

Cite as: K. V. Rosenberg *et al.*, *Science*  
10.1126/science.aaw1313 (2019).

# Decline of the North American avifauna

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Species extinctions have defined the global biodiversity crisis, but extinction begins with loss in abundance of individuals that can result in compositional and functional changes of ecosystems. Using multiple and independent monitoring networks, we report population losses across much of the North American avifauna over 48 years, including once common species and from most biomes. Integration of range-wide population trajectories and size estimates indicates a net loss approaching 3 billion birds, or 29% of 1970 abundance. A continent-wide weather radar network also reveals a similarly steep decline in biomass passage of migrating birds over a recent 10-year period. This loss of bird abundance signals an urgent need to address threats to avert future avifaunal collapse and associated loss of ecosystem integrity, function and services.

Slowing the loss of biodiversity is one of the defining environmental challenges of the 21<sup>st</sup> century (1–5). Habitat loss, climate change, unregulated harvest, and other forms of human-caused mortality (6, 7) have contributed to a thousand-fold increase in global extinctions in the Anthropocene compared to the presumed prehuman background rate, with profound effects on ecosystem functioning and services (8). The overwhelming focus on species extinctions, however, has underestimated the extent and consequences of biotic change, by ignoring the loss of abundance within still-common species and in aggregate across large species assemblages (2, 9). Declines in abundance can degrade ecosystem integrity, reducing vital ecological, evolutionary, economic, and social services that organisms provide to their environment (8, 10–15). Given the current pace of global environmental change, quantifying change in species abundances is essential to assess ecosystem impacts. Evaluating the magnitude of declines requires effective long-term monitoring of population sizes and trends, data which are rarely available for most taxa.

Birds are excellent indicators of environmental health and ecosystem integrity (16, 17), and our ability to monitor many species over vast spatial scales far exceeds that of any other animal group. We evaluated population change for 529 species of birds in the continental United States and Canada (76% of breeding species), drawing from multiple standardized bird-monitoring datasets, some of which provide close to fifty years of population data. We integrated range-wide estimates of population size and 48-year population trajectories,

along with their associated uncertainty, to quantify net change in numbers of birds across the avifauna over recent decades (18). We also used a network 143 weather radars (NEXRAD) across the contiguous U.S. to estimate long-term changes in nocturnal migratory passage of avian biomass through the airspace in spring from 2007 to 2017. The continuous operation and broad coverage of NEXRAD provide an automated and standardised monitoring tool with unrivaled temporal and spatial extent (19). Radar measures cumulative passage across all nocturnally migrating species, many of which breed in areas north of the contiguous U.S. that are poorly monitored by avian surveys. Radar thus expands the area and the proportion of the migratory avifauna that is sampled relative to ground surveys.

Results from long-term surveys, accounting for both increasing and declining species, reveal a net loss in total abundance of 2.9 billion (95% CI = 2.7–3.1 billion) birds across almost all biomes, a reduction of 29% (95% CI = 27–30%) since 1970 (Fig. 1 and Table 1). Analysis of NEXRAD data indicate a similarly steep decline in nocturnal passage of migratory biomass, a reduction of  $13.6 \pm 9.1\%$  since 2007 (Fig. 2A). Reduction in biomass passage occurred across the eastern U.S. (Fig. 2, C and D), where migration is dominated by large numbers of temperate- and boreal-breeding songbirds; we observed no consistent trend in the Central or Pacific flyway regions (Fig. 2, B to D, and table S5). Two completely different and independent monitoring techniques thus signal major population loss across the continental avifauna.

Species exhibiting declines (57%, 303/529) based on long-

term survey data span diverse ecological and taxonomic groups. Across breeding biomes, grassland birds showed the largest magnitude of total population loss since 1970—more than 700 million breeding individuals across 31 species— and the largest proportional loss (53%); 74% of grassland species are declining. (Fig. 1 and Table 1). All forest biomes experienced large avian loss, with a cumulative reduction of more than 1 billion birds. Wetland birds represent the only biome to show an overall net gain in numbers (13%), led by a 56% increase in waterfowl populations (Fig. 3 and Table 1). Surprisingly, we also found a large net loss (63%) across 10 introduced species (Fig. 3, D and E, and Table 1).

A total of 419 native migratory species experienced a net loss of 2.5 billion individuals, whereas 100 native resident species showed a small net increase (26 million). Species overwintering in temperate regions experienced the largest net reduction in abundance (1.4 billion), but proportional loss was greatest among species overwintering in coastal regions (42%), southwestern aridlands (42%), and South America (40%) (Table 1 and fig. S1). Shorebirds, most of which migrate long distances to winter along coasts throughout the hemisphere, are experiencing consistent, steep population loss (37%).

More than 90% of the total cumulative loss can be attributed to 12 bird families (Fig. 3A), including sparrows, warblers, blackbirds, and finches. Of 67 bird families surveyed, 38 showed a net loss in total abundance, whereas 29 showed gains (Fig. 3B), indicating recent changes in avifaunal composition (table S2). While not optimized for species-level analysis, our model indicates 19 widespread and abundant landbirds (including 2 introduced species) each experienced population reductions of >50 million birds (data S1). Abundant species also contribute strongly to the migratory passage detected by radar (19), and radar-derived trends provide a fully independent estimate of widespread declines of migratory birds.

Our study documents a long-developing but overlooked biodiversity crisis in North America—the cumulative loss of nearly 3 billion birds across the avifauna. Population loss is not restricted to rare and threatened species, but includes many widespread and common species that may be disproportionately influential components of food webs and ecosystem function. Furthermore, losses among habitat generalists and even introduced species indicate that declining species are not replaced by species that fare well in human-altered landscapes. Increases among waterfowl and a few other groups (e.g., raptors recovering after the banning of DDT) are insufficient to offset large losses among abundant species (Fig. 3). Importantly, our population loss estimates are conservative since we estimated loss only in breeding populations. The total loss and impact on communities and ecosystems could be even higher outside the breeding season

if we consider the amplifying effect of “missing” reproductive output from these lost breeders.

Extinction of the Passenger Pigeon (*Ectopistes migratorius*), once likely the most numerous bird on the planet, provides a poignant reminder that even abundant species can go extinct rapidly. Systematic monitoring and attention paid to population declines could have alerted society to its pending extinction (20). Today, monitoring data suggest that avian declines will likely continue without targeted conservation action, triggering additional endangered species listings at tremendous financial and social cost. Moreover, because birds provide numerous benefits to ecosystems (e.g., seed dispersal, pollination, pest control) and economies (47 million people spend 9.3 billion U.S. dollars per year through bird-related activities in the U.S. (21)), their population reductions and possible extinctions will have severe direct and indirect consequences (10, 22). Population declines can be reversed, as evidenced by the remarkable recovery of waterfowl populations under adaptive harvest management (23) and the associated allocation of billions of dollars devoted to wetland protection and restoration, providing a model for proactive conservation in other widespread native habitats such as grasslands.

Steep declines in North American birds parallel patterns of avian declines emerging globally (14, 15, 22, 24). In particular, depletion of native grassland bird populations in North America, driven by habitat loss and more toxic pesticide use in both breeding and wintering areas (25), mirrors loss of farmland birds throughout Europe and elsewhere (15). Even declines among introduced species match similar declines within these same species’ native ranges (26). Agricultural intensification and urbanization have been similarly linked to declines in insect diversity and biomass (27), with cascading impacts on birds and other consumers (24, 28, 29). Given that birds are one of the best monitored animal groups, birds may also represent the tip of the iceberg, indicating similar or greater losses in other taxonomic groups (28, 30).

Pervasiveness of avian loss across biomes and bird families suggests multiple and interacting threats. Isolating spatio-temporal limiting factors for individual species and populations will require additional study, however, since migratory species with complex life histories are in contact with many threats throughout their annual cycles. A focus on breeding season biology hampers our ability to understand how seasonal interactions drive population change (31), although recent continent-wide analyses affirm the importance of events during the non-breeding season (19, 32). Targeted research to identify limiting factors must be coupled with effective policies and societal change that emphasize reducing threats to breeding and non-breeding habitats and minimizing avoidable anthropogenic mortality year-round. Endangered species legislation and international treaties, such as

the 1916 Migratory Bird Treaty between Canada and the United States, have prevented extinctions and promoted recovery of once-depleted bird species. History shows that conservation action and legislation works. Our results signal an urgent need to address the ongoing threats of habitat loss, agricultural intensification, coastal disturbance, and direct anthropogenic mortality, all exacerbated by climate change, to avert continued biodiversity loss and potential collapse of the continental avifauna.

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## ACKNOWLEDGMENTS

This paper is a contribution of The Partners in Flight International Science Committee and the American Ornithologist Society Conservation Committee, and the study benefited from many discussions with these groups. Steve Bessinger, John Fitzpatrick, Scott Loss, T. Scott Sillett, Wesley Hochachka, Daniel Fink, Steve Kelling, Viviana Ruiz-Gutierrez, Orin Robinson, Eliot Miller, Amanda Rodewald, and three anonymous reviewers made suggestions to improve the paper. Jillian Ditner and Matt Strimas-Mackey helped with figures and graphics. Tim Meehan provided an analysis of trends from National Audubon's Christmas Bird Count. We thank the hundreds of volunteer citizen-scientists who contributed to long-term bird-monitoring programs in North America and the institutions that manage these programs. Photos in Fig. 3 from Macaulay Library, Cornell Lab of Ornithology. **Funding:** NSF LTREB DEB1242584 to PPM; AWS Cloud Credits for Research to AMD; NSF ABI Innovation DBI-1661259. **Author contributions:** All authors conceived of the idea for the paper; ACS, PJB, AMD, JRS, PAS, and JCS conducted analyses; KVR, AMD and PPM primarily wrote the paper, although all authors contributed to the final manuscript. **Competing interests:** M. P. is President, and a member of the Board of Directors of American Bird Conservancy. All remaining authors declare no competing interests. **Data and materials availability:** All data and software are archived and available on Zenodo (33–35) and will be published in future versions of the Avian Conservation Assessment Database (<http://pif.birdconservancy.org/ACAD/>).

## SUPPLEMENTARY MATERIALS

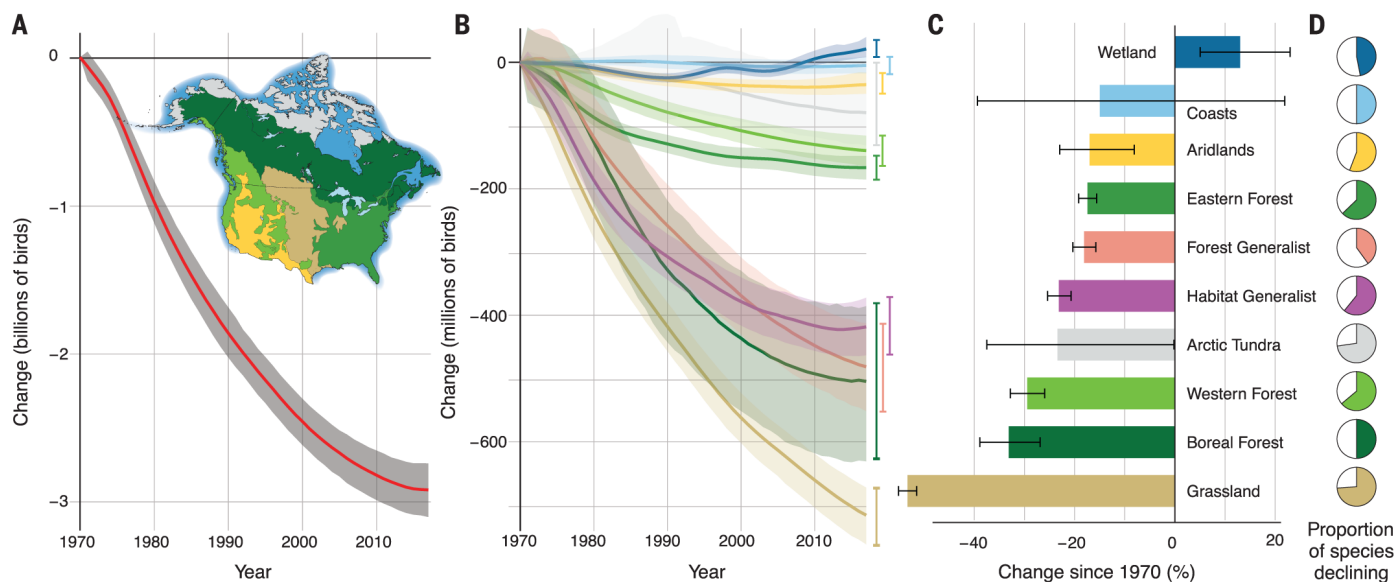
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References (36–101)

20 November 2018; resubmitted 23 May 2019

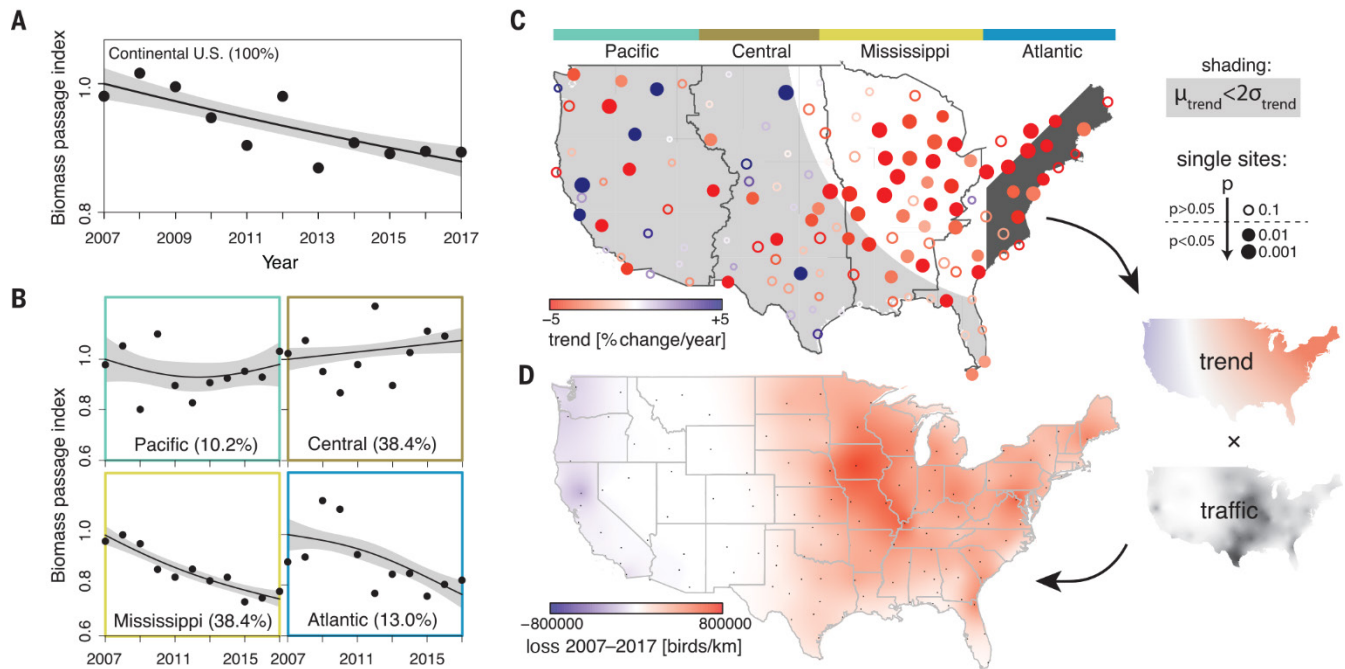
Accepted 5 September 2019

Published online 19 September 2019

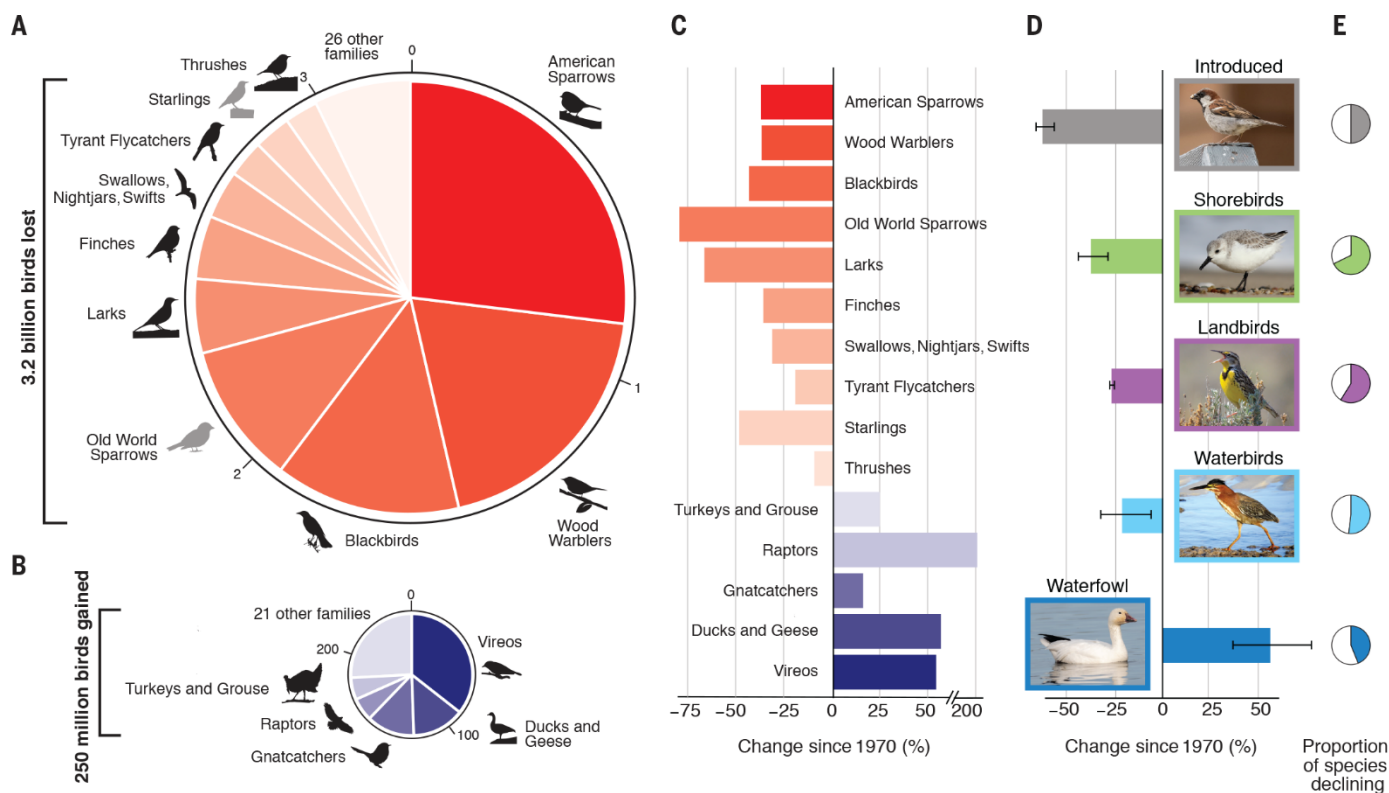
10.1126/science.aaw1313



**Fig. 1. Net population change in North American birds.** (A) By integrating population size estimates and trajectories for 529 species (18), we show a net loss of 2.9 billion breeding birds across the continental avifauna since 1970. Gray shading represents  $\pm 95\%$  credible intervals around total estimated loss. Map shows color-coded breeding biomes based on Bird Conservation Regions and land cover classification (18). (B) Net loss of abundance occurred across all major breeding biomes except wetlands (see Table 1). (C) Proportional net population change relative to 1970,  $\pm 95\%$  C.I. (D) Proportion of species declining in each biome.



**Fig. 2. NEXRAD radar monitoring of nocturnal bird migration across the contiguous U.S.** (A) Annual change in biomass passage for the full continental U.S. (black) and (B) the Pacific (green), Central (brown), Mississippi (yellow), and Atlantic (blue) flyways (borders indicated in panel C), with percentage of total biomass passage (migration traffic) for each flyway indicated; Declines are significant only for the full U.S. and the Mississippi and Atlantic flyways (tables S3 to S5). (C) Single-site trends in seasonal biomass passage at 143 NEXRAD stations in spring (1 Mar – 1 Jul), estimated for the period 2007-2017. Darker red colors indicate higher declines and loss of biomass passage, while blue colors indicate biomass increase. Circle size indicates trend significance, with closed circles being significant at a 95% confidence level. Only areas outside gray shading have a spatially consistent trend signal separated from background variability. (D) 10-year cumulative loss in biomass passage, estimated as the product of a spatially-explicit (generalized additive model) trend, times the surface of average cumulative spring biomass passage.



**Fig. 3. Gains and losses across the North American avifauna over the last half century.** (A) Bird families were categorized as having a net loss (red) or gain (blue). Total loss of 3.2 billion birds occurred across 38 families; each family with losses greater than 50 million individuals is shown as a proportion of total loss, including two introduced families (gray). Swallows, nightjars, and swifts together show loss within the aerial insectivore guild. (B) 29 families show a total gain of 250 million individual birds; the five families with gains greater than 15 million individuals are shown as a proportion of total gain. Four families of raptors are shown as a single group. Note that combining total gain and total loss yields a net loss of 2.9 billion birds across the entire avifauna. (C) For each individually represented family in B and C, proportional population change within that family is shown. See Table S2 for statistics on each individual family. (D) *Left*, proportion of species with declining trends and, *Right*, percentage population change among introduced and each of four management groups (18). A representative species from each group is shown (top to bottom, house sparrow, *Passer domesticus*; sanderling, *Calidris alba*; western meadowlark, *Sturnella neglecta*; green heron, *Butorides virescens*; and snow goose, *Anser caerulescens*).

**Table 1. Net change in abundance across the North American avifauna, 1970-2017.** Species are grouped into native and introduced species, management groups (landbirds, shorebirds, waterbirds, waterfowl), major breeding biomes, and nonbreeding biomes (see data S1 in (18) for assignments and definitions of groups and biomes). Net change in abundance is expressed in millions of breeding individuals, with upper and lower 95% credible intervals (CI) shown. Percentage of species in each group with negative trend trajectories are also noted. Values in bold indicate declines and loss; those in italics indicate gains.

| Species Group            | Number of Species | Net Abundance Change (Millions) & 95% CI |          |          | Percent Change & 95% CIs |        |        | Proportion Species in Decline |
|--------------------------|-------------------|------------------------------------------|----------|----------|--------------------------|--------|--------|-------------------------------|
|                          |                   | Change                                   | LC95     | UC95     | Change                   | LC95   | UC95   |                               |
| Species Summary          |                   |                                          |          |          |                          |        |        |                               |
| All N. Am. Species       | 529               | -2,911.9                                 | -3,097.5 | -2,732.9 | -28.8%                   | -30.2% | -27.3% | 57.3%                         |
| All Native Species       | 519               | -2,521.0                                 | -2,698.5 | -2,347.6 | -26.5%                   | -28.0% | -24.9% | 57.4%                         |
| Introduced Species       | 10                | -391.6                                   | -442.3   | -336.6   | -62.9%                   | -66.5% | -56.4% | 50.0%                         |
| Native Migratory Species | 419               | -2,547.7                                 | -2,723.7 | -2,374.5 | -28.3%                   | -29.8% | -26.7% | 58.2%                         |
| Native Resident Species  | 100               | 26.3                                     | 7.3      | 46.9     | 5.3%                     | 1.4%   | 9.6%   | 54.0%                         |
| Landbirds                | 357               | -2,516.5                                 | -2,692.2 | -2,346.0 | -27.1%                   | -28.6% | -25.5% | 58.8%                         |
| Shorebirds               | 44                | -17.1                                    | -21.8    | -12.6    | -37.4%                   | -45.0% | -28.8% | 68.2%                         |
| Waterbirds               | 77                | -22.5                                    | -37.8    | -6.3     | -21.5%                   | -33.1% | -6.2%  | 51.9%                         |
| Waterfowl                | 41                | 34.8                                     | 24.5     | 48.3     | 56.0%                    | 37.9%  | 79.4%  | 43.9%                         |
| Aerial Insectivores      | 26                | -156.8                                   | -183.8   | -127.0   | -31.8%                   | -36.4% | -26.1% | 73.1%                         |
| Breeding Biome           |                   |                                          |          |          |                          |        |        |                               |
| Grassland                | 31                | -717.5                                   | -763.9   | -673.3   | -53.3%                   | -55.1% | -51.5% | 74.2%                         |
| Boreal forest            | 34                | -500.7                                   | -627.1   | -381.0   | -33.1%                   | -38.9% | -26.9% | 50.0%                         |
| Forest Generalist        | 40                | -482.2                                   | -552.5   | -413.4   | -18.1%                   | -20.4% | -15.8% | 40.0%                         |
| Habitat Generalist       | 38                | -417.3                                   | -462.1   | -371.3   | -23.1%                   | -25.4% | -20.7% | 60.5%                         |
| Eastern Forest           | 63                | -166.7                                   | -185.8   | -147.7   | -17.4%                   | -19.2% | -15.6% | 63.5%                         |
| Western forest           | 67                | -139.7                                   | -163.8   | -116.1   | -29.5%                   | -32.8% | -26.0% | 64.2%                         |
| Arctic Tundra            | 51                | -79.9                                    | -131.2   | -0.7     | -23.4%                   | -37.5% | -0.2%  | 56.5%                         |
| Aridlands                | 62                | -35.6                                    | -49.7    | -17.0    | -17.0%                   | -23.0% | -8.1%  | 56.5%                         |
| Coasts                   | 38                | -6.1                                     | -18.9    | 8.5      | -15.0%                   | -39.4% | 21.9%  | 50.0%                         |
| Wetlands                 | 95                | 20.6                                     | 8.3      | 35.3     | 13.0%                    | 5.1%   | 23.0%  | 47.4%                         |
| Nonbreeding Biome        |                   |                                          |          |          |                          |        |        |                               |
| Temperate North America  | 192               | -1,413.0                                 | -1,521.5 | -1,292.3 | -27.4%                   | -29.3% | -25.3% | 55.2%                         |
| South America            | 41                | -537.4                                   | -651.1   | -432.6   | -40.1%                   | -45.2% | -34.6% | 75.6%                         |
| Southwestern Aridlands   | 50                | -238.1                                   | -261.2   | -215.6   | -41.9%                   | -44.5% | -39.2% | 74.0%                         |
| Mexico-Central America   | 76                | -155.3                                   | -187.8   | -122.0   | -15.5%                   | -18.3% | -12.6% | 52.6%                         |
| Widespread Neotropical   | 22                | -126.0                                   | -171.2   | -86.1    | -26.8%                   | -33.4% | -19.3% | 45.5%                         |
| Widespread               | 60                | -31.6                                    | -63.1    | 1.6      | -3.7%                    | -7.4%  | 0.2%   | 43.3%                         |
| Marine                   | 26                | -16.3                                    | -29.7    | -1.2     | -30.8%                   | -49.1% | -2.5%  | 61.5%                         |
| Coastal                  | 44                | -11.0                                    | -14.9    | -6.7     | -42.0%                   | -51.8% | -26.7% | 68.2%                         |
| Caribbean                | 8                 | -6.0                                     | 1.4      | -15.7    | 12.1%                    | -2.8%  | 31.7%  | 25.0%                         |

## Decline of the North American avifauna

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published online September 19, 2019 originally published online September 19, 2019

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