Changes in Bird Abundance in Eastern North America: Urban Sprawl and Global Footprint?

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The abundance of birds recorded in the North American Breeding Bird Survey decreased by up to 18 percent between 1966 and 2005. The abundance of US and Canadian resident species decreased by 30 percent, and that of migrants within the United States and Canada decreased by 19 percent. By contrast, Neotropical migrants increased by up to 20 percent. Land-cover changes in northern latitudes therefore seem more consequential for bird populations than those occurring in Neotropical habitats. Lower abundances were most marked for resident breeding birds that used open, edge, and wetland habitats, the environments most affected by human disturbances—particularly urban sprawl—in northern latitudes. The abundance of resident and migrant forest-dwelling birds increased (although trends varied from species to species), with the increases seeming to follow the 20th-century expansion of forest area in northern latitudes, rather than the loss of Neotropical forests. The geographic footprint of changes in bird abundance linked to habitat changes in North America may thus be extending southward, with negative effects on birds that use open habitats and positive effects on forest birds.

Keywords: temperate avifauna, tropical avifauna, loss of birds, habitat losses

Experienced observers and scientists aver that there have been significant reductions in the abundance of birds breeding in North America across the last half-century (Robbins et al. 1989, King and Rappole 2003, National Audubon Society 2004), perhaps owing, among other factors, to the influence of global atmospheric changes (Sillett et al. 2000, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Valiela and Bowen 2003, Anders and Post 2006) or to the loss of North American breeding habitats or Neotropical wintering habitats (Andren and Angelstam 1988, Temple and Cary 1988, Terborgh 1989, Böhning-Gaese et al. 1993, Brook et al. 2003, Johnson et al. 2005, Stratford and Robinson 2005). The loss of Neotropical wintering habitat has been given special attention because of the many reports, both in the scientific literature and in the popular press, of continuing alteration of tropical landscapes (Melillo et al. 1985, Woodwell et al. 1987, Sader and Joyce 1988, Houghton et al. 2000, Brook et al 2003, Hirsch et al. 2004, Marris 2005).

In this article we use the remarkably data-rich long-term (1966–present) record of breeding birds in the North American Breeding Bird Survey (BBS) to pursue three lines of inquiry: (1) to ascertain whether the abundance of eastern and central North American breeding birds indeed decreased during recent decades; (2) to see whether the abundance of birds that breed in North America was affected by the loss of habitat in the locations where the birds spend their winters; and (3) to determine whether changes in the abundance of North American breeders differed among birds that used different habitats.

The BBS data have been collected annually since 1966 in surveys staffed by skilled observers surveying set routes during the breeding season to record the abundance and identity of breeding birds. The data sets are massive: There are about 3700 routes defined in the BBS, and, on average, about 2900 of them are surveyed annually in the states and provinces

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of the United States and Canada. The routes were located so as to sample habitats that are representative of the regions. The survey of each 40-kilometer (km) route consists of 50 stops at 0.8-km intervals. Data on the numbers and species of breeding birds are recorded at each stop for 3 minutes, and all observations are added for the route; then all the route data are added for the state or province, and eventually reported (USGS 2005).

The BBS counts, repeated across years (and, when feasible, along the same routes) by qualified personnel, are intended to assess the relative abundance of breeding birds rather than to yield a complete count of them. Statistical issues arising from BBS counts are reviewed (Robbins et al. 1989, Böhning-Gaese et al. 1993, Peterjohn et al. 1995), and BBS abundance data have been used, albeit with some criticism, in previous papers (Böhning-Gaese et al. 1993, Keitt and Stanley 1998, Anders and Post 2006). Survey data such as those of the BBS have been subjected to a variety of normalizing procedures aimed at reducing bias and statistical irregularities. As appropriate as such corrections and modifications may be, it seems nearly impossible to fully correct for all potential statistical flaws (there has even been concern about the effects of the age of observers [and the consequent loss of aural acuity], interference by changing traffic frequency, sampling species that could be detected near roads, and more such variables). Tools for assessing the influence of all potential biasing variables are simply not available.

Most statistical problems arise at the level of the specific count. We avoided such problems as much as possible by pooling all of the observations made in all of the provinces and states within the Atlantic and Mississippi flyways. Pooling such large numbers of observations diminishes the impact of the inherent sampling problems to some degree. In addition, we focused on interpreting broad decadal trends (increases, decreases, or no change over the entire record) rather than attempting to interpret shorter-term interannual changes. Moreover, all normalizing corrections add variation as propagated error and produce transformed variables that might be less transparent than the straightforward "birds per kilometer of transect." Since the effects of corrections in many cases were modest or variable, and given the difficulty of fully normalizing the data, we eschewed transformations and simply used pooled counts, keeping the data real and readily accessible. Although the BBS data may have biases and limitations, the BBS's long-term span, remarkably large number of observa-

tions, and regional coverage make these records attractive for comparative examination of long-term changes.

Previous studies have analyzed BBS data within restricted time periods, along selected routes, or in separate regions, or have focused on a single bird species or subset of the species recorded. We include the entire BBS data set for all data from the Atlantic and Mississippi flyways (figure 1), including all years, all routes, and all species. We therefore focus on the overall longer decadal trends, and use the entire data set to depict the changes in the avifauna as comprehensively as possible. This approach minimizes the influences of short-term inter-
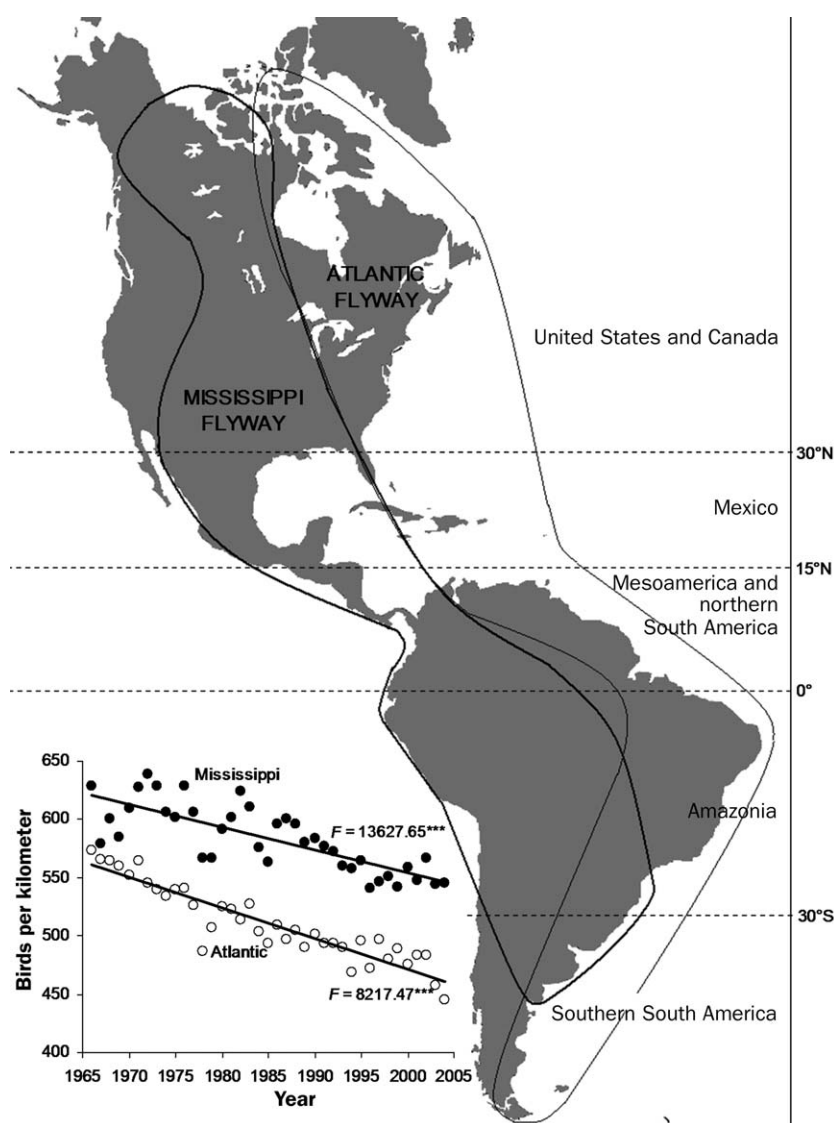
Figure 1. Approximate bounds of the Mississippi and Atlantic migratory flyways over the Americas. The dashed horizontal lines indicate the latitudinal ranges into which we stratified the North American Breeding Bird Survey (BBS) data. The inset graph shows the abundance of breeding birds recorded in the BBS from 1966 to 2004. Linear regressions were fit to BBS records from states and provinces that provided breeding areas for birds that used the Misssissippi and Atlantic flyways.

annual trends and of differences among specific bird species that we knew were present in the record.

Reduction in breeding bird abundance

Our central finding was that the total number of birds recorded as nesting in the eastern and central United States and Canada has steadily decreased since 1966 (figure 1 inset). The long-term trend in the number of nesting birds revealed decreases of about 12 percent and 18 percent in the Mississippi and Atlantic records, respectively, for the period 1966–2004. These losses took place at rates of 0.3 to 0.5 percent per year. The abundance of nesting birds was consistently higher in the Mississippi than in the Atlantic flyway, and there was a degree of year-to-year variation (figure 1).

We initially examined the possible association of changes in bird abundance with changes in mean temperature and precipitation for winter and summer over the eastern United States, using data from the NOAA Satellite and Information Service (*www.ncdc.noaa.gov/oa/climate/research/monitoring. html*), for the years covered by BBS records. The year-to-year variation was probably a result of large-scale interannual climatic shifts (Sillett et al. 2000, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Valiela and Bowen 2003, Anders and Post 2006), although we found no evident correlation between (a) eastern North American temperatures and precipitation and (b) the year-to-year variations in bird abundance shown in figure 1. The interannual changes merit further study, but here we focus on the overall decadal-scale trends. For simplicity, and because of the relatively similar time courses, we pooled data for the two flyways. The decadal-scale losses of numbers of nesting birds that have taken place across large regions of North America over the more than 40 years of the BBS record pose a question: What are the possible causes?

The effect of overwintering range on the abundance of breeding birds

To discern whether the reduction in the numbers of birds that breed in eastern and central North America was associated with factors (particularly habitat losses) related to the latitudinal range where the birds either bred or spent the boreal winter, we partitioned the BBS data in terms of species that (a) were fully resident within the United States and Canada, or (b) migrated south during the boreal winter to more southern areas of the United States, to Mexico, to Mesoamerica and northern South America, to the Amazon basin and other areas east of the Andes, or to southern South America (figure 1). The idea here was that residents were exposed to conditions in the northern latitudes year-round, but migrants were exposed to the effects of spending part of the year in the United States and Canada as well as to the hazards of spending the boreal winter in the more southerly wintering range. If, as has been suggested, the loss of Neotropical habitats has been detrimental for Neotropical migrants, we might see different time courses of abundance among resident and migrant species, particularly those migrants that overwinter in the Neotropics, where extensive habitat loss has been reported. The species listed in the BBS records, and our classification of their migratory status, are included in table 1.

Nesting bird abundance decreased most clearly and consistently in species that either resided (19 percent overall loss) or migrated within the United States and Canada (30 percent loss; figure 2). The slopes of the time trends for these two groups were similar (figure 2), suggesting that the effect of living in the United States and Canada part-time or year-round was about the same: Migrants did not incur relatively greater losses.
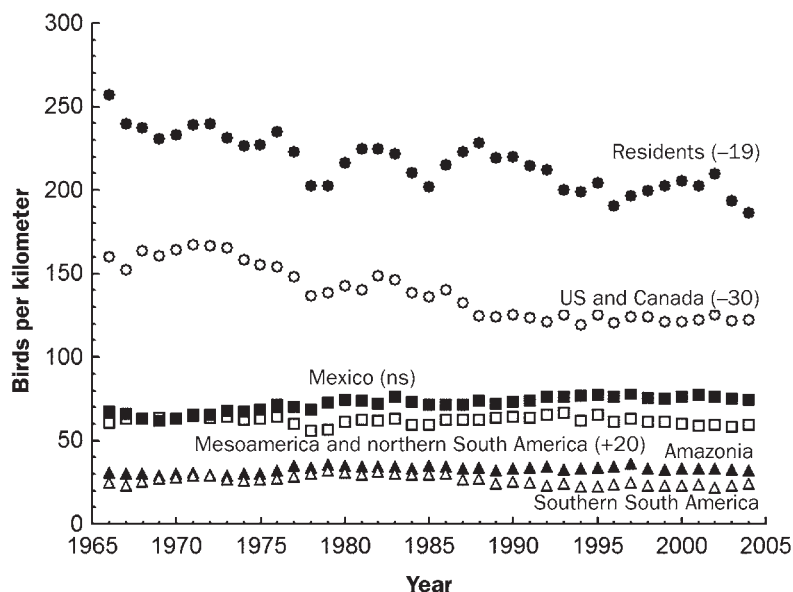

Figure 2. *Abundance of birds breeding in central and eastern North America that either were resident (black circles) or migrated farther south in the United States and Canada (white circles), to Mexico (black squares), to Mesoamerica and northern South America (white squares), to Amazonia (black triangles), or to southern South America (white triangles; cf. figure 1) during the boreal winter, 1966–2004. Numbers in parentheses on the right indicate the percentage of change, calculated as the difference between initial (1966) and final (2004) bird abundances using regression equations fitted to the entire data sets (for residents,* $F = 91.099$, $R^2 = 0.711$, $p < 0.001$; *for migrants within the United States and Canada,* $F = 208.166$, $p < 0.001$, $R^2 = 0.849$; *for migrants to Mexico,* $F = 1.837$, $p = 0.183$, $R^2 = 0.047$; *for migrants to Mesoamerica and northern South America,* $F = 115.026$, $p < 0.001$, $R^2 = 0.757$; *for migrants to Amazonia,* $F = 12.373$, $p < 0.001$, $R^2 = 0.251$; *and for migrants to southern South America,* $F = 16.146$, $p < 0.001$, $R^2 = 0.304$). *Where data scatter was such that* R^2 *was too low to be predictive (Prairie 1996), no numbers are included. Abbreviation: ns, not significant.*

Table 1. Species recorded in the North American Breeding Bird Survey, sorted by boreal winter area and habitat use.

Species (by migratory pattern)	Habitat type	Species (by migratory pattern)	Habitat type
Resident within United States and Canada		*Dendrocygna bicolor*	Wetland
		Plegadis falcinellus	Wetland
Coragyps atratus	Open	*Ardea herodias*	Wetland
Athene cunicularia	Open	*Rallus elegans*	Wetland
Bubulcus ibis	Open	*Aramus guarauna*	Wetland
Corvus corax	Open	*Sula leucogaster*	Coastal
Caracara cheriway	Open	*Corvus ossifragus*	Coastal
Sturnella magna	Open	*Fregata magnificens*	Coastal
Perdix perdix	Open	**Migrant within United States and Canada**	
Tympanuchus cupido	Open		
Geococcyx californianus	Open	*Aquila chrysaetus*	Open
Eremophila alpestris	Open	*Ammodramus henslowii*	Open
Phasianus colchicus	Open	*Falco mexicanus*	Open
Columbia livia	Open	*Buteo lagopus*	Open
Tympanuchus phasianellus	Open	*Cathartes aura*	Open
Buteo brachyurus	Open	*Chordeiles minor*	Open
Anas rubripes	Forest	*Sturnella neglecta*	Open
Picoides dorsalis	Forest	*Caprimulgus vociferus*	Open
Strix varia	Forest	*Certhia americana*	Forest
Picoides arcticus	Forest	*Wilsonia canadensis*	Forest
Poecile hudsonica	Forest	*Regulus satrapa*	Forest
Sitta pusilla	Forest	*Accipiter gentilis*	Forest
Accipiter cooperii	Forest	*Aegolius acadicus*	Forest
Megascops asio	Forest	*Dendroica pinus*	Forest
Coccothraustes vespertinus	Forest	*Carpodacus purpureus*	Forest
Strix nebulosa	Forest	*Accipiter striatus*	Forest
Bubo virginianus	Forest	*Loxia leucoptera*	Forest
Asio otus	Forest	*Catharus guttatus*	Forest
Dryocopus pileatus	Forest	*Dendroica palmarum*	Forest
Carduelis pinus	Forest	*Regulus calendula*	Forest
Loxia curvirostra	Forest	*Carduelis tristis*	Edge
Sitta canadensis	Forest	*Turdus migratorius*	Edge
Picoides borealis	Forest	*Toxostoma rufum*	Edge
Amazona viridigenalis	Forest	*Quiscalus quiscula*	Edge
Bonasa umbellus	Forest	*Passerella iliaca*	Edge
Junco hyemalis	Forest	*Melanerpes erythrocephalus*	Edge
Falcipennis canadensis	Forest	*Buteo jamaicensis*	Edge
Tyto alba	Edge	*Euphagus carolinus*	Edge
Thryomanes bewickii	Edge	*Zonotrichia albicollis*	Edge
Pica hudsonia	Edge	*Troglodytes troglodytes*	Edge
Poecile atricapillus	Edge	*Vireo solitarius*	Edge
Cyanocitta cristata	Edge	*Sayornis phoebe*	Edge
Quiscalus major	Edge	*Spizella pusilla*	Edge
Poecile carolinensis	Edge	*Ammodramus leconteii*	Edge
Thryothorus ludovicianus	Edge	*Dendroica coronata*	Edge
Columbina passerina	Edge	*Pooecetes gramineus*	Edge
Acridotheres tristis	Edge	*Sphyrapicus varius*	Edge
Picoides pubescens	Edge	*Anas rubripes*	Open water
Sialia sialis	Edge	*Larus philadelphia*	Open water
Pipilo erythrophthalmus	Edge	*Bucephala albeola*	Open water
Streptopelia decaocto	Edge	*Bucephala clangula*	Open water
Passer montanus	Edge	*Mergus merganser*	Open water
Sturnus vulgaris	Edge	*Podiceps auritus*	Open water
Aphelocoma coerulescens	Edge	*Anas platyrhynchos*	Open water
Perisoreus canadensis	Edge	*Mergus serrator*	Open water
Quiscalus mexicanus	Edge	*Cygnus buccinator*	Open water
Picoides villosus	Edge	*Aix sponsa*	Open water
Carpodacus mexicanus	Edge	*Aythya valisineria*	Open water
Passer domesticus	Edge	*Anas crecca*	Open water
Columbia inca	Edge	*Aythya americana*	Open water
Coccyzus minor	Edge	*Oxyura jamaicensis*	Open water
Myiopsitta monachus	Edge	*Pelecanus erythrorhynchos*	Open water
Zenaida macroura	Edge	*Larus argentatus*	Open water
Colinus virginianus	Edge	*Aythya affinis*	Open water
Cardinalis cardinalis	Edge	*Aechmophorus occidentalis*	Open water
Colaptes auratus	Edge	*Mycteria americana*	Wetland
Mimus polyglottos	Edge	*Scolopax minor*	Wetland
Melanerpes carolinus	Edge	*Anhinga anhinga*	Wetland
Streptopelia risoria	Edge	*Haliaeetus leucocephalus*	Wetland
Molothrus bonariensis	Edge	*Laterallus jamaicensis*	Wetland
Crotophaga ani	Edge	*Branta canadensis*	Wetland
Baeolophus bicolor	Edge	*Rallus longirostris*	Wetland
Sitta carolinensis	Edge	*Limosa fedoa*	Wetland
Zenaida asiatica	Edge	*Circus cyaneus*	Wetland
Meleagris gallopavo	Edge	*Agelaius phoeniceus*	Wetland
Lophodytes cucullatus	Open water		
Anas fulvigula	Open water		
Cygnus olor	Open water		
Dendrocygna autumnalis	Wetland		

Table 1. *(continued)*

Species (by migratory pattern)	Habitat type	Species (by migratory pattern)	Habitat type
Ammodramus caudacutus	Wetland	*Sterna nilotica*	Coastal
Cistothorus platensis	Wetland	*Larus delawarensis*	Coastal
Rostrhamus sociabilis	Wetland	*Sterna forsteri*	Coastal
Eudocimus albus	Wetland	*Sterna maxima*	Coastal
Coturnicops noveboracensis	Wetland	*Sterna sandvicensis*	Coastal
Grus canadensis	Wetland	**Migrant wintering in Mesoamerica and northern South America**	
Passerculus sandwichensis	Wetland		
Asio flammeus	Wetland	*Charadrius vociferous*	Open
Melospiza georgiana	Wetland	*Falco peregrinus*	Open
Gallinago delicata	Wetland	*Empidonax virescens*	Forest
Somateria mollissima	Coastal	*Dendroica castanea*	Forest
Gavia immer	Coastal	*Ceryle alcyon*	Forest
Larus marinus	Coastal	*Dendroica virens*	Forest
Sula dactylatra	Coastal	*Passerina caerulea*	Forest
Podiceps grisegena	Coastal	*Vermivora pinus*	Forest
Sterna caspia	Coastal	*Dendroica pensylvanica*	Forest
Charadrius melodus	Coastal	*Oporornis agilis*	Forest
Migrant wintering in Mexico		*Vermivora chrysoptera*	Forest
		Catharus minimus	Forest
Ammodramus bairdii	Open	*Wilsonia citrina*	Forest
Euphagus cyanocephalus	Open	*Oporornis formosus*	Forest
Poecile rufescens	Open	*Empidonax minimus*	Forest
Ammodramus savannarum	Open	*Seiurus motacilla*	Forest
Chondestes grammacus	Open	*Dendroica magnolia*	Forest
Melospiza lincolnii	Open	*Oporornis philadelphia*	Forest
Lanius ludovicianus	Open	*Seiurus noveboracensis*	Forest
Stelgidopteryx serripennis	Open	*Seiurus aurocapilla*	Forest
Sayornis saya	Open	*Vireo philadelphicus*	Forest
Anthus spragueii	Open	*Dendroica discolor*	Forest
Tachycineta bicolor	Open	*Protonotaria citrea*	Forest
Vireo bellii	Forest	*Pheucticus ludovicianus*	Forest
Vireo solitarius	Forest	*Catharus ustulatus*	Forest
Vermivora leucobronchialis	Forest	*Vermivora peregrina*	Forest
Carduelis lawrencei	Forest	*Hylocichla mustelina*	Forest
Vermivora ruficapilla	Forest	*Helmitheros vermivorus*	Forest
Pinicola enucleator	Forest	*Vireo flavifrons*	Forest
Vireo gilvus	Forest	*Dendroica fusca*	Forest
Vireo griseus	Forest	*Piranga rubra*	Forest
Mniotilta varia	Forest	*Dendroica caerulescens*	Forest
Parula americana	Forest	*Icterus galbula*	Edge
Polioptila caerulea	Edge	*Bombycilla cedrorum*	Edge
Molothrus aeneus	Edge	*Caprimulgus carolinensis*	Edge
Molothrus ater	Edge	*Geothlypis trichas*	Edge
Spizella passerina	Edge	*Spiza americana*	Edge
Spizella pallida	Edge	*Dumetella carolinensis*	Edge
Troglodytes aedon	Edge	*Tyrannus dominicensis*	Edge
Buteo lineatus	Edge	*Myiarchus crinitus*	Edge
Melospiza melodia	Edge	*Passerina cyanea*	Edge
Pyrocephalus rubinus	Edge	*Contopus cooperi*	Edge
Tyrannus verticalis	Edge	*Icterus spurius*	Edge
Falco columbarius	Edge	*Passerina ciris*	Edge
Wilsonia pusilla	Edge	*Archilochus colubris*	Edge
Falco sparverius	Edge	*Tyrannus forficatus*	Edge
Dendroica petechia	Edge	*Empidonax flaviventris)*	Edge
Limnothlypis swainsonii	Edge	*Icteria virens*	Edge
Dendroica dominica	Edge	*Ceryle alcyon*	Open water
Gallinula chloropus	Open water	*Anas discors*	Open water
Podiceps nigricollis	Open water	*Pelecanus occidentalis*	Open water
Anas strepera	Open water	*Podilymbus podiceps*	Open water
Anas acuta	Open water	*Ardea alba*	Wetland
Anas clypeata	Open water	*Egretta caerulea*	Wetland
Anas americana	Open water	*Pandion haliaetus*	Wetland
Aythya collaris	Open water	*Porphyrula martinica*	Wetland
Botaurus lentiginosus	Wetland	*Xanthocephalus xanthocephalus*	Wetland
Nycticorax nycticorax	Wetland	*Egretta tricolor*	Wetland
Butorides virescens	Wetland	*Tringa flavipes*	Wetland
Cistothorus palustris	Wetland	*Rhynchops niger*	Coastal
Egretta rufescens	Wetland	*Chlidonias niger*	Coastal
Egretta thula	Wetland	*Larus atricilla*	Coastal
Porzana carolina	Wetland	*Charadrius alexandrinus*	Coastal
Plegadis chihi	Wetland	**Migrant wintering in Amazonia**	
Nyctanassa violacea	Wetland		
Haematopus palliatus	Wetland	*Chordeiles gundlachii*	Open
Recurvirostra americana	Wetland	*Progne subis*	Open
Himantopus mexicanus	Wetland	*Chaetura pelagica*	Open
Ajaia ajaja	Wetland	*Empidonax alnorum*	Forest
Rallus limicola	Wetland	*Coccyzus erythrophthalmus*	Forest
Fulica americana	Wetland	*Vireo altiloquus*	Forest
Phalacrocorax auritus	Coastal	*Dendroica cerulea*	Forest

Table 1. (continued)

Species (by migratory pattern)	Habitat type
Contopus virens	Forest
Vireo olivaceus	Forest
Piranga olivacea	Forest
Catharus fuscescens	Forest
Setophaga ruticilla	Forest
Dendroica tigrina	Forest
Tyrannus tyrannus	Edge
Buteo platypterus	Edge
Elanoides forficatus	Wetland
Ictinia mississippiensis	Wetland
Larus pipixcan	Coastal
Sterna antillarum	Coastal
Sterna dougallii	Coastal
Migrant wintering in southern South America	
Riparia riparia	Open
Dolichonyx oryzivorus	Open
Petrochelidon pyrrhonota	Open
Buteo swainsonii	Open
Bartramia longicaudata	Open
Coccyzus americanus	Forest
Empidonax traillii	Forest
Dendroica striata	Forest
Hirundo rustica	Edge
Actitis macularius	Edge
Catoptrophorus semipalmatus	Wetland
Ixobrychus exilis	Wetland
Charadrius wilsonia	Coastal
Sterna hirundo	Coastal
Phalaropus tricolor	Coastal

In contrast, the abundance of nesters that migrated farther south after the nesting season did not diminish. Species that migrated to Mexico, Amazonia, or southern South America showed no significant change, while migrants to Mesoamerica and northern South America increased by 20 percent across the later 20th century (figure 2). In all cases, there were multiyear increases and decreases over more than four decades, perhaps related to climatic shifts, but for present purposes the salient feature of figure 2 is the consistent loss of abundance of nesting species that spend their lives within the United States and Canada, compared with the increased abundance or lack of change in abundance of Neotropical migrants.

We have so far dealt with the total abundance of breeding birds. It seems useful to add species-specific information on abundance. To examine the time course of the many species recorded in the BBS, we fitted regressions of abundance for each species for each year, and used the calculated F_{reg} value as an approximate way to assess the significance of the changes in abundance (increases or decreases, noted by the sign of the slope of the regressions) between 1966 and 2004. Among US and Canada residents, 38 percent of the species increased significantly, while 21 percent decreased significantly in abundance (table 2). For Neotropical migrant species, 51 percent of the species increased significantly and 25 percent decreased significantly in abundance. It is not surprising, therefore,

that previous reports show a variety of results, some claiming increases, some decreases, depending on the taxa included. Ratios of numbers of species that increased significantly relative to those that decreased significantly in abundance were somewhat higher for migrants (2.1) than for residents (1.8; table 2). We focus here on the contrasts among species that migrate different distances, but other traits may be important—for example, whether the species feed on other birds, mammals, invertebrates, leaves, fruits, or seeds—since climate change and habitat loss may differentially affect these groups of birds. Such features need further study.

The abundance of specific species in the BBS record varied: Almost half the species increased significantly in numbers, and less than a quarter decreased significantly (table 2), during the last half of the past century. There were substantial differences in the time trends among species with different migratory behavior. Of the species that reside year-round or migrate within the eastern United States and Canada, 38 percent increased significantly in abundance (including the mourning dove, house finch, Carolina wren, and Canada goose, among other prominent species), and only 21 percent decreased in abundance (the common grackle, red-winged blackbird, eastern meadowlark, house sparrow, and field sparrow, among others). Thus, increases in abundance were about twice as common as decreases for these species of birds.

The trends for US and Canadian species that migrate to more southern latitudes contrast with the trends for those that do not do so (table 2). More than half the species that migrate south of the United States and Canada increased significantly in numbers, and a quarter of the species decreased significantly in abundance (table 2). Surprisingly, therefore, conditions between 1966 and 2004 for Neotropical migrant species seemed somewhat better than, or at least not as problematic as, conditions for species resident in the United States and Canada.

In spite of the significant reductions in total abundance (figure 1), less than a quarter of the individual species in the BBS significantly decreased in abundance (table 2). This suggests that the considerable reductions in abundance seen in figure

Table 2. Number of resident or migrant bird species with significant or nonsignificant increases or decreases in abundance in the breeding areas between 1966 and 2004.

Migratory pattern	Species showing increases in abundance		Species showing decreases in abundance	
	Significant	Nonsignificant	Significant	Nonsignificant
Resident or migrant within the United States and Canada	42	22	23	24
Migrant south of United States and Canada	115	32	55	22
Total	157	54	78	46

Note: Trend for each species (increase or decrease) was determined by fitting regressions to the 1966–2004 data sets from the North American Breeding Bird Survey for each species and noting the sign of the slope; significance was assigned at the 0.05 probability level for the calculated values of F_{reg} for each species.

1 (inset) may have largely resulted from losses incurred by a handful of relatively common species.

Effect of habitat preference on changes in the abundance of breeding birds

To determine whether reductions in abundance were disproportionate among species that preferred different terrestrial (open, edge, forest) or aquatic (open-water, coastal, wetland) habitats, we sorted BBS data accordingly (table 1). Sorting species of birds into a few simple habitat preference categories and migratory ranges involved some arbitrary

assignments. Many species use a variety of habitats; in such cases, we assigned the species to the principal habitat used, on the basis of facts provided in Poole and Gill's (2006) excellent and comprehensive review of North American avifauna, supplemented by information from several other bird guidebooks and confirmed by personal experience.

Terrestrial species. There were notable differences in the decadal trends of abundances of resident and migrant bird species that used different terrestrial habitats (figure 3). Terrestrial species that were resident or migrated within the
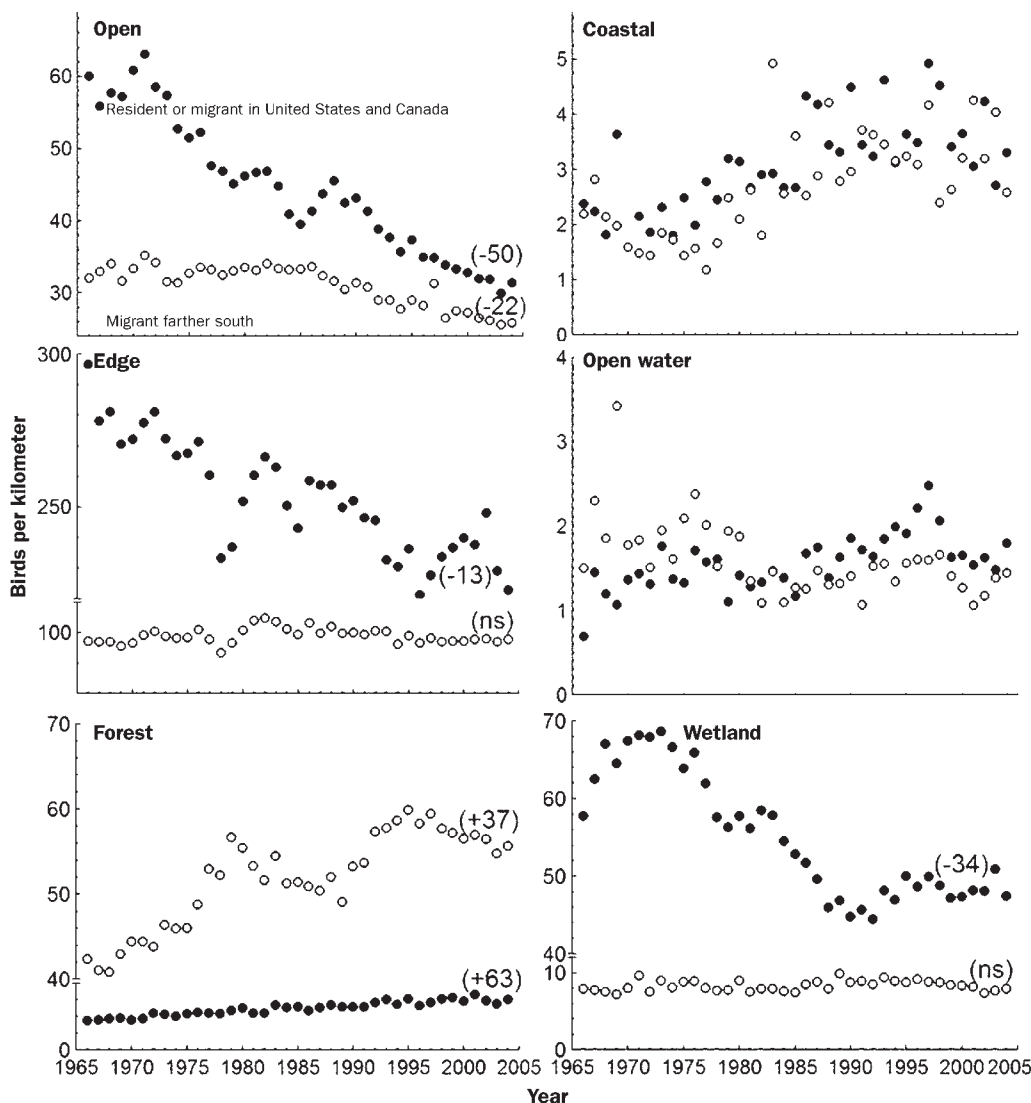

Figure 3. Abundance of breeding birds in the North American Breeding Bird Survey (BBS) data, stratified into two classifications: first, species that were resident or migrated within the United States (black circles) or migrants that spent the boreal winter farther south (white circles); second, species that used open (top left), edge (center left), or forest (bottom left) terrestrial habitats, or used coastal (top right), open water (center right), or wetland (bottom right) habitats. Numbers in parentheses show the percentage change between the start and end of the time course, calculated by comparing the start and end values from regressions fitted to the data. Where data scatter was such that R^2 was too low to be predictive (Prairie 1996), no numbers are included. Abbreviation: ns, not significant.

United States and Canada and preferred open habitats suffered a 50 percent decrease in abundance (figure 3). This group included species such as the eastern meadowlark, rock pigeon, common nighthawk, gray partridge, and greater prairie chicken. There were also considerable reductions (13 percent) in the abundance of species that preferred edge habitats (figure 3). Among the affected species were the blue jay, yellow-shafted flicker, and European starling. In striking contrast, the abundance of the few resident species that preferred forests—such as the brown-headed nuthatch, pine warbler, and pileated woodpecker—increased by about 63 percent (figure 3).

Such shifts in abundance in resident breeding birds may be linked to the substantial land-cover changes (Goss-Custard et al. 1994) taking place in North America during the period covered by the BBS. The expansion of urban sprawl at the expense of agricultural area, for example, may be associated with loss of birds of open habitats. We use "urban sprawl" here to describe a pattern of landscape cover that is not truly urbanization, but rather a complex mosaic of suburban, industrial, and other human-affected land covers that is proliferating across most of the developed world, and North America in particular. Detailed surveys of land-cover changes across the second half of the 20th century (figure 4) demonstrate that urban sprawl has recently expanded throughout eastern North America, at the expense of open (mainly agricultural) land covers and, to a more variable extent, of forest area (figure 4, top). Moreover, the extent of urban sprawl continues to increase (figure 4, bottom). The extent of this transition is impressive: About 14 and 32 percent, respectively, of the area of the states that fall within the Mississippi and Atlantic flyways falls into a land-use classification that has been defined as the "wildland–urban interface," a land cover consisting of a reticulate mosaic of remnant natural and new residential parcels (Radeloff et al. 2005).

The shift to more wildland–urban interface should, however, have furnished considerably more edge habitat, but the BBS records show significantly decreased rather than increased abundance of North American edge-loving birds (figure 3). This suggests that the increased edge habitat undoubtedly provided by the remarkable proliferation of wildland–urban interface is somehow inadequate as bird habitat, perhaps owing to overfragmentation or poor quality for bird use.

The increased abundance of resident forest species (figure 3) may be related to expansion of area of northern forests during much of the 20th century. The changes in forest area vary geographically (hence the wide scatter of the losses and gains of forest area seen in figure 4). Although we record mostly losses of forest area, forest cover increased in, for example, New England during much of the 20th century, as felled areas were reforested (Foster and Aber 2004). Such increases may have tapered off during the last 20 years or so (figure 3), as recovered forest area has been newly altered to "wildland–urban" land covers.

The history of the abundance of terrestrial migrant species that spend the boreal winter south of the United States
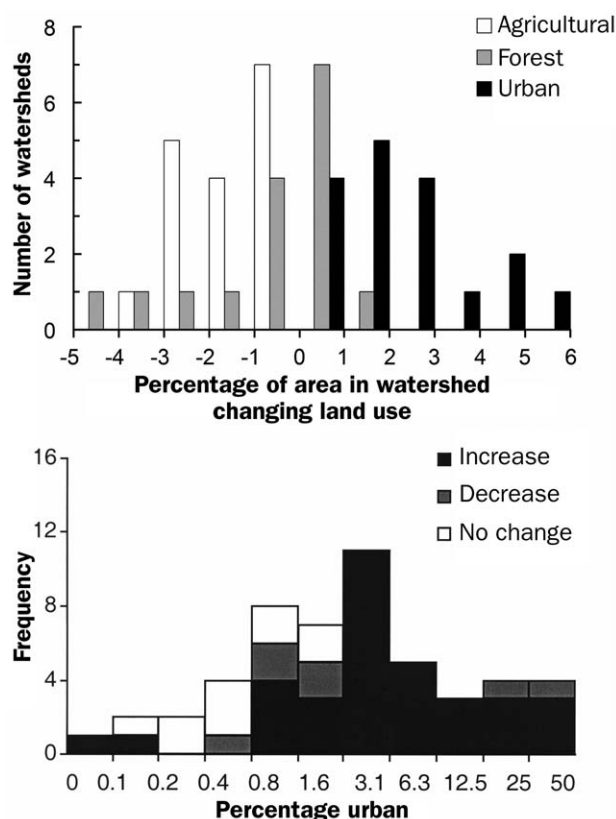

Figure 4. Top: Frequency distributions of gains and losses of area covered by agricultural, forest, or urbanized land cover, 1982–1992, in 16 watersheds of the eastern United States. Bottom: Number of watersheds with different percentages of urbanized land cover within 51 eastern US watersheds. Each bar is divided into watersheds where the population within urbanized areas was increasing, decreasing, or not changing across the previous decade. Modified from Valiela (2006); data are from Van Breemen and colleagues (2002) and Dow and DeWalle (2000).

differed from those of bird species that spend their life within the United States and Canada; in addition, there were clear differences among migrants that prefer open, edge, or forest habitats (figure 3). There was about a 22 percent loss of abundance of migrant open-habitat species between 1966 and 2004 (figure 3). Because of the widespread conversion of Neotropical forest to pastures (Melillo et al. 1985, Woodwell et al. 1987, Sader and Joyce 1988, Houghton et al. 2000, Brook et al. 2003, Hirsch et al. 2004, Marris 2005), with the provision of extensive open areas, we conjecture that the decrease in migrant open-habitat birds might not be related to the loss of Neotropical habitat area, but rather may be a measure of the spreading footprint of loss of suitable open breeding habitats in the United States and Canada, an impact that may be spreading to affect the bird fauna of the entire Americas. We note that this seems to have occurred in the group

of species that showed the greatest loss within the breeding areas (open-habitat birds), so it seems reasonable to find that this is the group that may show the first signs of the incipient global effects of the loss of North American breeding habitat.

In contrast to the trends for migrant open-habitat birds, there were no obvious changes in migrant edge species across the 38 years of BBS data (figure 3). For species that use edge habitats, the footprint of the loss or impoverishment of northern breeding habitats still seems to be constrained to their northern place of origin.

In further contrast to the time courses of migrants that prefer open and edge habitats, there was a clear increase in the numbers of forest-loving migrants, amounting to about 37 percent (figure 3). This increase suggests that the well-documented loss of forest in the Neotropics (Melillo et al. 1985, Woodwell et al. 1987, Sader and Joyce 1988, Houghton et al. 2000, Brook et al. 2003, Hirsch et al. 2004, Marris 2005) has not been paralleled by reductions in the total abundance of migrant forest species that nest in the United States and Canada. The increases in both the resident and the migrant forest species (figure 3) point out another instance of a possible spreading ecological footprint. The expansion of North American forest habitat area in the earlier 20th century might have altered—in this case positively—the abundance of the bird fauna of the Americas. It is unclear, however, how long this increase might continue, since in the breeding areas there is much conversion of forest to urban cover, and in the Neotropics the prediction is that in coming years agricultural expansion will consume about 40 percent of the Amazon forests (Silveira Soares-Filho et al. 2005). There is no evidence as yet (figure 3) that the reported losses of Neotropical forest area can be associated with lower total abundance of birds migrating to Neotropical forest habitats during the boreal winter. We do not know at what point migrant forest species might, as a group, begin to show negative effects from the continuing loss of suitable habitats.

Aquatic species. The time courses of abundance of the relatively few open-water or coastal birds that reside or migrate within the United States and Canada were quite variable (figure 3). In contrast to the relatively modest changes in time course for open-water and coastal species, resident US and Canadian wetland birds—which made up the majority of aquatic birds—suffered about a 34 percent reduction in abundance since the late 1960s (figure 3). The marked reduction in the numbers of wetland species may be a little-known consequence of the considerable loss of wetland habitats that has taken place in North America during the last century (Mitsch and Gosselink 2000, Valiela et al. 2001, 2004, Valiela 2006). Perhaps 50 percent of the area of salt marshes of the United States has been lost, and there have been comparable losses of freshwater wetlands, so it does not seem unreasonable to find repercussions in the abundance of birds dependent on northern wetlands.

In stark contrast to the data for resident wetland birds, there was no evident loss of abundance of wetland birds that migrated south of the United States (figure 3). The lack of change in the abundance of migrant wetland birds is puzzling. We are unaware of the status of freshwater wetlands in Mexico, Central America, and South America, but about 38 percent of the mangrove area of the Americas has been lost during the past two decades, at a record rate of 3.6 percent per year (Valiela et al. 2001). We have no information on other coastal wetlands for the area, but the BBS data (figure 3) suggest that whatever Neotropical wetlands remain, they still support the migrant bird species arriving from northern breeding areas.

Differences in decadal trends of abundance among resident aquatic birds suggest that the availability of open and coastal water habitats might have not changed sufficiently to alter the abundances of birds. The lack of significant change in the abundances of the Neotropical migrant wetland species also suggests that the considerable losses of wetland birds breeding within the United States and Canada may be related more to losses of suitable habitat in northern latitudes than to losses of wetlands in Neotropical latitudes. In this case, however, the ecological footprint seems to have so far remained within the original northern area.

The abundance of birds must be affected by many variables, including global atmospheric changes as well as local changes in habitats. We failed to find correlations between bird abundance and atmospheric variables such as temperature and precipitation across the latter half of the previous century. On the other hand, from the data presented here, there appear to be human-mediated changes in land covers and habitats that may be associated with changes in bird abundance. We cannot claim a direct causal link between anthropogenic land-cover change and changes in bird populations, but there is substantial circumstantial evidence. Birds that spend their lives in the United States and Canada, and prefer open, edge, or wetland habitats—the environments that suffered the greatest changes across the period—suffered significant decreases in total abundance in the last century. This suggests that something about full-year residence within North American environments lowers bird numbers. We are fully aware of the major changes in land cover throughout the continent, and we need to further examine the impacts on habitat quality resulting from the urban sprawl that affects surprisingly large portions of the landscape of eastern and central North America, and the effect of these impacts on natural populations, including birds.

Changes in habitat availability that have taken place in the Neotropics may have reduced the abundance of certain species (Andren and Angelstam 1988, Temple and Cary 1988, Robbins et al. 1989, Terborgh 1989, Böhning-Gaese et al. 1993, Marra et al. 1998, Brook et al. 2003, King and Rappole 2003, National Audubon Society 2004, Johnson et al. 2005, Stratford and Robinson 2005). Considering the BBS data on the basis of individual species, we found that the abundance of many migrant species increased, while that of other species

decreased. More specifically, however, the evidence suggests that alterations in the northern parts of the ranges dominate the time courses of increases or decreases in abundance of migrant breeding birds.

Human domination of the world's ecosystems by a variety of agents of change has been detailed in a number of recent reviews (Vitousek et al. 1997, Sala and Huber-Sannwald 2001, Millennium Ecosystem Assessment 2005). In certain cases (e.g., emission of greenhouse gases, export of alien species, coral bleaching, sea level rise), human activities in one part of the world turn out to have much larger footprints, extending to far reaches of the world, and hence have global-scale impacts.

For the considerable reductions in breeding bird populations we report here, the perturbations of certain habitats (open land and forest), largely in North America, may have begun to have consequences that extend across a wide swath of latitudes, with negative results for species of migrant birds that prefer open habitats, and positive results for forest-loving birds. These expanding footprints seem at an incipient stage. For other groups of bird species, the effects of losses in the highly disturbed North American environments are restricted to the continent where the disturbances occurred, and, as far as can be determined, have not as yet expanded to the avian fauna of the entire Americas. We might expect that in other parts of the world, such as the European–African flyways, where human disturbance of boreal breeding areas might have longer and more intensive histories, such expanding ecological footprints might be more prominent.

Acknowledgments

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