitarius*)	15	>1 (0–4)	0.6 ± 1.0 (161)
Yellow-rumped Warbler (*Dendroica coronata*)	12	0 (0–3)	0.8 ± 1.1 (133)
Dark-eyed Junco (*Junco hyemalis*)	16	0 (0–8)	1.8 ± 2.7 (147)
Long-distance Neotropical migrants			
Least Flycatcher (*Empidonax minimus*)	17	1 (0–57)	13.0 ± 17.3 (133)
Veery (*Catharus fuscescens*)	30	3 (>1–6)	2.6 ± 1.3 (49)
Swainson's Thrush (*Catharus ustulatus*)	27	3 (0–11)	4.1 ± 3.3 (81)
Wood Thrush (*Hylocichla mustelina*)	22	1 (0–9)	2.9 ± 3.1 (108)
Philadelphia Vireo (*Vireo philadelphicus*)	14	0 (0–8)	1.8 ± 2.3 (129)
Red-eyed Vireo (*Vireo olivaceus*)	30	22 (13–31)	21.7 ± 4.3 (20)
Black-throated Green Warbler (*Dendroica virens*)	30	10 (6–18)	11.2 ± 3.7 (33)
Black-throated Blue Warbler (*Dendroica caerulescens*)	30	11 (4–16)	10.7 ± 2.9 (27)
Blackburnian Warbler (*Dendroica fusca*)	26	2 (0–7)	2.5 ± 2.0 (82)
Ovenbird (*Seiurus aurocapillus*)	30	11 (6–22)	12.5 ± 4.0 (32)
American Redstart (*Setophaga ruticilla*)	30	21 (2–44)	21.5 ± 11.5 (54)
Scarlet Tanager (*Piranga olivacea*)	30	3 (2–8)	3.5 ± 1.8 (52)
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	30	4 (>1–10)	4.5 ± 2.4 (54)

[a] Number of years in which one or more individuals (pairs) bred on Hubbard Brook plot.

[b] Median number (and range) of individuals breeding on 10 ha Hubbard Brook plot, 1969–1998.

[c] Mean ±1 SD of total number of adult birds (males plus females) occupying 10 ha plot 1969–1998. SD and Coefficient of Variation (CV) are given only as approximate descriptors of variability in numbers within species populations over the 30 year period (see text).

ritories of each species were then determined from those maps, by drawing boundaries encompassing each cluster of observations. Those were compared to the number of singing males recorded on the timed censuses and to the number of captures in mist nets (when available), and any discrepancies led to reexamination of all data to determine best estimates of bird abundances. Number of individuals of each species occupying the 10 ha plot was then determined by counting the number of whole or fractional territories, taking into account the mating status of each territorial male. Mating status was determined by the presence of females, nests, or food delivery by males. Data therefore represent total number of adult individuals (males plus females) of each species per 10 ha, and represent best estimates of absolute densities of each species on a 10 ha area of northern hardwood forest (Holmes and Sturges 1975).

For this paper, we consider population trends of the 24 most abundant and regularly occurring breeding species in the northern hardwood forests, grouped by migratory status (see Table 2). We excluded from trend analysis species that occurred sporadically (present in ≤4 of the 30 years of study;

e.g. Red-breasted Nuthatch, *Sitta canadensis*; American Robin, *Turdus migratorius*; Black-and-white Warbler, *Mniotilta varia*; Canada Warbler, *Wilsonia canadensis*; and Purple Finch, *Carpodacus purpureus*), as well as those that were regular breeders but present at very low densities (e.g. Ruby-throated Hummingbird, *Archilochus colubris*; Pileated Woodpecker, *Dryocopus pileatus*; Eastern Wood Pewee, *Contopus virens*; and Blue Jay, *Cyanocitta cristata*). Abundances of these species, when present, were included in estimates of total numbers of birds on the study plot (see Fig. 1).

Because some species occurred at very low densities or because their abundances changed markedly over the 30 year study period, no one measure of central tendency or variability adequately described the data. As a result, we present several descriptive measures of the abundance data for each of the 24 species (*n* = 30 years): median, range, mean (±SD), coefficient of variation (CV = SD × 100/mean), and frequency of years present on the study area. Because SD and CV may not be appropriate for many of the species-specific trends, they are presented here only as approximate descriptors of annual variability
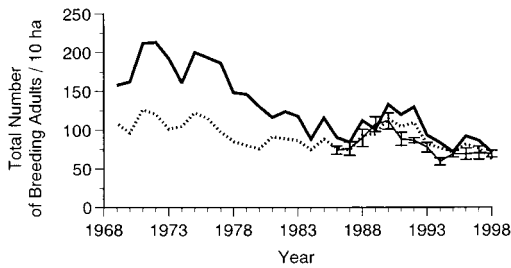
FIG. 1.   Total numbers of adult birds (males plus females, all species combined) breeding on the 10 ha study plot at Hubbard Brook, 1969–1998, and on three replicate 10 ha sites (mean ±1 SE) in nearby parts of the White Mountain National Forest, 1986–1998. Dashed line indicates total numbers of adult birds minus those of Least Flycatcher, Wood Thrush, Philadelphia Vireo, and American Redstart, four species most likely to have declined due to changes related to forest succession (see text).

within each species population. They also allow for comparisons with previous analyses of those data (Holmes et al. 1986, Holmes and Sherry 1988).

Population trends were determined from linear regression models for the abundance of each species over time, following procedures of Holmes and Sherry (1988). Population changes were transformed to units of average percentage annual change: $(t-1)(100)$, where t = trend. Trends were considered significant when linear regressions had slopes that were statistically different from zero ($P \leq 0.05$), based on F-tests. F-tests are approximate in this case because annual abundance of a species in one year may not be independent among years. Thus, significance levels should be considered as estimates of whether or not slopes differ from zero.

Data on bird abundances from the replicate plots in the nearby White Mountain National Forest were averaged for each year, and are given as means ±1 SE (n = 3). Those patterns of abundance on nearby sites are presented here only for general comparisons of density levels and abundance trends with the 30 year patterns for each species at Hubbard Brook. More detailed analyses of the similarities and differences in abundance patterns among those replicate plots for individual species will be presented elsewhere (R. T. Holmes and P. J. Doran unpubl. data).

For comparison at the statewide level, we used trends in abundance for the same bird species on the 22–24 BBS routes in New Hampshire for the years 1969 through 1998, obtained from the Patuxent Wildlife Research Center (J. R. Sauer pers. comm.). BBS trends were calculated on the basis of the linear route regression method (Peterjohn et al. 1997), which yielded bootstrap estimates for each species of the median ''trend'' from which the average percentage annual change was calculated, along with an esti-

mate of variance of these trends among routes for each species. Statistical significance was determined with z-tests.

Vegetation on the Hubbard Brook plot was quantified using the point quarter method (Cottam and Curtis 1956) and foliage profiles (MacArthur and Horn 1969). For the former, 40 points were located at 50 m intervals on the census grid, and the nearest tree identified to the point in each of the four quadrants delineated by cardinal compass directions and in each of three size classes: 2–10, 10.1–20, and >20 cm diameter at breast height (DBH). Vegetation was reinventoried at the same points at 5–9 year intervals between 1973–1999. Foliage profile measurements were conducted along six randomly placed sample lines at 20 sites located 100 m apart (in 1973) or at 40 sites located 50 m apart (in 1993) on the census grid. Along each line, six measurements were taken of distances to nearest leaf, both downwards to the ground using a plumb line, and upwards to the canopy using the focusing of a single lens reflex camera to measure distances to intersecting leaves (see MacArthur and Horn 1969). Profiles were calculated using the methods of MacArthur and Horn, and values were averaged for all points on the study area and divided by the height of each stratum. Student's t-tests were used to compare foliage density separately within each stratum between two sampling periods.

RESULTS

Trends in bird community patterns.—Of the 24 relatively common and regularly-occurring species on the study sites, 4 were permanent residents, 7 were short distance migrants, and 13 were long-distance migrants that winter in the Neotropics (Table 2). Only 11 of the 24 species were present as breeders on the Hubbard Brook plot in all 30 years, with the remainder absent in 1 to as many as 18 years. Several species were present and sometimes very abundant during the early years of study but then were absent for a long series of years, leading to wide ranges in abundance and higher mean than median values due to highly skewed frequency distributions in annual abundances (e.g. Least Flycatcher, Wood Thrush, Swainson's Thrush, Philadelphia Vireo, American Redstart, Dark-eyed Junco—Table 2; and see individual species accounts below). Similarly, other species occurred at low densities but fluctuated considerably in abundance from year to year, with low median and mean abundances and high SD and CV (e.g. Black-capped Chickadee, Brown Creeper, Winter Wren, Blue-headed Vireo, Blackburnian Warbler—Table 2).

TABLE 3.   Population trends of forest birds on 10 ha study plot in the Hubbard Brook Experimental Forest, New Hampshire and on Breeding Bird Survey (BBS) routes in New Hampshire, grouped by migratory status.

Bird species	Hubbard Brook (1969–1998)		BBS (1969–1998)
	Regression slope[a]	% annual change[b]	% annual change[c]
North temperate residents			
Downy Woodpecker	−0.055***	−5.38	+0.22
Hairy Woodpecker	−0.014	−1.42	−0.40
White-breasted Nuthatch	−0.023*	−2.28	+2.65**
Black-capped Chickadee	−0.014	+1.40	+2.65**
Short distance migrants			
Brown Creeper	+0.013	+1.25	−0.73
Winter Wren	−0.012	−1.23	+5.00**
Hermit Thrush	−0.017	−1.69	+5.02***
Blue-headed Vireo	−0.002	−0.19	+0.20
Yellow-rumped Warbler	+0.039**	+4.01	+3.47**
Dark-eyed Junco	−0.086***	−8.30	−1.45
Long-distance Neotropical migrants			
Yellow-bellied Sapsucker	−0.028	−2.73	+3.07*
Least Flycatcher	−0.188***	−17.17	−4.83***
Veery	+0.009	+0.93	−1.50**
Swainson's Thrush	−0.084***	−8.04	NA[d]
Wood Thrush	−0.118***	−11.13	−4.55***
Philadelphia Vireo	−0.222***	−8.04	NA
Red-eyed Vireo	−0.010*	−0.96	−1.33***
Black-throated Green Warbler	+0.023***	+2.32	−1.80
Black-throated Blue Warbler	+0.002	+0.19	+0.21
Blackburnian Warbler	−0.056**	−5.45	−4.08
Ovenbird	+0.013*	+1.27	+0.85
American Redstart	−0.050***	−4.85	−3.10*
Scarlet Tanager	−0.023**	−2.32	−2.50***
Rose-breasted Grosbeak	−0.052***	−5.08	−2.34*

[a] Regression slope of bird abundance against time (mean ± SE, n = 30 years). Asterisks indicate approximate probability that slopes differ from zero (see text). *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

[b] Percentage annual change on Hubbard Brook plot.

[c] Percentage annual change on BBS routes, using route regression method (see text).

[d] New Hampshire BBS data insufficient for trend analysis.

Trends in total abundance.—The total number of adult birds breeding on the 10 ha Hubbard Brook study area (all species combined) declined from a peak of about 210–220 in the early 1970s to 70–90 in the late 1990s (Fig. 1), a highly significant decline ($y = -4.15 + 196.48$, $R^2 = 0.72$, $P < 0.001$). From 1986–1998, mean total abundances of all species on the three replicate plots averaged slightly lower than those at Hubbard Brook, but showed the same temporal pattern, with numbers increasing from 1986 to the early 1990s, decreasing through 1994–1995, and then remaining relatively stable through 1998 (Fig. 1).

Population trends of resident species.—Of the four species that were permanently resident in the study area, two (White-breasted Nuthatch, Downy Woodpecker) declined significantly at Hubbard Brook (Table 3). Nuthatch numbers

were high in 1969, the first year of this study, dropping in the two subsequent years, and then remained relatively stable in abundance through 1998 (Fig. 2). Downy Woodpeckers declined more gradually from 2–4 individuals per 10 ha in the early years of the study to <1 individual, on average, in the last 10 years (Fig. 2). During the same period, both Downy Woodpecker and White-breasted Nuthatch increased in abundance statewide in New Hampshire, a trend that was highly significant for the nuthatch (Table 3).

Populations of Hairy Woodpecker and Black-capped Chickadee at Hubbard Brook remained relatively stable between 1969 and 1998 at Hubbard Brook and between 1986–1998 on the replicate plots (Fig. 2, Table 3). On the New Hampshire BBS routes, Hairy Woodpeckers were
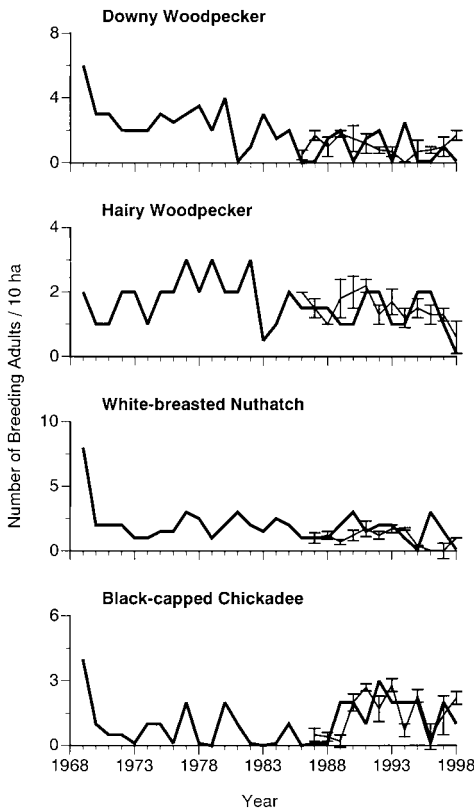
FIG. 2. Population trends of permanently resident species at Hubbard Brook, 1969–1998, and on three replicate sites (mean ± 1 SE), 1986–1998. Note differences in scale on y-axes.

relatively stable, but the chickadee showed a significantly increasing trend (Table 3).

Population trends of short distance migrants.— Of the seven short-distance migrant species, five (Yellow-bellied Sapsucker, Brown Creeper, Winter Wren, Hermit Thrush, and to an extent Blue-headed Vireo) had stable population trends on the Hubbard Brook plot (Table 3). On the replicate plots, there were generally similar trends in abundance, especially for the creeper, Winter Wren and thrush, but not for the vireo (Fig. 3). On the larger regional scale, the creeper and the vireo also maintained stable or slightly increasing population trends, whereas abundances of the wren, thrush, and sapsucker increased significantly on the New Hampshire BBS routes (Table 3). One short-distance migrant, the Yellow-rumped Warbler, had a significantly increasing trend at Hubbard Brook, but occurred at lower average densities on the
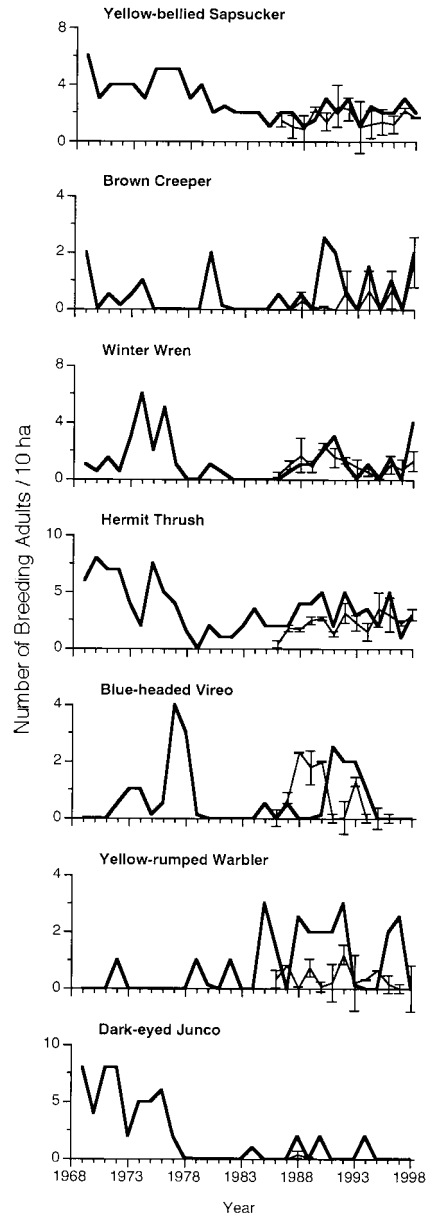

FIG. 3. Population trends of short-distance migrant species at Hubbard Brook, 1969–1998, and on three replicate sites (mean ± 1 SE), 1986–1998. Note differences in scale on y-axes.

replicate plots (Fig. 3). That species increased significantly on BBS counts in New Hampshire between 1969 and 1998 (Table 3). Finally, the Dark-eyed Junco was relatively abundant in the first 10 years of this study, but then declined to local extinction on the Hubbard Brook plot by
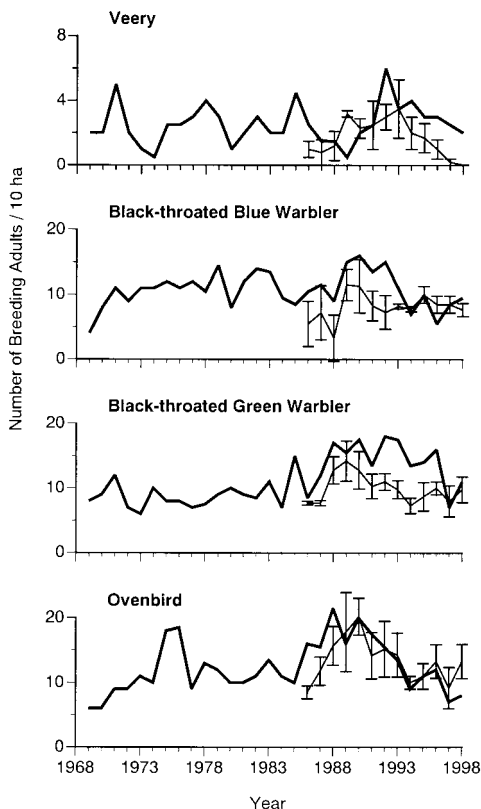
FIG. 4. Population trends of long-distance Neo-
tropical migrants with either constant (Veery, Black-
throated Blue Warbler) or significantly increasing
(Black-throated Green Warbler, Ovenbird) abun-
dance trends at Hubbard Brook, 1969–1998, and on
three replicate sites (mean ± 1 SE), 1986–1998. Note
differences in scale on *y*-axes.

1978. After that time, it was recorded only spo-
radically, and was essentially absent from the
replicate plots between 1986–1998 (Fig. 3). That
species exhibited a declining but nonsignifi-
cant trend on New Hampshire BBS routes over
the 30 year time period (Table 3).

Population trends of long-distance migrants.—
Of the 13 Neotropical migrant species, two
maintained relatively constant population lev-
els, two increased in abundance, and nine de-
clined (Table 3). Abundance trends for those
species are described below and in Figures 4–
6, grouped by trend pattern.

Veeries and Black-throated Blue Warblers
maintained relatively constant populations at
Hubbard Brook between 1969 and 1998 (Table
3) and on the replicate plots since 1986 (Fig. 4).
On New Hampshire BBS routes for that same

period, the Black-throated Blue Warbler exhib-
ited a stable trend, whereas the Veery declined
significantly (Table 3).

In contrast, Ovenbirds and Black-throated
Green Warblers increased significantly in
abundance at Hubbard Brook between 1969
and 1998 (Table 3), and showed strikingly par-
allel patterns of population change on the rep-
licate plots since 1986 (Fig. 4). On BBS routes,
both species maintained relatively stable abun-
dances between 1969 and 1998 (Table 3).

Of the nine long-distance migrant species
that declined, three (Least Flycatcher, Wood
Thrush, and Philadelphia Vireo) disappeared
entirely from the Hubbard Brook plot by the
early 1980s (Fig. 5). For the first 10 years of
study, Least Flycatchers were very common,
and in fact were the most abundant species in
the study area between 1970–1975, reaching a
peak of 57 individuals occupying the 10 ha
study area in 1973. Though not as numerous,
Wood Thrushes were also common in the first
15 years of the study, but dropped in numbers
in the late 1970s and then were absent by the
late 1980s (Fig. 5). Philadelphia Vireos, though
never as numerous as the two preceding spe-
cies, gradually declined from a maximum of 8
individuals (4 pairs) in 1972 to zero in 1983.
Thus, all three species had disappeared entire-
ly from the Hubbard Brook plot by the mid to
late 1980s. All three were also rare or absent on
the replicate plots for the period 1986–1998
(Fig. 5). On BBS routes in New Hampshire,
Least Flycatchers, and Wood Thrushes showed
similar highly significant declining trends in
abundance (Table 3). Philadelphia Vireos oc-
curred too infrequently on BBS routes for state-
wide estimates.

Two other long-distance migrants, Swain-
son's Thrush and American Redstart, also de-
clined significantly in abundance at Hubbard
Brook during the first 20 years of the study, but
their populations then stabilized at low densi-
ties by the mid to late 1980s and remained low
thereafter (Fig. 5). The average abundance of
redstarts on the replicate plots closely matched
those at Hubbard Brook, whereas Swainson's
Thrushes were absent from two of the three
replicate sites, resulting in lower mean densi-
ties on those latter sites (Fig. 5). On BBS state-
wide estimates, redstart abundances declined
significantly between 1969 and 1998 (Table 3).
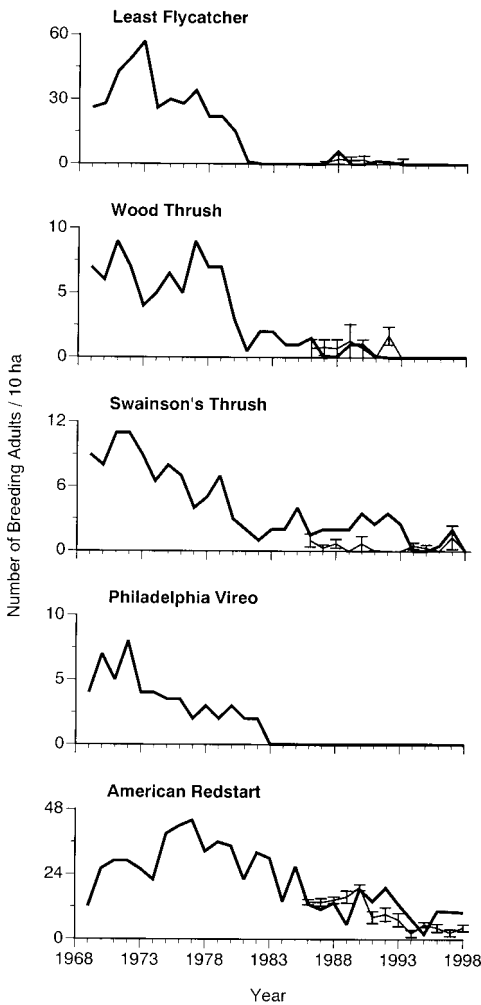Occurrences of Swainson's Thrush on BBS

FIG. 5.   Population trends of long-distance Neo-tropical migrant species that exhibited statistically significant and dramatic declines in abundance at Hubbard Brook, 1969–1998, and on three replicate sites (mean ± 1 SE), 1986–1998. Note differences in scale on *y*-axes.

FIG. 6.   Population trends of long-distance Neo-tropical migrant species that exhibited statistically significant but less pronounced declines in abundance at Hubbard Brook, 1969–1998, and on three replicate sites (mean ± 1 SE), 1986–1998. Note differences in scale on *y*-axes.

routes were too infrequent for statewide estimates.

Finally, four other long-distance migrants (Red-eyed Vireos, Blackburnian Warblers, Scarlet Tanagers, and Rose-breasted Grosbeaks) exhibited significantly declining trends in abundance at Hubbard Brook between 1969–1998 (Fig. 6, Table 3). Similar densities and trends were evident for all four species on the three replicate plots between 1986–1998 (Fig. 6), and BBS trends for all four species on New
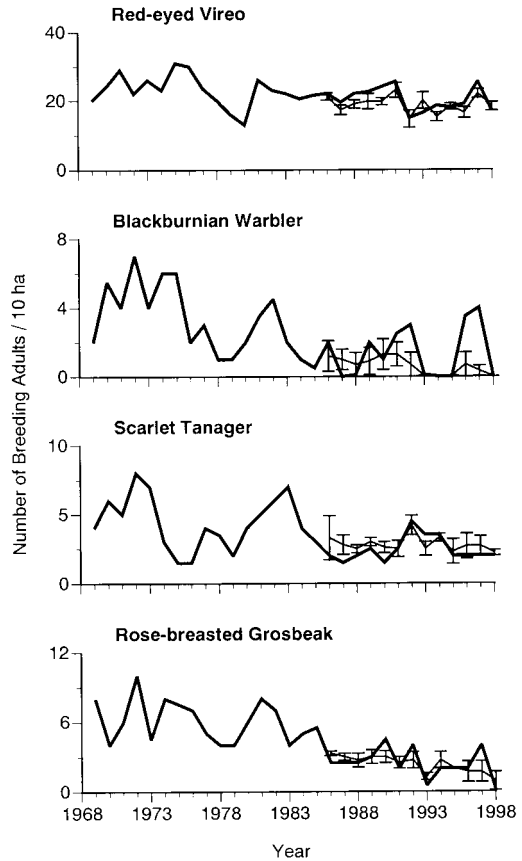
Hampshire BBS routes were also significantly negative (Table 3).

Overall trends in bird abundances.—To summarize, 12 of the 24 species exhibited significant declines in abundance at Hubbard Brook between 1969–1998 (nine long-distance migrants, one short-distance migrant, two permanent residents). Three species increased significantly (two Neotropical migrants, one short-distance migrant), whereas nine species maintained relatively constant population levels (two resident, five short-distance migrants, and two long-distance migrant species). Mean densities of most species were generally similar on the replicate study sites (Figs. 2–6), suggesting the patterns at Hubbard Brook were

TABLE 4. Summary of population trends for 24 forest bird species at Hubbard Brook (HB) from 1969–1998 and on Breeding Bird Surveys (BBS) in New Hampshire (NH), and their major wintering areas.

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

[a] Trends based on linear regression analyses for Hubbard Brook and route regression method for BBS (see Table 2).

[b] Data from New Hampshire BBS routes insufficient for classification, but population trends stable for these two species on continent-wide BBS data (Peterjohn et al. 1995).

representative for those species in that habitat type in central New Hampshire.

Comparisons with New Hampshire BBS data indicate that a majority (17 of 24) of species had similar trends at the local (Hubbard Brook plot) and regional (New Hampshire statewide) scale (Table 4). Of those 17 species, 11 maintained stable or had increasing abundances at both Hubbard Brook and regional levels over the 30 year period, whereas 6 showed strongly significant declines in both data sets. The former group contained species that were permanent residents, short-distance migrants, and Neotropical migrants, but the latter (declining) group consisted exclusively of Neotropical migrants (Table 4). Of those six declining species, three have wintering distributions in South America, two in Central America, and one in both Central America and the Caribbean (Table 4). Conflicting trends between Hubbard Brook and the regional BBS level were found for seven species: six showed declines locally at Hubbard

Brook with stable or increasing trends statewide and one (Veery) was stable at Hubbard Brook, but declined statewide (Table 4).

Vegetation changes at Hubbard Brook.—Inventories of woody plants on the Hubbard Brook census plot indicate that although some components of the forest remained relatively constant, other aspects changed markedly. The density and relative importance of the large (>20 cm DBH) canopy tree species remained relatively constant over the course of the study, with only a slight increase in sugar maple and a decrease in American beech (Table 5). In the 10–20 cm DBH tree size class, yellow birch declined in frequency and importance value, beech increased in relative importance, and sugar maple remained relatively constant (Table 5). The most striking changes were in the density and species composition of the smallest (2–10 cm DBH) size class of trees, with sugar maple and yellow birch declining sharply both in density and relative importance values,

TABLE 5. Density and relative importance values of trees on the Hubbard Brook study area between 1973 and 1999, as measured by the point-quarter method (Cottam and Curtis 1956).

Size class/tree species	Number of stems/ha (Importance value,[a] %)				
	1973	1982	1987	1993	1999
2–10 cm DBH[b]					
Sugar maple	154 (42.8)	115 (42.5)	126 (32.8)	92 (24.9)	78 (14.5)
American beech	150 (37.2)	138 (44.4)	262 (50.4)	334 (55.6)	655 (69.7)
Yellow birch	16 (7.2)	0 (0.0)	5 (1.4)	5 (1.8)	4 (0.7)
Striped maple	14 (4.3)	20 (7.2)	48 (11.0)	61 (12.3)	121 (13.7)
Red spruce	5 (1.8)	9 (3.3)	9 (2.4)	13 (3.8)	4 (0.9)
Others	28 (6.7)	3 (2.6)	9 (2.0)	8 (1.6)	9 (0.5)
10.1–20 cm DBH					
Sugar maple	55 (36.5)	47 (40.6)	54 (43.1)	53 (44.4)	51 (39.3)
American beech	39 (27.8)	42 (36.7)	48 (40.1)	47 (38.9)	66 (48.5)
Yellow birch	34 (25.3)	12 (13.7)	8 (9.2)	9 (9.4)	8 (7.3)
White ash	1 (0.6)	0 (0.0)	1 (0.6)	0 (0.0)	0 (0.0)
Striped maple	10 (7.3)	3 (3.9)	2 (1.7)	2 (2.2)	5 (4.3)
Red spruce	2 (1.8)	3 (3.9)	2 (1.7)	2 (2.2)	0 (0.0)
Others	1 (0.7)	3 (3.6)	4 (4.5)	4 (3.9)	1 (0.6)
>20 cm DBH					
Sugar maple	86 (38.4)	91 (39.8)	92 (39.7)	75 (39.6)	102 (44.7)
American beech	55 (26.8)	53 (29.6)	60 (25.6)	44 (24.6)	51 (20.9)
Yellow birch	60 (27.4)	44 (21.2)	48 (22.5)	48 (26.8)	50 (23.3)
White ash	10 (5.9)	13 (8.0)	18 (10.4)	12 (6.9)	15 (9.4)
Other	3 (1.5)	3 (1.4)	4 (1.8)	5 (2.7)	3 (1.7)

[a] Importance value = 100 (relative basal area + relative density + relative frequency)/3.
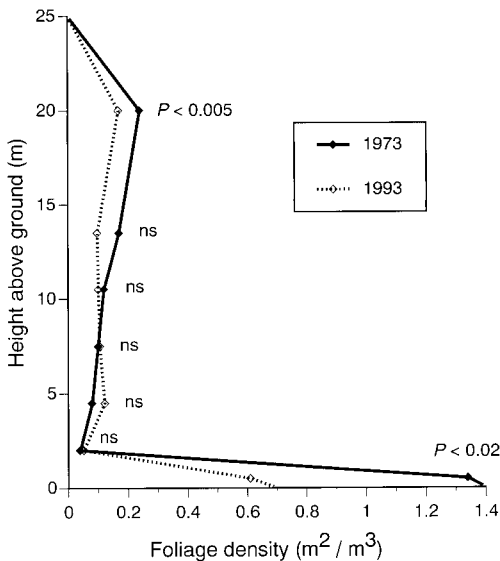
[b] DBH = diameter at breast height.

FIG. 7. Foliage density profile (leaf area per unit volume) for the Hubbard census plot in 1972–1973 (solid line) and in 1993 (broken line), as measured by methods of MacArthur and Horn (1969). Units represent projected leaf surface area per cubic meter. Results of *t*-tests for differences between means at each of seven height intervals are indicated (NS = nonsignificant, $P > 0.05$).

whereas striped maple and especially beech increased dramatically (Table 5). The decline, absence, or both of yellow birch and white ash in the smaller size classes is consistent with the shade-intolerance of seedlings and the special germination requirements of these midsuccessional tree species (Forcier 1975). Changes also occurred in the distribution of foliage over the vertical profile of the forest (Fig. 7). Between 1973 and 1993, foliage density was significantly reduced in both canopy and low shrub strata, resulting in a more equal vertical distribution of foliage (Fig. 7, see also Holmes et al. 1986). The forest therefore changed from one characterized by a dense, fairly closed canopy, with an open subcanopy and a low, dense shrub layer in the late 1960s to one with a more open and patchy canopy, a denser and taller shrub/subcanopy layer composed disproportionately of beech thickets, and a more sparse, low shrub layer in the 1990s.

DISCUSSION

In this study, we have shown that the bird community of an undisturbed, unfragmented, and relatively mature deciduous forest in New Hampshire changed dramatically over a 30

year period between 1969 and 1998. Total number of individuals, all species combined, occupying the 10 ha study area declined by ~60%, from a peak of about 210–220 in the early 1970s to 70–90 in the late 1990s. Twelve species exhibited long-term, statistically significant declines. Several of those disappeared entirely from the study area, including one (Least Flycatcher) that in 1970–1975 had been the most abundant species there (see Fig. 3, Holmes et al. 1986). Three species increased significantly in abundance, whereas nine others fluctuated in numbers but with no long-term positive or negative trend. These findings, which were largely corroborated by similar patterns at larger regional scales on replicate study sites in nearby sections of the White Mountains and from BBS routes located across the state of New Hampshire, demonstrate that bird abundances in those intact, relatively mature northern hardwood forests do not (necessarily) remain stable over time. Indeed, the longer our study has continued the more evident such fluctuations have become, indicating the value and necessity of long-term continuous studies for detecting and measuring population trends and variability. That is important for two reasons. First, investigators comparing bird populations or communities on the same site separated by long time intervals should not assume stasis or any other pattern for the intervening years. In particular, attempts to deduce long-term population changes from a simple repeat census after a long interval should be done with great caution. Secondly, the different population trajectories occurring on different time scales among cooccurring species suggest that no single common factor or event can account for the observed changes and that generalizations from one species to another are tenuous at best (see also Holmes et al. 1986, Taper et al. 1995).

Given such caveats and the fact that causes of population changes, especially when based on correlational evidence, are often difficult to identify (Wilcove and Terborgh 1984, Sauer et al. 1996), below we consider and evaluate possible explanations for the population changes observed at Hubbard Brook, specifically the effects of (1) habitat change in the breeding area, (2) summer food availability, (3) interspecific competitive interactions, (4) nest predators and brood parasites, and (5) nonbreeding season mortality.

Effects of habitat change.—Bird species have long been known to vary in abundance along successional (Johnston and Odum 1956, Martin 1960, Shugart and James 1973, Morgan and Freedman 1986, Thompson and Capen 1988) and environmental (Bond 1957, Smith 1977) gradients, often in accordance with changes in habitat structure (Wiens and Rotenberry 1981, James and Wamer 1982). Bird-species composition and abundance also change with forestry practices and management, most of which involve alterations in habitat structure (e.g. DeGraaf et al. 1998). Even though the forest at Hubbard Brook was considered to be relatively mature at the start of our study (see above), changes in vegetation structure did occur during the subsequent 30 years (see below). Those changes were mostly due to normal processes of natural succession (e.g. increasing frequency of treefall gaps associated with a more even vertical distribution of foliage; Aber 1979), sometimes in combination with local disturbances, for instance due to storm damage or disease. Damage due to high winds or to heavy icing during the winter sometimes topple large trees (especially those weakened by disease, see below) or result in broken tree crowns and branches, thus creating gaps and other changes in the structure of the forest canopy (Irland 1998, R. T. Holmes pers. obs.). Perhaps the most important disturbance factor in the last 30 years has been the occurrence of beech bark disease (*Nectria coccinea*), first detected at Hubbard Brook in the 1970s (T. G. Siccama pers. comm.). That fungal pathogen not only results in weakening and eventual death of large beeches (Shigo 1972, Twery and Patterson 1984), but also leads to a subsequent release of beech sprouts or suckers from the roots of the dying trees (Houston 1975, E. Hane and T. G. Siccama pers. comm.). With increased light admitted through the more open canopy, those beech suckers (and some other understory shrubs such as striped maple) grow rapidly, and produce dense shrub-layer thickets. Such dense stands, dominated by beech saplings, were prevalent in our study area in the late 1980s (see Table 5), and by the mid to late 1990s, those young beeches had grown 3–8 m tall (but many still <5 cm DBH), forming a tall, dense shrub and subcanopy layer in parts of the study area. At that time, the ground cover beneath those beech thickets, although containing

herbs, ferns, and other low-lying vegetation, had fewer other woody plants, such as hobblebush or small tree seedlings, which in the earlier years of this study had formed dense patches at the low (<1 m) shrub level (R. T. Holmes pers. obs.). A recent experimental manipulation at Hubbard Brook indicates that the proliferation of small beech negatively affects the growth and survival of sugar maple seedlings and saplings (E. Hane unpubl. data), which may explain the observed decline in small sugar maples (see Table 5). A similar interspecific competitive effect may have also resulted in a reduction in hobblebush in some parts of the study area (R. T. Holmes pers. obs.). Thus, even though the forest at Hubbard Brook has remained free of logging and other direct human influences since the early 1900s, it has continued to change in diverse and substantial ways even during the last 30 years when it appeared to be a relatively mature forest. As indicated above, the most noticeable changes during the period were in its physical structure, particularly the openness of the canopy and the distribution of foliage among strata.

To what degree can these changes in habitat structure account for the trends in bird abundances that we have documented? Four of the five species that have shown the most dramatic declines in abundance or have disappeared from the forest at Hubbard Brook (Least Flycatcher, Wood Thrush, American Redstart, and Philadelphia Vireo) are most strongly associated with midsuccessional forests. If the abundances of those four strongly declining species are removed from the community totals, the overall decline in total bird numbers at Hubbard Brook is less dramatic (see Fig. 1), although still significantly declining ($y = -1.13 + 110.6$, $R^2 = 0.35$, $P < 0.001$). Below, we review the evidence, most of which is correlational, for succession and other vegetation change as the cause of population trends for those and other Hubbard Brook species.

Least Flycatchers are often locally abundant in well-stratified forests, with a relatively open subcanopy beneath a dense upper canopy (Breckenridge 1956, Sherry 1979, Briskie 1994). In northern hardwood succession, that structure is characteristic of 40–60 year old forests, whereas the canopy in older stands becomes opened by tree falls and other forms of disturbance, resulting in a greater variety of tree

ages, sizes, and shapes (Aber 1979). Similarly, Bond (1957) in his ordination of birds among plant communities in Wisconsin forests found that Least Flycatchers reached greatest abundance midway along the vegetation (partly a successional) gradient. At Hubbard Brook, Least Flycatchers disappeared from the census plot in the late 1970s, but they continued to occur in other nearby parts of the forest through the late 1980s to early 1990s (Sherry and Holmes 1985, T. W. Sherry and R. T. Holmes pers. obs.). The areas where they persisted were at elevations and on slopes that had been most severely damaged by a major hurricane in 1938. That storm had blown down many trees in those areas, creating patches of earlier successional forests (Merrens and Peart 1992, R. T. Holmes pers. obs.), which were in effect 40–50 years of age in the 1980s when they were still occupied by the flycatchers. That species disappeared from even those areas by the mid 1990s, and it was recorded only once during systematic censuses of all bird species in the 3000 ha Hubbard Brook valley in 1999–2000 (P. J. Doran unpubl. data). Thus, by the late 1990s, the Least Flycatcher no longer occurred in that forest. We hypothesize that is due to an increase in canopy gaps and other changes in vegetation structure that have occurred in the last 20–30 years in that forest, making that site unsuitable for that species, and that maturing of the forests in New Hampshire and perhaps New England as a whole (see Litvitas 1993, Hunt 1998) may account for the Least Flycatcher's regional decline in recent years.

Wood Thrushes are typically a species of mesic deciduous and mixed deciduous–coniferous forests. They are also found commonly along edges, in suburban areas, and in fragmented forest patches (Dilger 1956, James et al. 1984, Roth et al. 1996), which suggests extensive use of disturbed and human-modified woodlands. Wood Thrushes occur at highest densities in forests with tall canopies, few small trees, a well-developed but sparse understory shrub layer, and a fairly open forest floor (James et al. 1984, Roth et al. 1996), characteristics that correspond to midsuccessional northern hardwood forests in New England (Aber 1979). Similarly, in Bond's (1957) ordinations, Wood Thrush abundance peaked in midsuccessional plant communities. Like Least Flycatchers, Wood Thrushes disappeared from the Hub-

bard Brook census plot in the late 1970s, but remained in areas that had been severely affected by a hurricane in 1938 for 10–15 years after they had disappeared from the census plot (R. T. Holmes pers. obs.). Thus, the gradual decline of the Wood Thrush on the Hubbard Brook plot could have been expedited, if not caused, by subtle forest changes associated with secondary succession (but see below for an alternative explanation).

American Redstarts have been shown through both empirical and modeling studies to occur more frequently in early and midsuccessional forest habitat (Hunt 1996, 1998). Hunt showed that redstart abundance was positively correlated with amount of early successional habitat and that their decline in recent decades in New England was coincident with forest maturation in the region. In addition, a greater proportion of older, presumably more experienced redstarts were found in early successional sites, and individuals in those sites had smaller territories and higher mating success (Hunt 1996). These findings suggest that early successional forests are more suitable for this species in terms of reproduction and probably survival.

Philadelphia Vireos are also a species primarily of early to midsuccessional woodlands, aspen parklands, and shrub thickets (Moskoff and Robinson 1996). Their disappearance from Hubbard Brook seems consistent with the hypothesis that forest maturation has decreased the suitability of the forest.

Finally, habitat change can also improve conditions for some species. At Hubbard Brook, abundance of Ovenbird, Black-throated Green and Yellow-rumped warblers have gradually increased over the last 30 years as the forest has become older. All three species are typically found in structurally diverse, mature forests. The Ovenbird is typically found in deciduous forests with relatively open understories (Van Horn and Donovan 1994), and the data from Hubbard Brook suggest that the shrub layer has become less dense in recent years (see Fig. 7, and above). The Black-throated Green and Yellow-rumped warblers are most common in mature coniferous or mixed deciduous–coniferous stands (Morse 1993, Hunt and Flaspohler 1998).

Most of the above discussion about effects of habitat change has relied on correlational evidence, and points to the fact that we know very little about how changes in vegetation structure influence habitat choice and hence local abundance patterns. Do these population changes relate in some way to the structure of the habitat per se, or to associated changes in food abundance or availability (Robinson and Holmes 1982, Parrish 1995), predation risk to adults or to young, microclimate, availability of nest sites, or other factors that determine habitat suitability that influence reproductive success and survival? Identifying such mechanisms and processes, which involves behavioral, ecological and demographic studies, is essential for understanding how habitat change affects these species and their population trends, as well as being critical for developing scientifically based management plans.

Effects of summer food availability.—Studies at Hubbard Brook have shown that fluctuations in the availability of food, specifically Lepidoptera larvae, influence the reproductive success of several bird species (Holmes 1988, Holmes et al. 1991, 1992; Rodenhouse and Holmes 1992, Sillett et al. 2000). In turn, for American Redstarts and Black-throated Blue Warblers, the mean number of young fledged annually per female correlates with the number of yearlings recruited into populations in the following season (Sherry and Holmes 1991, Holmes et al. 1992, Sillett et al. 2000), illustrating the importance of breeding-ground events in maintaining local breeding populations of those species.

In the first three years of this study, caterpillars were unusually abundant on the Hubbard Brook study area due to a broad, regional irruption of a defoliating caterpillar, the saddled prominent (*Heterocampa guttivita*: Notodontidae, Lepidoptera). The maximum bird numbers on the study area (see Fig. 1) were coincident with, or lagged slightly after, that irruption, suggesting that food abundance influenced population sizes of many forest-bird species (Holmes and Sturges 1975, Holmes et al. 1986, Holmes and Sherry 1988). In addition, several species bred on the study area only during those years (e.g. American Robin, Purple Finch), and others typically found in more coniferous habitat (e.g. Swainson's Thrush, Dark-eyed Junco), may have increased in our study area due to the locally high abundance of food in those years. There has been no other major irruption of any defoliating caterpillar since the

early 1970s, although small, localized out-breaks of a looper (*Itame pustularia,* Geometridae) occurred in 1977, 1981–1983, and 1991–1992 (Holmes et al. 1986, R. T. Holmes unpubl. data). Those small irruptions were all short term, occurred early in the breeding season, and appeared to have relatively little effect on bird reproductive output. Therefore, during most years since 1972, Lepidoptera larvae have been low in abundance, averaging 3–5 caterpillars per 1,000 leaves (all Lepidoptera species combined; R. T. Holmes unpubl. data). That level could represent limiting conditions for many forest birds (Holmes et al. 1991, Rodenhouse and Holmes 1992).

Additional evidence that food abundance can influence forest-bird populations comes from the association of reproductive success of Black-throated Blue Warblers at Hubbard Brook with El Niño Southern Oscillation (ENSO; Sillett et al. 2000). From 1986 to 1999, warbler reproductive output was higher during the La Niña phase of ENSO, as was mass of young at fledging and the abundance of Lepidoptera larvae. Thus, changes in food abundance related to global climate events appear to affect bird reproduction, and those in turn influence recruitment into winter and subsequent breeding populations (Sillett et al. 2000). However, the extent to which those climate-mediated changes in reproductive parameters contributed to the long-term population changes of any species we studied, is unknown. For example, the population of Black-throated Blue Warblers, the subject of the above-cited study, has shown no net change in abundance at Hubbard Brook in the last 30 years (see Fig. 4), and the Black-throated Green Warbler, another species that depends extensively on caterpillars for food (Morse 1993), significantly increased in abundance at Hubbard Brook during the course of this study. Finally, with the available data, we can not rule out the possibility that declines in those species that we have attributed to habitat change were not exacerbated by low food supply following the major caterpillar irruption in the early 1970s. For example, the abrupt decline in caterpillar abundance in 1972 following the collapse of the defoliator outbreak could have contributed to the subsequent decline of the Least Flycatcher and Philadelphia Vireo. The degree or extent to which food determines habitat quality and influences local densities of those forest bird species requires further study.

Effects of interspecific competitive interactions.—Studies at Hubbard Brook have shown that competitive interactions between certain pairs of bird species influence local patterns of distribution and abundance of other species (Sherry 1979, Robinson 1981, Sherry and Holmes 1988). That was most evident when American Redstarts shifted their distribution in response to the presence and then absence of Least Flycatchers, a pattern that was verified through experimental manipulations (Sherry and Holmes 1988). This interspecific effect could have contributed to the increase in redstart abundance in the mid 1970s as Least Flycatchers declined (see Fig. 3), but does not account for either the disappearance of the flycatcher, nor the subsequent decline of the redstart. It is important to consider such competitive interactions, however, because they can affect local patterns of abundance and thus be important when assessing short-term changes in abundance at the local scale.

Effects of nest depredation and brood parasitism.—Depredation of eggs and nestlings is the major factor affecting nesting success for birds at Hubbard Brook (Sherry and Holmes 1991, Holmes et al. 1992, Sloan et al. 1998) and for most passerine birds (Martin 1995). Nest depredation also has been shown to increase when habitats are fragmented or disturbed, and has been cited as a major factor influencing breeding success and ultimately the abundances of songbirds (Wilcove and Robinson 1990). At Hubbard Brook, annual nesting success, as measured by the Mayfield method, has varied 20–74% ($n = 9$ years) for American Redstarts (Sherry and Holmes 1992) and 46–79% ($n = 12$ years) in Black-throated Blue Warblers (Holmes et al. 1992, 1996; R. T. Holmes unpubl. data). Such variation in nest survival among years is related largely to differences in the abundance of major nest predators (e.g. Eastern chipmunks, *Tamias striatus*; and red squirrels, *Tamiasciurus hudsonicus*), which in turn is related to the intermittent but highly synchronous production of seeds by forest trees (Ostfeld and Keesing 2000, R. T. Holmes pers. obs.). The result is a highly variable pattern of nest predation from year to year, but not one that shows either an increasing or decreasing trend over long time intervals (R. T. Holmes unpubl. data).

Thus, it seems unlikely that nest depredation over this 30 year period could be a factor responsible for long-term increases or declines in the abundances of any particular bird species in this unfragmented forest.

Brood parasitism has been proposed as a major factor contributing to declines of Neotropical migrants (e.g. Brittingham and Temple 1983, Robinson et al. 1995a). Brood parasitism, however, was not a factor affecting bird populations at Hubbard Brook during this 30 year study. Even though cowbirds occur in agricultural areas within several kilometers of our study area, they have rarely been seen within the extensive forest where our study plots are located, and only then in mid and late summer in the early 1970s during the defoliator irruption (Holmes and Sturges 1975, Holmes 1990). In 30 years of intensive field work, only one sighting of a cowbird fledgling has been made within the forest at Hubbard Brook (S. K. Robinson pers. comm., Holmes 1990) and none on the replicate plots (R. T. Holmes unpubl. data). Similarly, in bird censuses covering the entire Hubbard Brook valley in 1999 and 2000, only one cowbird was recorded in more than 1,000 point counts each season (P. J. Doran unpubl. data). This lack of cowbirds in these New Hampshire forests contrasts sharply with the situation in woodlots and forest edges in the midwestern United States and other areas where cowbirds are abundant and frequently parasitize bird nests (Brittingham and Temple 1983, Robinson et al. 1995a,b; Fauth 2000), even penetrating many kilometers into the forest (Morse and Robinson 1999).

Effects of events during the nonbreeding period.—Another possible cause of bird-population changes observed at Hubbard Brook is mortality occurring in the nonbreeding season. The best evidence for winter limitation from Hubbard Brook comes from data early in our study on species permanently resident at Hubbard Brook (e.g. woodpeckers, chickadees) and on short-distance migrants that winter in the southern United States (e.g. Hermit Thrushes and Dark-eyed Juncos). For both sets of species during the late 1960s to mid 1970s, abundances in summer at Hubbard Brook declined following severe winters in the northeastern and southeastern United States (Holmes et al. 1986, Holmes and Sherry 1988).

For long-distance Neotropical migrants, it is more difficult to identify changes in abundance that could be attributed to events in their wintering areas (Wilcove and Terborgh 1984, Holmes et al. 1986, Rappole and McDonald 1994, Sherry and Holmes 1996), partly because individuals from local breeding areas apparently scatter widely through the species' winter quarters (Chamberlain et al. 1997), making the effects of local winter events on breeding populations difficult to detect. However, survivorship analyses incorporating recapture and resighting probabilities for Black-throated Blue Warblers in both breeding and wintering areas suggest that increased mortality resulting from El Niño conditions during the winter affects survival and subsequent recruitment of individuals into breeding populations (Sillett et al. 2000, T. S. Sillett and R. T. Holmes unpubl. data). Similarly, Marra et al. (1998), using a habitat-specific isotope tracer, showed that winter-habitat quality lowered overwinter body condition and delayed spring departure schedules of American Redstarts, influencing in turn arrival times and, potentially, reproductive output. Those latter two studies suggest that winter habitat conditions affect migrant bird demography that have carryover effects into the breeding season. They also highlight the need for the development of new methods and approaches for assessing the effects of events in different seasons and places on the abundances of these long-distance migrant species.

With respect to winter habitat loss causing population declines, it could be argued that migrant species that commonly inhabit second-growth and other disturbed habitats in winter should not be affected (or should at least be less affected) by winter habitat loss than those species utilizing tropical forests. By this line of reasoning, the declines at Hubbard Brook of Least Flycatcher, American Redstart, and Philadelphia Vireo, all of which winter commonly in second-growth and edge habitats in Central America, the Caribbean, or both (Holmes et al. 1989, Greenberg 1992, Moskoff and Robinson 1996, Greenberg et al. 1997) do not seem to be ascribable to availability of their habitats in the winter areas. As a caveat to that argument, however, we note that just because those species are found in second-growth habitats in winter does not mean that those habitats are

necessarily of the highest quality; that is, those most suitable for maintaining body condition and survival over the winter period. In Jamaica, for instance, American Redstarts compete for high quality habitats that are the more heavily forested ones. For that species, the more subordinate individuals are forced into second-growth scrub where they are less able to maintain body condition and survive less well compared to the more dominant birds occupying forested sites (Marra and Holberton 1998, Marra and Holmes 2001). In this case, it is possible that the conversion of tropical forest to second-growth habitats over recent decades may have resulted in an overall decline in both quantity and quality of habitat for wintering redstarts (and perhaps other migrants), and that could have contributed to its general population decline. No comparable habitat-specific demographic data are available from the winter grounds for Least Flycatchers or Philadelphia Vireos or for most other Neotropical migrant songbirds. Such information is needed before discounting the winter period as being unimportant in affecting migratory bird populations.

Species of long-distance migratory songbirds that depend more exclusively on mature forests in the Neotropics could be affected by the loss or degradation of those habitats through deforestation. The Wood Thrush is a good example of such a species (Roth et al. 1996), and it is at least plausible to hypothesize that winter habitat loss could be a cause for its population decline (Rappole et al. 1992, Morton 1992). However, the alternative hypothesis that population decline of Wood Thrushes is due to the loss of suitable breeding sites due to forest succession (see above) or to effects of fragmentation (Robinson et al. 1995a) seems equally likely, and of course, both may be occurring simultaneously. This illustrates the difficulty of identifying the factors limiting those populations and the need for understanding the influence of factors operating at different parts of the annual cycle.

Correspondence of trends at different spatial scales.—For many of the species studied, we identified similar trends at three different spatial scales: local (Hubbard Brook Experimental Forest; Table 3, Figs. 2–6), regional (southwestern White Mountains of New Hampshire, on the basis of three replicate plots; Figs. 2–6), and statewide (on the basis of BBS surveys, see Tables 3 and 4). Thus, similar population trends

for a species occurring at the local level tended to be representative of those at larger scales. That may be related to the general maturing of forest habitat in New England as a whole during the last 30 years (Irland 1982, Litvitas 1993, Hunt 1998), providing an increasingly forested landscape, which provides increasingly favorable habitat for some species but negatively affects others. For species declining within that region, the lack of recruitment of new individuals into those more mature habitats or even into local patches of suitable habitat within the more mature habitat matrix could be affected by the absence of nearby source areas (see Robinson et al. 1995b, Simons et al. 2000). The landscape context, coupled with dispersal abilities and habitat preferences of each species, may be important in determining whether populations increase or decrease within a given area.

Finally, the lack of congruence in trends between the local Hubbard Brook plot and larger scale BBS trends for several species (see Tables 3 and 4) may be an artifact of sampling, especially because most of those species were represented in the Hubbard Brook study plot and often in the BBS data set by a very small number of individuals. Also, for four of those seven species (Swainson's Thrush, Philadelphia Vireo, Blackburnian Warbler, Dark-eyed Junco), northern hardwood probably represents marginal breeding habitat, where populations may fluctuate more.

In conclusion, our long-term data from Hubbard Brook demonstrate that bird populations within that unfragmented and largely undisturbed forest fluctuate widely in abundance and that those fluctuations are evident at local and often regional (statewide) spatial scales. Our focus in this paper has been on the factors causing local changes in abundances, which are shown to be multiple and complex, to vary among species, and to operate at different temporal and spatial scales. We have shown those factors to include forest history (e.g. timing and intensity of logging), natural successional processes, disturbances such as pathogens (beech-bark disease), and climatic events such as wind and ice storms that affect forest structure. We identified structural changes in the forest over time, especially those related to natural forest succession, as particularly important in affecting bird-population changes at Hubbard Brook. This latter finding, in particular, implies

that studies examining causes of bird-population change, including those concerned with the effects of habitat fragmentation, cowbird parasitism, etc., need to control for concomitant changes in habitat quality due to succession and other factors.

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Associate Editor: A. Powell