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Population declines in North American birds that migrate to the neotropics

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ABSTRACT **Using data from the North American Breeding Bird Survey, we determined that most neotropical migrant bird species that breed in forests of the eastern United States and Canada have recently (1978–1987) declined in abundance after a period of stable or increasing populations. Most permanent residents and temperate-zone migrants did not show a general pattern of decrease during this period. Field data from Mexico were used to classify a subset of the neotropical migrants as using forest or scrub habitats during winter. Population declines during 1978–1987 were significantly greater among the forest-wintering species, while populations of scrub-wintering species increased. The same subset of neotropical migrants also showed overall declines in forest-breeding species, but no significant differences existed between species breeding in forest and scrub habitats. Neotropical migrant species that primarily use forested habitats in either wintering or breeding areas are declining, but a statistically significant association between habitat and population declines was detected only in the tropics.**

The majority of birds that breed in the forests of Canada and the United States winter in the neotropics (1). Tropical deforestation, now proceeding at an annual rate of 1–3.5% (2), has attracted much recent attention as a potential cause of declines of neotropical migrant species (3–15). Most neotropical migrants also need extensive forest habitat during the breeding season, because their short nesting season, small clutch size, open nests, and nesting sites, which for many species are on or near the ground, leave these migrants vulnerable to increased rates of predation and nest parasitism in small woodlots and forest edges (4–15). Deforestation and fragmentation of both temperate and tropical forests dramatically reduce the suitability of a region for neotropical migrants (12). However, despite widespread concern regarding the status of this group, convincing evidence of regional population declines has not been presented (3). In fact, until quite recently no long-term data have been gathered on a sufficiently large scale to detect regional and continental population changes in neotropical migrant birds.

The North American Breeding Bird Survey (BBS), an annual roadside survey of United States and Canadian birds initiated in 1966 (16), is the only quantitative source of information regarding regional changes in breeding populations of neotropical migrant birds. BBS data can be used to estimate population trends for about 370 of the more common species of North American birds. These estimates are based on counts conducted each June along approximately 2000 randomly distributed roadside "routes." Experienced volunteers recruited by state and provincial coordinators use uniform procedures to sample bird populations at 50 stops at 0.8-km intervals along secondary roads; observers start 0.5 hr before local sunrise and at each stop count all birds detected within a 0.4-km radius during a 3-min period.

METHODS

Preliminary examination of annual population means for the Eastern BBS Region (the United States east of the Mississippi River and corresponding parts of eastern and central Canada) suggested that many neotropical migrant species began to decline in abundance during the period 1978–1980. To quantify this decline, we calculated population trend estimates for two consecutive time periods, 1966–1978 and 1978–1987, for eastern populations of 62 neotropical migrant species (Table 1). A species was included in this analysis if the majority of the population winters in the tropics and breeds in scrub or forest habitats.

The population trend for each BBS route was calculated using linear regression to estimate the slope of the logarithmically transformed annual counts. Observers were included as a covariable in the analysis. The trends for individual routes were then averaged to give state, regional, and continental trends; in this process the individual routes were weighted to compensate for density of routes, consistency of coverage, and relative abundance of the species. Variances were estimated by "bootstrapping," and z tests were used to examine the null hypothesis of no change over the interval (16).

If changes had resulted from systematically biased BBS data, population trends for nonmigratory and temperate-zone migrant species should have been similarly affected. We therefore performed separate trend analyses of 13 common species that are primarily nonmigratory (permanent residents) in the eastern region (Table 2) and 19 common temperate-zone migrant species that winter primarily north of the tropics (Table 3). We used Wilcoxon signed-rank tests to examine the null hypothesis that median trends for a group of species equaled 0.0, and Mann–Whitney tests to test for differences in median trends between time periods or groups of species. Unfortunately, comparisons of population trends of permanent resident and temperate-zone migrant species with trends in neotropical migrant species cannot be used to examine the hypothesis that changing habitat conditions are associated with population changes in neotropical migrants. This is because differences among groups can be attributed to several causes, including loss of breeding habitat from forest fragmentation, to which neotropical migrants are particularly susceptible (7, 8), hazards of migration, which affect the two groups of migrants, and severe weather during winter, which periodically impacts the two control groups (16).

Because habitat changes in wintering and breeding areas are often cited as a potential cause of population declines in songbirds (3–15), we examined the hypothesis that patterns of winter or breeding habitat use by neotropical migrant species were associated with population trends. In the breed-

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Abbreviation: BBS, North American Breeding Bird Survey.

Table 1. Neotropical migrant species examined, with population trends for 1966–1978 and 1978–1987

Species		Trend, %/year		Species		Trend, %/year	
Common name	Latin name*	1966–1978	1978–1987	Common name	Latin name*	1966–1978	1978–1987
Broad-winged hawk	*Buteo platypterus*	1.5†	−0.8	Cape May warbler	*Dendroica tigrina*	19.3	−2.3
Black-billed cuckoo	*Coccyzus erythropthalmus*	13.4	−5.9‡	Black-throated blue warbler	*Dendroica caerulescens*	−0.9	1.7
Yellow-billed cuckoo	*Coccyzus americanus*	1.8‡	−5.0‡	Black-throated green warbler	*Dendroica virens*^{f,2}	0.3	−3.1‡
Chuck-will's-widow	*Caprimulgus carolinensis*	0.6	−2.0	Blackburnian warbler	*Dendroica fusca*	1.3	−1.1
Whip-poor-will	*Caprimulgus vociferus*	0.6	−0.8	Yellow-throated warbler	*Dendroica dominica*^{f,1}	2.0†	−0.4
Ruby-throated hummingbird	*Archilochus colubris*^{s,1}	0.4	1.8†	Prairie warbler	*Dendroica discolor*	−3.7‡	−0.4
Olive-sided flycatcher	*Contopus borealis*	3.6	−5.7†	Bay-breasted warbler	*Dendroica castanea*	10.2	−15.8‡
Eastern wood-pewee	*Contopus virens*^{f,1}	−2.1‡	−0.7	Blackpoll warbler	*Dendroica striata*	18.9	−6.3
Yellow-bellied flycatcher	*Empidonax flaviventris*	14.9†	3.6	Cerulean warbler	*Dendroica cerulea*	−3.9‡	−0.9
Acadian flycatcher	*Empidonax virescens*	1.2†	−1.3†	Black-and-white warbler	*Mniotilta varia*^{f,2}	1.4	1.4†
Least flycatcher	*Empidonax minimus*^{f,1}	−1.6†	−0.2	American redstart	*Setophaga ruticilla*^{f,2}	1.3	−1.2
Great crested flycatcher	*Myiarchus crinitus*^{f,2}	0.4	−0.3	Prothonotary warbler	*Protonotaria citrea*	4.4‡	1.1
Blue-gray gnatcatcher	*Polioptila caerulea*^{f,1}	0.5	1.4	Worm-eating warbler	*Helmitheros vermivorus*^{f,2}	1.8‡	−2.0
Veery	*Catharus fuscescens*	1.6†	−2.4†	Swainson's warbler	*Limnothlypis swainsonii*	6.6†	0.0
Swainson's thrush	*Catharus ustulatus*^{f,2}	3.4‡	−0.2	Ovenbird	*Seiurus aurocapillus*^{f,2}	1.0	−1.0†
Wood thrush	*Hylocichla mustelina*^{f,2}	1.3‡	−4.0‡	Northern waterthrush	*Seiurus noveboracensis*	5.3‡	5.8
Gray catbird	*Dumetella carolinensis*^{3}	0.6†	−1.4†	Louisiana waterthrush	*Seiurus motacilla*	−1.0	−0.4
White-eyed vireo	*Vireo griseus*^{s,2}	0.3	−1.2†	Kentucky warbler	*Oporornis formosus*^{f,2}	−0.3	−1.6
Solitary vireo	*Vireo solitarius*	6.1‡	−0.1	Mourning warbler	*Oporornis philadelphia*	1.1	−1.6
Yellow-throated vireo	*Vireo flavifrons*^{f,2}	−0.2	−0.9	Common yellowthroat	*Geothlypis trichas*^{s,1}	0.2	−1.9‡
Warbling vireo	*Vireo gilvus*	0.2	0.3	Hooded warbler	*Wilsonia citrina*^{f,2}	0.9	0.4
Philadelphia vireo	*Vireo philadelphicus*	−0.2	0.2	Wilson's warbler	*Wilsonia pusilla*	9.8	−6.5
Red-eyed vireo	*Vireo olivaceus*^{f,2}	2.8‡	0.2	Canada warbler	*Wilsonia canadensis*	−2.7	−2.7‡
Blue-winged warbler	*Vermivora pinus*^{s,2}	1.0	−1.0	Yellow-breasted chat	*Icteria virens*^{s,1}	−4.5‡	1.2‡
Golden-winged warbler	*Vermivora chrysoptera*	−2.2†	−1.9	Summer tanager	*Piranga rubra*^{3}	−0.6	−0.8
Tennessee warbler	*Vermivora peregrina*	18.6	−11.6†	Scarlet tanager	*Piranga olivacea*	2.6‡	−1.2‡
Nashville warbler	*Vermivora ruficapilla*	0.0	2.7	Rose-breasted grosbeak	*Pheucticus ludovicianus*^{f,1}	6.1‡	−4.1‡
Northern parula	*Parula americana*^{3}	1.2	−2.1‡	Blue grosbeak	*Guiraca caerulea*^{s,1}	2.4†	2.7†
Yellow warbler	*Dendroica petechia*^{s,1}	0.9†	1.6‡	Indigo bunting	*Passerina cyanea*^{s,1}	0.4	−0.7‡
Chestnut-sided warbler	*Dendroica pensylvanica*^{s,2}	2.2‡	−3.8‡	Orchard oriole	*Icterus spurius*^{s,1}	−0.3	1.1
Magnolia warbler	*Dendroica magnolia*^{f,2}	3.3†	0.0	Northern oriole	*Icterus galbula*	2.0†	−2.9†

*Superscripts indicate nesting and wintering habitats: f, forest-nesting; s, scrub-nesting; 1, scrub-wintering; 2, forest-wintering; 3, winter-habitat generalist.
†$P < 0.05$.
‡$P < 0.01$.

ing-season analysis, birds were categorized as forest interior or forest edge/scrub species (5).

Habitat use by migratory birds in the tropics is largely unquantified. We categorized nonbreeding-season habitat use based on data gathered in weekly censuses along six 1-km transects at the Sian Ka'an Biosphere Reserve in Quintana Roo, Mexico, during the winters from October 1987 through March 1989. These censuses, part of an unrelated study, were designed to determine the distribution of migrants across a successional gradient from pasture to mature forest. The censuses included all migrants seen or heard within 20 m of the transect. Two transects were placed in each of three major habitats: recently cleared forest, 5- to 7-year-old scrub, and closed canopy forest. Each pair of transects was representative of distinct forms of the different major habitats. The recently cleared forest included a pasture and an abandoned cornfield, the secondary scrub was either grazed or ungrazed, and the forest was of low (11-m canopy) or medium (17-m) stature. Species were included in the analysis if at least five individuals were observed on a total of at least 5 days. A species was classified as a forest species if more individuals per kilometer were observed in forest than in other habitats. Early successional species were those with lowest densities occurring in forests. Generalist species exhibited no clear habitat preferences. For this analysis no distinction was made between secondary and primary forest. All migrants detected during the period October through March were included in the analysis; 25 species were present in mid-winter, 4 in the late fall only, and 2 in the late winter. We have included some transients (eastern wood-pewee, red-eyed vireo) because observations made during their long tenure in Mexico suggest a dependence on these habitats. Additionally, their habitat use in the Yucatán correlates well with our observations in other tropical areas. Because data were collected systematically from only one site in Mexico, habitat information was available for only 31 species from our sample of neotropical migrants. We suggest that the generality of the results be tested with habitat-use data from other points in the neotropics. Breeding and wintering habitat analyses were conducted only on those species that could be classified in both areas.

RESULTS

Neotropical Migrant Trends. Striking differences in trends are evident between the two periods (Table 1). During the first period, 15 species (24.2%) had negative trends, of which 6 were significant ($P < 0.05$). Positive trends occurred in 47 species (75.8%), 23 of which were significant. In contrast, during the second period 44 of the species showed negative trends (71.0%) with 20 significant, and only 18 species had positive trends (29.0%), of which 4 were significant. The difference in median trends between the periods is highly significant (Mann–Whitney test: 1966–1978 median slope = 1.17%/year, 1978–1987 median slope = −0.97; $P < 0.0001$).

Permanent Resident and Temperate-Zone Migrant Trends. Population trends of the permanent residents and temperature-zone migrants differed strongly from trends of neotropical migrants. Among the 13 permanent resident species, 5 (38.5%) had positive trends in the first period and 7 (53.8%) had positive trends in the second period (Table 2). Median population trends of permanent resident species did not differ between the two time periods (1966–1978 median trend = −0.2, 1978–1987 median trend = 0.6; $P > 0.12$). Nine (47.4%) and 10 (52.6%) of the 19 temperate-zone migrant species had positive trends in the two time periods, respectively (Table 3). As with permanent residents, median trends did not differ between the time periods for temperate-zone migrants (1966–1978 median trend = 0.0, 1978–1987 median trend = 0.3; $P > 0.26$).

Winter Habitat Use by Neotropical Migrants. Of 31 migrants and winter residents present in the study area in Quintana Roo, 16 were categorized as occurring in forest interior and 12 in open scrub habitats; the other 3 were classified as habitat generalists and were not included in the following analyses (Table 1). To detect negative impacts on previously increasing populations, we examined the difference between 1966–1978 and 1978–1987 trends. Forest-wintering species showed a much greater decline in trend (median change = −2.30; Mann–Whitney test of null hypothesis that median change = 0.0, $P < 0.001$) between periods than did scrub species (median change = 0.74; $P > 0.78$). The difference in median changes between forest and scrub-wintering species is highly significant ($P < 0.0001$). Species wintering in forest also had lower median trends in the 1978–1987 period (median trend = −1.03; $P < 0.005$) than those wintering in scrub habitat (median trend = 0.46; $P > 0.54$) (test of null hypothesis of no difference in trends between groups, $P < 0.06$).

Breeding Habitat Use by Neotropical Migrants. Forest-breeding species also exhibited a decline in trends between periods (median change = −2.20; $n = 18$; $P < 0.005$), and a nonsignificant decline occurred in scrub-breeding species (median change = −0.4; $n = 10$; $P > 0.54$). Although forest-breeding species showed a larger median decline than scrub-breeding species, the median changes between the groups were not statistically significant ($P > 0.12$). Species breeding in forest also had lower median trends in the 1978–1987 period (median trend = −0.55; $P < 0.03$) than

Table 2. Permanent resident species examined, with population trends for 1966–1978 and 1978–1987

Species		Trend, %/year	
Common name	Latin name	1966–1978	1978–1987
Northern bobwhite	*Colinus virginianus*	−3.6‡	−0.8
Great horned owl	*Bubo virginianus*	0.8	2.0†
Downy woodpecker	*Picoides pubescens*	−0.2	−0.7
Hairy woodpecker	*Picoides villosus*	1.8	1.6
Pileated woodpecker	*Dryocopus pileatus*	1.2	2.6
Black-capped chickadee	*Parus atricapillus*	1.8†	3.4‡
Carolina chickadee	*Parus carolinensis*	0.0	−0.5
Tufted titmouse	*Parus bicolor*	−2.0‡	3.5‡
Brown-headed nuthatch	*Sitta pusilla*	−1.9	−3.3
Carolina wren	*Thryothorus ludovicianus*	1.2‡	5.4‡
Northern mockingbird	*Mimus polyglottos*	−1.7‡	0.0
Northern cardinal	*Cardinalis cardinalis*	−0.9‡	0.6†
House sparrow	*Passer domesticus*	−1.4‡	−1.4‡

†$P < 0.05$.
‡$P < 0.01$.

Table 3. Temperate-zone migrants examined, with population trends for 1966–1978 and 1978–1987

Species		Trend, %/year	
Common name	Latin name	1966–1978	1978–1987
Turkey vulture	*Cathartes aura*	1.4	1.8
Black vulture	*Coragyps atratus*	2.3	−2.0
American kestrel	*Falco sparverius*	2.4‡	−0.9
Mourning dove	*Zenaida macroura*	1.9‡	1.2‡
Belted kingfisher	*Ceryle alcyon*	0.0	−0.1
Northern flicker	*Colaptes auratus*	−4.4‡	−1.2†
Red-bellied woodpecker	*Melanerpes carolinus*	0.2	0.3
Yellow-bellied sapsucker	*Sphyrapicus varius*	−5.4‡	−0.6
Horned lark	*Eremophila alpestris*	0.7	1.5†
Blue jay	*Cyanocitta cristata*	−1.3†	−2.3‡
Brown creeper	*Certhia americana*	2.7†	2.0
Winter wren	*Troglodytes troglodytes*	−7.1‡	7.0‡
Golden-crowned kinglet	*Regulus satrapa*	−2.4	4.1
Eastern bluebird	*Sialia sialis*	−6.3‡	9.8‡
American robin	*Turdus migratorius*	1.1‡	2.9‡
Chipping sparrow	*Spizella passerina*	−1.9‡	2.3‡
White-throated sparrow	*Zonotrichia albicollis*	−0.1	−0.2
Red-winged blackbird	*Agelaius phoeniceus*	1.0‡	−2.8‡
Common grackle	*Quiscalus quiscula*	−0.1	−1.5‡

†$P < 0.05$.
‡$P < 0.01$.

those breeding in scrub habitat (median trend = 0.20; $P > 0.88$) (test of null hypothesis of no difference in trends between groups, $P > 0.30$).

Species with Seasonal Change in Habitat Use. Eight species change habitat use between breeding and wintering seasons. The species that breed in scrub but winter in forested habitat (white-eyed vireo, blue-winged warbler, and chestnut-sided warbler) had lower trends in the later period than in the earlier period, while three of five species that breed in forested but winter in scrub habitat (eastern wood-pewee, least flycatcher, and blue-gray gnatcatcher, but not yellow-throated warbler or rose-breasted grosbeak) showed increased trends in the later period.

DISCUSSION

A number of studies have shown long-term declines of neotropical migrant birds at census sites in the forests of eastern North America (17, 18). In addition, many forest-breeding neotropical migrants are rare or missing from small tracts of forest, suggesting that declines have occurred at these sites since their isolation (4–8). The data summarized in this paper, however, show a general decline in neotropical migrants throughout eastern North America.

Good evidence supports the proposition that deforestation at local sites on both the breeding and wintering grounds leads to declines in forest-dwelling specialists at the sites. Therefore, both types of deforestation could lead to continental declines in neotropical migrants. However, forest cover within North America has remained relatively stable compared to the large net loss of tropical forests (19). Declines because of cowbird parasitism have been cited as a side effect of forest clearing on the breeding ground (20), but BBS data indicate that the brown-headed cowbird (*Molothrus ater*) has declined significantly (−2.35% per year) since 1966 in the eastern United States. Unfortunately, the relative contribution of habitat destruction on the wintering grounds toward breeding population declines has been difficult to assess and is thus controversial.

Patterns of decline at the regional or continental scale can be used to test for an effect of tropical deforestation. Our analysis of habitat distribution shows a significant association between the use of forests in the Yucatán and the tendency of species to show a negative slope change in their population trends over the past 9 years. Our analysis also indicates that neotropical migrants that primarily use forested habitats during either the breeding or the wintering season have been declining in recent years. However, only in winter does a significant difference exist between median trends of species that use forested versus scrub habitats. This result suggests that tropical deforestation is having a more direct impact on neotropical migrants than is loss and fragmentation of forest habitats in North America.

Unfortunately, because most species use the same general habitat types in both winter and summer, it is difficult to separate winter habitat effects from summer habitat effects. Species that switch habitat use between breeding and wintering seasons provide the only information on differential effects of wintering and breeding habitats. Species that winter in a more mature habitat than that in which they breed show negative slope changes, whereas those that winter in earlier successional habitats generally show positive slope changes. This suggests that the effects of winter habitat destruction are detectable at the continental level. Given the difficulty of quantifying the effects of nonbreeding-season events on breeding populations, we suggest that this analysis represents the strongest evidence to date that tropical deforestation is contributing to declines in migratory bird populations.

Although the pattern of decline in the past 9 years and its correlation with winter habitat use are evident, the reasons for the increases during the early years of the BBS are unclear. One possible explanation is the decline in use of persistent pesticides in Canada and the United States. Another is that the late 1970s was a period when large areas of the Caribbean slope of Mexico and Central America were opening for development (21) and North American forest cover had reached a peak and was beginning to decline after decades of increase (refs. 22 and 23; T. W. Birch, personal communication).

Habitat degradation in North America and the neotropics should not be viewed as alternative hypotheses for the population declines of neotropical migrants. Rather, evidence now supports the view that human activities in both regions are having dramatic impacts on the populations of migratory birds. Given the patterns of increasing forest destruction and fragmentation in both breeding and wintering areas of neotropical migrant birds, we predict that populations of migratory forest birds will continue to decline.

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