

## DECLINE OF THE RUFIOUS-SIDED TOWHEE IN THE EASTERN UNITED STATES

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**ABSTRACT.**—The Rufous-sided Towhee (*Pipilo erythrophthalmus*) is a forest-generalist species that migrates short distances, with most of its range confined to the contiguous United States. Using migration count data from the northeastern United States, national Breeding Bird Survey data, and regional Christmas Bird Count data, I show that the towhee is making one of the most dramatic declines of a non-endangered species yet reported in the United States. Breeding Bird Survey data from New England states show that the towhee has been declining monotonically at about 8 to 10% per year. Populations in the Northeast are now at levels only about 13% of what they were when the Breeding Bird Survey began in 1966. Christmas Bird Count data from the southeastern United States also showed a decline in towhees, whereas Breeding Bird Survey data from the same region showed smaller declines, or no declines. This suggests that declines in wintering migratory towhees from the Northeast might explain most of the declines found in the Southeast using Christmas Bird Count data. The most likely explanation for this long-term, chronic decline in New England towhees is a gradual reversion of southern New England from a landscape with much early-successional habitat to a more forested landscape. Natural forest succession, following human-induced forest changes earlier in this century, may explain the current declines in towhees. Received 2 March 1992, accepted 25 November 1992.

CONSERVATION CONCERN for many migratory birds has burgeoned in recent years, especially for Neotropical species, those that breed in the Nearctic biogeographic region and winter in the Neotropical region (see Terborgh 1989, Askins et al. 1990, papers in Hagan and Johnston 1992). This is partly because several long-term monitoring programs have finally accumulated enough years of data that trends can be revealed over the noise inherent in such data (e.g. Robbins et al. 1989, Hagan et al. 1992, Hussell et al. 1992, Sauer and Droege 1992).

Concern has centered heavily on Neotropical migrants for at least two reasons. First, wintering habitat in the Neotropics is known to be rapidly disappearing, particularly mature tropical forest (Gradwohl and Greenberg 1988). Second, on the breeding grounds, many Neotropical migrants have been described as "forest-interior" species. Such species appear to be especially vulnerable to brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and nest predation, both of which are intensified near forest edges (e.g. Brittingham and Temple 1983, Wilcove 1985a, b, Robinson 1992). Thus, Neotropical migrants face serious, international threats to their survival. However, declines in migratory landbirds are not restricted to this group of species. Because all species occupy

unique niches, each can be vulnerable to an individualized problem or set of problems.

The Rufous-sided Towhee (*Pipilo erythrophthalmus*) is not a Neotropical migrant. Most of its wintering and breeding range is confined to the contiguous United States (AOU 1983). Towhees in the northern United States are migratory, spending their winters in the southern United States, while towhees breeding in the southern United States are nonmigratory. In the southern United States during winter, migratory northern-breeding towhees overwinter sympatrically with southern, nonmigratory towhees.

The towhee is also not a forest-interior species. Rather, it is typically found in edge and early successional habitats, or forest if there is sufficient density of understory vegetation (Forman et al. 1976, Casey and Hein 1983). It is perceived to be a habitat generalist that can do well in both large and small woodlots, and in both mature forests and regenerating second growth. In both habitat and distribution, the towhee is the antithesis of the forest-interior Neotropical migrant. Though forest-dwelling Neotropical migrants are generally perceived to be more vulnerable to population declines than nonforest generalists, the Rufous-sided Towhee is showing one of the most dramatic

declines of any North American landbird species. In this paper I draw on three data sources to document the decline of this species in the eastern United States: (1) regional migration capture data from Manomet Bird Observatory in Massachusetts; (2) continental Breeding Bird Survey (BBS) data; and (3) Christmas Bird Count data.

#### METHODS

Since 1970 Manomet Bird Observatory has operated a standardized banding program on Cape Cod Bay, Massachusetts (41°50'N, 70°30'W). Fifty mist nets (30-mm mesh) are opened five days each week during spring and fall migration, except during unusually severe cold or rain. Because the procedures are standardized, and because records are kept of daily effort (net hours), these data can be used to quantify long-term regional changes in bird populations (see Hagan et al. 1992). This data set was recently analyzed for population trends of 52 bird species (Hagan et al. 1992). In this paper I use only fall data for the Rufous-sided Towhee because some individuals are captured in traps in the spring, and trapping effort was not recorded. Methods of calculating annual indices accommodate slight changes in effort (net hours) from year to year and analyses are restricted to captures only during the time in fall when towhees are migratory. A complete description of the methods can be found in Hagan et al. (1992).

Because migration capture data from a single banding site are representative of only regional population changes, I also obtained Breeding Bird Survey (BBS) data from the U.S. Fish and Wildlife Service. These data are continental in coverage, span the period from 1966 to present, and involve several thousand qualified volunteer observers who survey breeding birds along rural roadsides one morning each summer. In this paper I use data from 1966 through 1989. Surveys are standardized by the Fish and Wildlife Service, and observers are screened by Fish and Wildlife Service biologists. Each survey consists of a 40-km rural roadside route with sampling stops at 0.8-km intervals (total of 50 stops). At each stop the observer counts all birds seen or heard within 400 m during a 3-min period. For a more detailed description of the method, see Robbins et al. (1986).

Trends were analyzed for each state of the United States where towhees occur and by individual route. Analyses by state were conducted as follows: For each year, the number of routes surveyed in each state was tallied. Then, the numbers of towhees counted on all routes were summed. From these values I calculated the mean number of towhees seen per route, per state, and per year. To calculate the state trend, I log transformed these values and ran a linear regression, with population index as the dependent variable and year

as the independent variable. From the slope of this regression, the percent annual change was calculated following Holmes and Sherry (1988). Although linear regression assumes a linear pattern of change through time, this appears to be an appropriate assumption for this species (see below).

To examine trends on a more spatially-precise scale, I also analyzed BBS data by individual route. The analysis techniques were the same as above except that averaging was not necessary because the regressions were performed on data from each route. Routes with fewer than 10 years of data were not included in these analyses, and samples identified as having some serious data problems (BBS code 7), or as being incomplete (BBS code 0; fewer than 46 stops sampled on a route), also were eliminated. I made no effort to adjust indices for year-to-year changes in observer in these analyses.

Christmas Bird Counts (CBCs) of wintering birds (organized by National Audubon Society) take place throughout the United States each year in late December. Observers can range from untrained observers to highly trained professional ornithologists. Each count area is represented by a circle 25 km (15 mi) in diameter. Counts must be confined to the circle, but effort (number of observers) can vary significantly among circles. Counts are tallied by local count coordinators and submitted to the National Audubon Society. Butcher (1990) provided a detailed description of the CBC. As of 1991, the Cornell Laboratory of Ornithology entered and stored CBC data in electronic format. I obtained all CBC data for the Rufous-sided Towhee from Cornell for the years 1966 to 1990. The information contained year of census, state, census-circle name, total number of towhees counted, total party hours (party = a group of observers traveling together), and total party miles. I generated a census-circle index for each year by dividing the number of towhees seen by the number of party hours of census (birds per party hour). I chose party hours instead of party miles because I felt effort expressed per unit time was more important than effort expressed as distance covered. However, the variables birds per party hour and birds per party mile were highly correlated, and conclusions drawn from the data would be the same regardless of which variable was used. I used the mean of all circles within a state as the annual index for that state. To calculate trend significance and rate of increase or decrease, I applied the same methods as described above for the BBS data, with the exception that no constant was added to the indices before log transformation (no indices were 0).

#### RESULTS

Of 52 species analyzed earlier for population trends using the Manomet migration data, the Rufous-sided Towhee showed the most dra-

matic population decline (Fig. 1). In the fall of 1970, about 2.7 towhees were captured per 1,000 net hours, but by 1988 only about 0.3 to 0.5 individuals were caught for the same amount of effort. This decline was significant using simple linear regression ( $P < 0.01$ ,  $n = 19$  years).

To determine whether the trends from migration capture data might be artifacts, or possibly only local in extent, I analyzed the Breeding Bird Survey data from throughout the towhee's range. Eighteen states and one Canadian province showed significant linear declines ( $P < 0.05$ ) in the number of Rufous-sided Towhees since 1966, with rates of decline (of those statistically significant) ranging from 1.2% (Tennessee) to 10.2% (New Hampshire) per year (Fig. 2a). There was a clear geographic pattern to these declines. First, most states showing declines were east of the Mississippi River (17 of 25 possible states [Connecticut and Rhode Island were combined for analysis]), and notably concentrated along the eastern seaboard (Fig. 2a). Second, the most severe declines were centered on the New England states, where rates of decline were all over 5% per year. Rates of decline, while still significant, diminished with distance from New England, but more slowly southward than westward (see Fig. 2a).

Ten states and two Canadian provinces showed increases in the number of towhees, with annual rates of increase ranging from 1.4% (Indiana) to 11.9% (Colorado; Fig. 2b). Again, there was a geographic pattern to these population changes, in which 8 of 10 states that showed an increase were west of the Mississippi River. Because western states are so much larger, on average, than eastern states, the area encompassed by significant increases is actually larger than the area of decline (compare Figs. 2a and 2b).

However, it is important to consider towhee density to properly understand the relative importance of these declines and increases. If large populations are increasing and small populations are decreasing, then species-level conservation concern might be unwarranted, although a range shift might be expected. If the reverse is true, and large populations are declining, then conservation concern should be heightened. A time-series plot at a five-year interval shows that the latter is the case for the Rufous-sided Towhee (Fig. 3). Populations were much denser in the East than in the Midwest and West in 1970. The mean state index in 1970

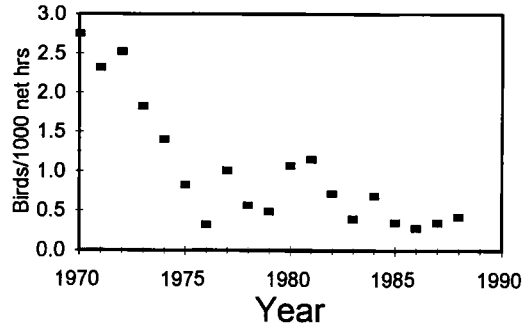


Fig. 1. Changes in abundance of Rufous-sided Towhees caught during fall migration at Manomet Bird Observatory, coastal Massachusetts, from 1970 to 1988.

for states that showed significant increases was only 2.6 birds per route ( $n = 10$  states reporting in 1970), while the same index for states showing decreases was 18.8 birds per route. Clearly, it has been the states (regions) with towhee populations of greater density that have shown declines. In 1985, for New England states where the decline has been most dramatic, the number of birds seen per route was down to 4.0 birds per route ( $n = 5$  states) from the 1970 value of 21.4 birds per route ( $n = 4$  states, Maine not reporting).

Because population declines were most severe in New England, I plotted raw data (birds route<sup>-1</sup> year<sup>-1</sup>) for each state (Fig. 4). The patterns of decline are remarkably linear and consistent among states. Unlike trend plots for many species, which show periods of increase and decrease (see trends reported in Robbins et al. 1989), the towhee in New England has been in constant decline ever since the BBS began in 1966.

Trends plotted by state, however, may not necessarily indicate that declines are spatially extensive. It is possible that state declines are driven by a few especially problematic routes. To explore this possibility I plotted the distribution of the number of routes showing various percent declines for New England states combined, New York, and Virginia and North Carolina combined (Fig. 5). The declines were not restricted to only a few routes. In New England, where towhees were reported for 87 routes, most routes showed declines of between 5 and 15% per year. Seventy-three of those routes (84%) showed statistically significant declines, and none showed a significant increase. A similar

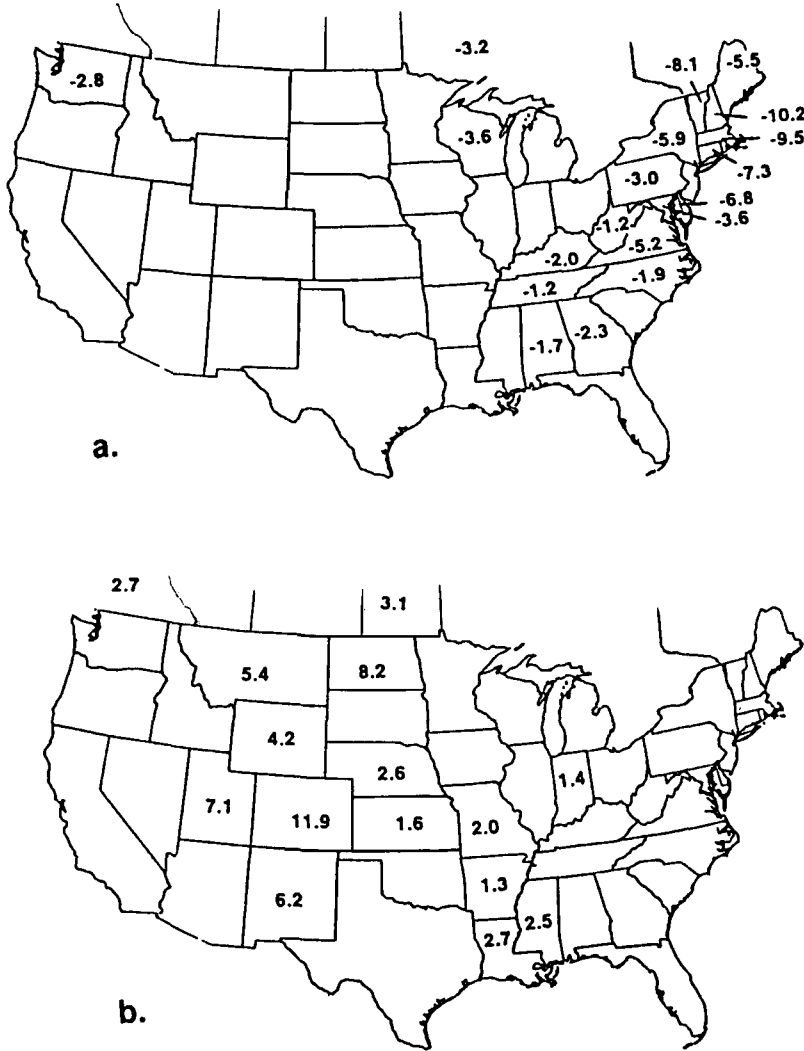


Fig. 2. (a) Percent annual change in Rufous-sided Towhees for each state that showed a significant linear decline ( $P < 0.05$ ) using 1966–1989 Breeding Bird Survey data; (b) percent annual change for each state that showed a significant linear increase using 1966–1989 Breeding Bird Survey data.

trend was observed for New York, and Virginia and North Carolina combined (see Fig. 5). Clearly, the majority of the routes are showing significant declines.

In New England, the widespread geographic distribution of routes that showed greater declines demonstrates the spatially extensive nature of the trend (Fig. 6). Routes showing the least severe declines tended to be concentrated on the northern fringe of the towhee range in northern Vermont and New Hampshire. Seven routes with especially severe declines (15% per year or greater) were scattered throughout New

England. Without visiting these routes individually, and exploring historical data about habitat changes through aerial photography, it will be difficult to determine what caused such severe declines on these routes. Two of the most severe declines occurred in the White Mountain National Forest, also in northern New Hampshire. Declines of 5 to 15% per year occurred throughout the New England states (Fig. 6).

Christmas Bird Counts in southeastern states include both southeastern nonmigratory breeders and northeastern wintering migrants. Using BBS data (see above), southeastern states showed

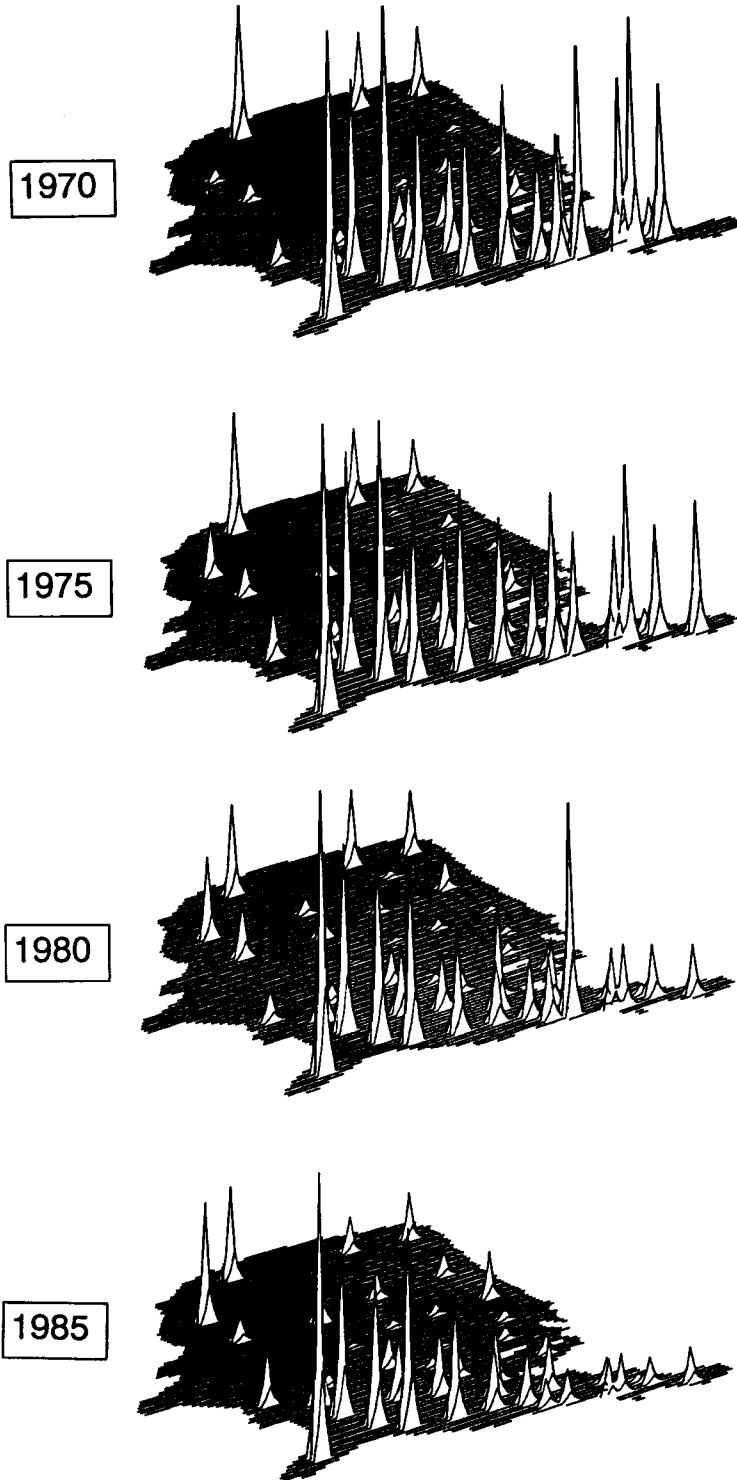


Fig. 3. Changes in relative densities of towhees across the United States at five-year intervals from 1970 to 1985 based on Breeding Bird Survey data.

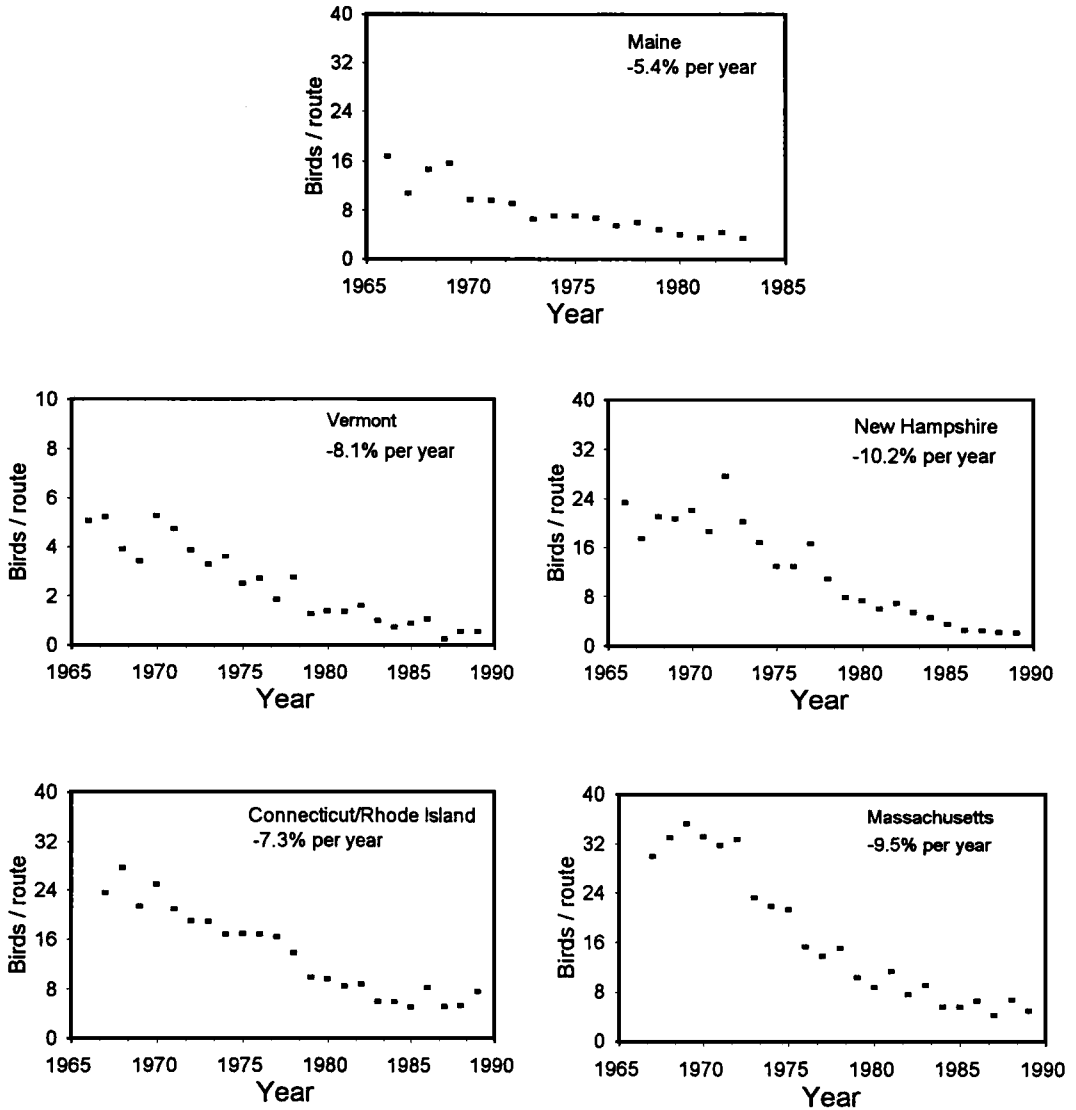


Fig. 4. Annual indices (birds per route) of Rufous-sided Towhees for each New England state based on Breeding Bird Survey data.

moderate declines (1 to 3% per year) or no declines. Christmas Bird Count data should show stronger declines because the counts are comprised partly of individuals from the precipitously declining populations of the Northeast. This prediction was upheld, with six southeastern states showing declines of 2 to 5% per year (see Fig. 7), all of which were stronger than shown by Breeding Bird Survey data for the same states. Moreover, plots of declines for these states were linear, as were the plots of breeding data from northeastern states.

DISCUSSION

The Rufous-sided Towhee is declining at a precipitous rate throughout the eastern United States, and especially in New England. Although there is heightened concern for species that winter in the tropics, the towhee is declining at faster rates than are most Neotropical migrant species. The median annual rate of decline for 62 Neotropical migrant species between 1978 and 1987 was 0.97%, although seven species showed declines of 5% or greater during

that time period (Robbins et al. 1989). However, all seven had been increasing in the previous decade (1966–1978). The towhee has been declining monotonically since 1966. It is unusual for a species to show such a long-term chronic decline. Such a pattern suggests a cause that is also chronic, and one that affects nearly all towhees in a region similarly.

Unfortunately, it is impossible to assign a cause to these declines because the data sets were not designed for that purpose. However, the magnitude of the declines in the East warrants discussion. It is especially relevant to consider whether the cause(s) for the declines are centered in the breeding or wintering grounds.

On a continental scale it is clear that declines have occurred primarily east of the Mississippi River in regions where towhees historically have been more abundant. If one can assume that towhees follow a generally north-south pattern of migration, as do some other passerines (Cooke 1904, Hutto 1985, Holmes and Sherry 1992), then it is logical to look for an explanation for the declines in the East as well. Although the most severe declines occurred in New England, towhees from this region overwinter in the southeastern United States, where poor survival in winter could affect breeding populations in the north. In a recent analysis of population trends of passerines that migrate through New England (Hagan et al. 1992), several southeastern United States wintering species were shown to have declined in numbers over the past two decades (Yellow-rumped Warbler [*Dendroica coronata*], Common Yellowthroat [*Geothlypis trichas*], Rufous-sided Towhee, Slate-colored Junco [*Junco hyemalis*], White-throated Sparrow [*Zonotrichia albicollis*], American Tree Sparrow [*Spizella arborea*], and Field Sparrow [*Spizella pusilla*]). These are all early-successional-habitat species in their wintering range. Two of these species breed north of the towhee range, but overlap in winter distribution (American Tree Sparrow and Yellow-rumped Warbler). If the cause for declines in these species was the same, it likely would be operating on the wintering grounds where they are sympatric for part of the year. These declines also spanned several taxonomic groups. The common feature of each species is a dependence on early-successional habitat.

However, that CBC data showed steeper declines than BBS data for six southeastern states suggests that the cause (if only one) for declines

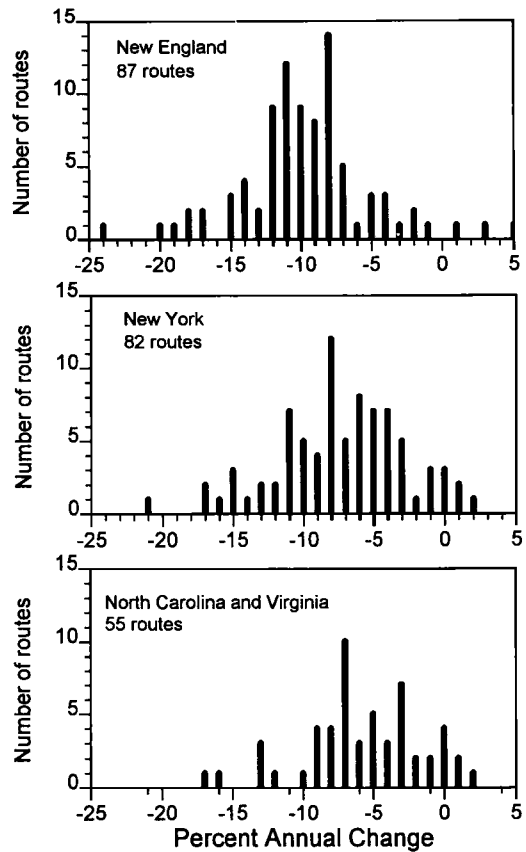


Fig. 5. Distribution of percent-change values for by-route regressions of Breeding Bird Survey data for the New England states combined, New York, and North Carolina and Virginia combined.

was a northeastern phenomenon. For example, BBS data from Florida showed a stable population, but CBC data (a mix of northern and southern towhees) showed a significant negative trend. This indicates that it was primarily the wintering migrant towhees that were driving the CBC trends, not the year-round resident towhees.

There is a strikingly linear pattern of decline shown by the data, especially for towhees in New England. The cause for such a monotonic erosion of populations must be equally constant in nature. Moreover, nearly every BBS route in New England showed a significant decline, providing further evidence for a cause or causes with broad spatial effects.

It is well known that New England forests have gradually matured over the past half-century with the abandonment of agriculture in

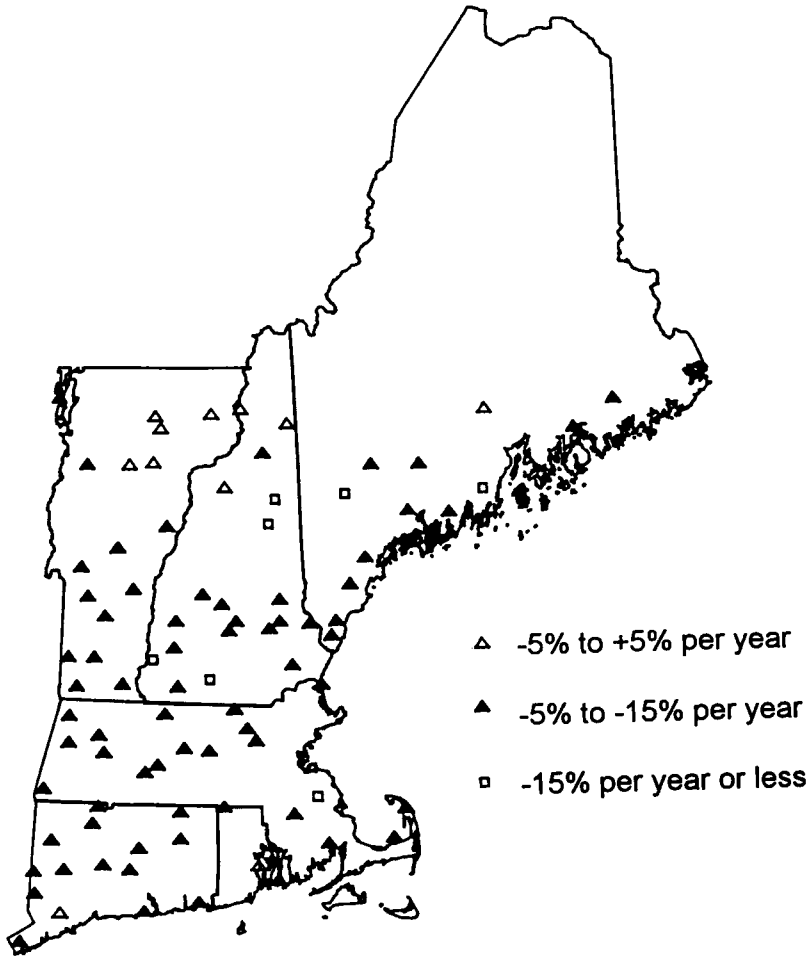


Fig. 6. Percentage change in Rufous-sided Towhees for each individual Breeding Bird Survey route in New England.

the region (Irland 1982, Brooks 1989). This succession has resulted in a taller, older forest with less understory vegetation, a seemingly important feature of towhee habitat. Witham and Hunter (1992) analyzed aerial photographs taken in the late 1960s of BBS routes in Maine, and compared them to more recent aerial photos. They found a significant loss of early-successional habitat. A midsuccessional species found breeding in New England, the Least Flycatcher (*Empidonax minimus*), has shown similar linear declines since the early 1940s (Hill and Hagan 1991). Holmes and Sherry (1988) attributed a decline in Least Flycatchers at the Hubbard Brook Experimental Forest in New Hampshire to loss of intermediate stages of forest

succession as a result of forest maturation. Declines in some bird species in New England, therefore, might reflect natural, regional changes in forest succession. The monotonic pattern of decline would be consistent with such an explanation. However, the rate of decline seems disproportionately severe. Declines of around 10% per year, which were observed in New England for the towhee, would result in populations of only about 13% of what they were 25 years ago (Fig. 8). Perhaps the effect of forest change on the towhee has been compounded by some yet unknown factor. For example, acid rain in the Northeast might have affected the food supply of the ground nesting, ground foraging towhee. A study of reproduc-



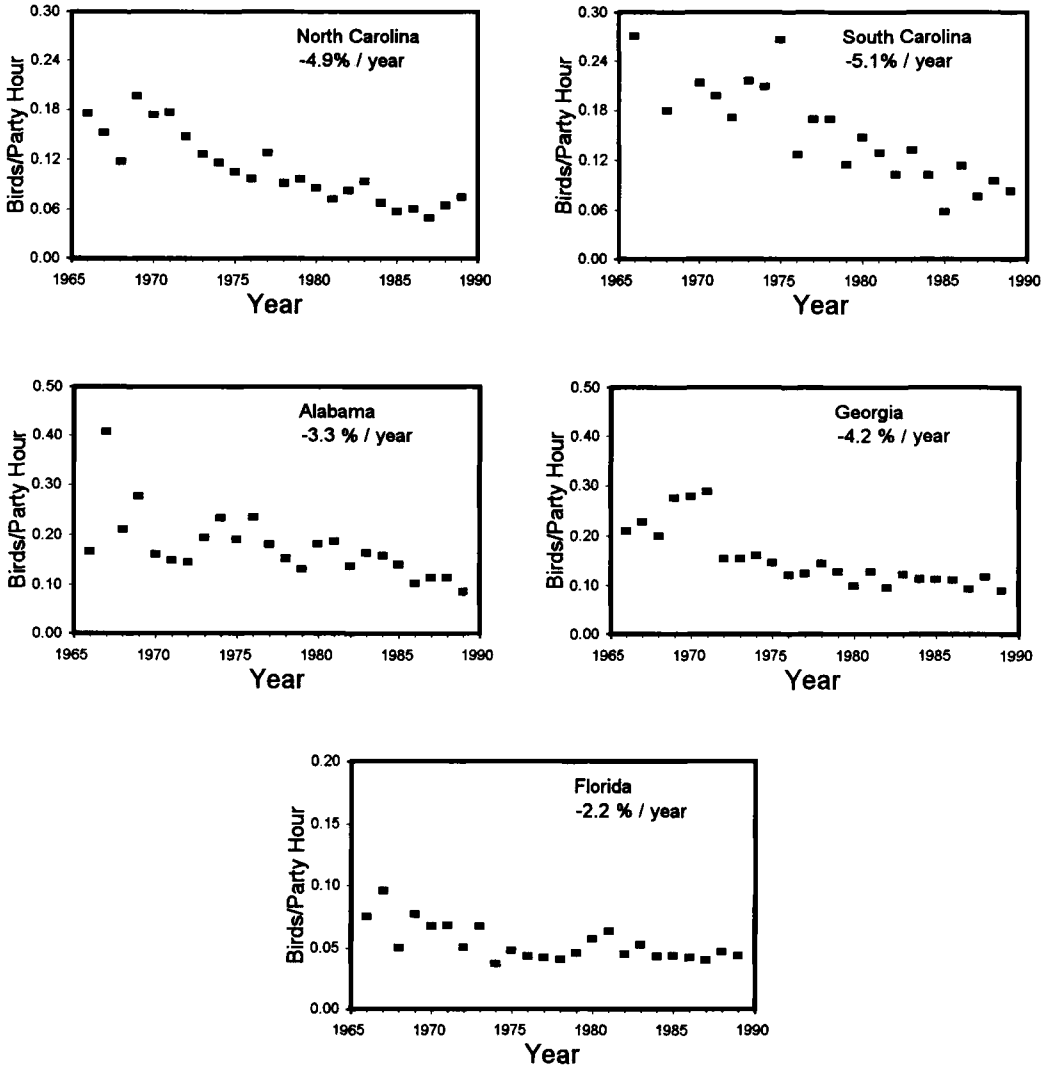


Fig. 7. Annual indices (birds/party hour) of Rufous-sided Towhees for states in the southeastern United States, based on Christmas Bird Count data.

tive success of New England towhees might shed light on whether adult survival, reproductive success, or both, explain the decline.

Browsing by white-tailed deer (*Odocoileus virginianus*) can dramatically reduce the amount of understory vegetation and, therefore, can reduce the densities of understory nesting birds (Dambach 1944, Casey and Hein 1983). Thus, population changes in white-tailed deer in New England might be relevant to population changes in towhees. I obtained deer-trend data

from Massachusetts and New Hampshire to compare with towhee trends. Deer densities in Massachusetts have been increasing at about 6% per year during the time span of this study (G. Vecellio unpubl. data; see Fig. 9), which is concordant with an hypothesis that deer browsing has caused the towhee decline. Data from New Hampshire, however, show generally declining deer populations during the same time period when towhees were declining (S. Williamson unpubl. data; see Fig. 9). The difference in deer

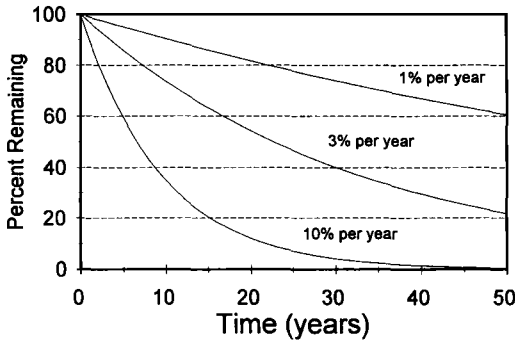


Fig. 8. Hypothetical population trends over time based on 1, 3, and 10% annual declines in numbers.

trends between these two adjacent states was apparently a result of different hunting regulations (S. Williamson pers. comm.). Thus, it seems unlikely that changing deer populations alone could explain changes in towhee populations in New England over the past 2.5 decades. In fact, DeGraaf et al. (1991) found little correlation between deer densities and numerous understory species (including the Rufous-sided Towhee) in experimental plots in central Massachusetts. Rather, the degree of forest thinning for timber management (which promoted development of an understory layer) superseded and countered the effects of deer browsing on understory birds. Thus, the general stage of forest development in New England might better explain the towhee decline. Brooks and Birch (1988) reported a significant decrease in the structural diversity of New England forests in just an 11-year period (1972–1982). This was a result of the gradual maturing of the forest, which has led to larger tree crowns, allowing less light to penetrate to the forest floor, thus reducing understory vegetation development.

The precipitous population declines of towhees in New England from 1966 to 1989 suggest cause for concern. However, it may be that the Rufous-sided Towhee is simply returning to pre-agricultural population levels of perhaps 200 years ago as New England forests age and former agricultural areas revert to forest. Unfortunately, the temporal scale of our population monitoring programs, many of which started in the 1960s, is relatively short, and it is difficult to find quantitative information on population levels before this time. Ludlow Griscom, an avid student of avian abundance and distribution in New England, wrote in 1949 that the towhee

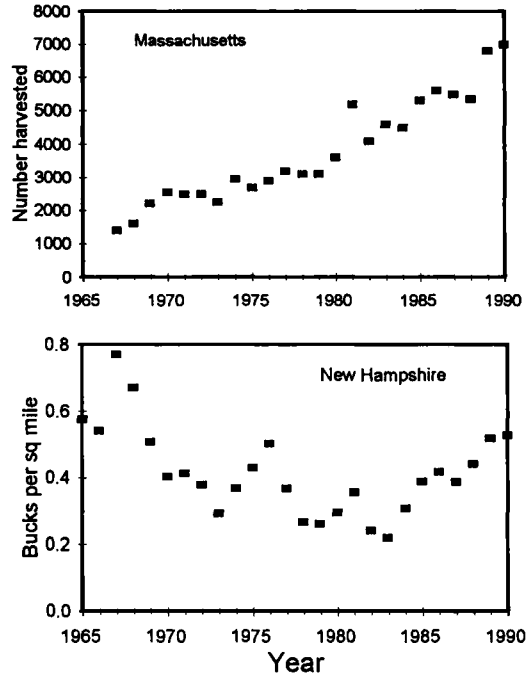


Fig. 9. Population indices of white-tailed deer in Massachusetts and New Hampshire from the mid-1960s to present.

was "now at its maximum abundance" (Griscom 1949). Griscom stated that the towhee "is the principal species to profit from lumbering, woodcutting, fires, and hurricanes, events which almost at once create a favorable habitat for several years." Griscom reported, however, that he did not know of any tangible density figures for the species.

Lack of historical, quantitative information does not preclude addressing conservation issues such as the effects of forest fragmentation or loss of early-successional habitat. Moreover, when a species declines at such rates as displayed by towhees in New England, thorough studies of population dynamics are warranted.

These results present the land manager with a dilemma. Habitat management for towhees would be different than that for edge-sensitive forest-interior Neotropical migrants, which are currently of great conservation concern. Decisions will have to be made regarding which species are more important as targets of land management. Moreover, geographic variation in population trends will mean that land-management strategies must be regionally specific. Regardless of which species become the focus

of land-management action in a region, this study indicates that one must be careful not to create new problems while attempting to solve others.

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