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Bird populations and species lost to Late Quaternary environmental change and human impact in the Bahamas

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Comparing distributional information derived from fossils with the modern distribution of species, we summarize the changing bird communities of the Bahamian Archipelago across deep ecological time. While our entire dataset consists of 7,600+ identified fossils from 32 sites on 15 islands (recording 137 species of resident and migratory birds), we focus on the landbirds from four islands with the best fossil records, three from the Late Pleistocene (~25 to 10 ka [1,000 y ago]) and one from the Holocene (~10 to 0 ka). The Late Pleistocene sites feature 51 resident species that have lost one or more Bahamian populations; 29 of these species do not occur in any of the younger Holocene sites (or in the Bahamas today). Of these 29 species, 17 have their closest affinities to species now or formerly living in Cuba and/or North America. A set of 27 species of landbirds, most of them extant somewhere today, was more widespread in the Bahamas in the prehistoric Holocene (~10 to 0.5 ka) than they are today; 16 of these 27 species were recorded as Pleistocene fossils as well. No single site adequately captures the entire landbird fauna of the combined focal islands. Information from all sites is required to assess changes in Bahamian biodiversity (including endemism) since the Late Pleistocene. The Bahamian islands are smaller, flatter, lower, and more biotically depauperate than the Greater Antilles, resulting in more vulnerable bird communities.

Significance

Among the 90 resident species of landbirds known from Bahamian fossils, 62 species (69%) have different distributions today from in the recent past, ranging from single-island extirpations to global extinction. Placing the modern bird communities in a deeper time perspective shows how dynamic geographic ranges are through time, including providing explanations for illogical modern distributions and apparent endemism in the Caribbean. The fragmented existing Bahamian bird communities have withstood 1,000 y of human impact, and thus represent species with some resiliency. They nevertheless face an uncertain future because the factors that have fueled extirpations and extinctions through time are still at play.

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The authors declare no competing interest.

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trending ridges on the eastern or northern (Atlantic) sides, with a total land area of \( \sim 12,000 \text{ km}^2 \). For roughly 90\% of the last half-million years (440 k of the past 492 k y), however, sea level was 40 to 120 m lower than present, so that the Great Bahama Bank (GBB) and Little Bahama Bank (LBB) each consisted of a single large island, with all modern separate islands on any given bank connected \((5, 6)\). The land areas of all other Bahamian banks (e.g., San Salvador, Crooked-Acklins, Caicos, etc.) also expanded. These lower sea levels occurred during the last six Pleistocene glacial intervals (the even-numbered marine isotope stages [MISs], from MIS 12 to 2), when the total land area of the archipelago averaged \( \sim 131,000 \text{ km}^2 \) (estimated land areas and elevations are from ref. 6). The resulting large Bahamian islands during glacial intervals (maximum elevations from \( \sim 120 \) to \( \sim 180 \) m) were situated closer to the Greater Antilles (especially Cuba) than today; these largerBahamian “superislands” \((5)\) sustained terrestrial habitats for the landbirds that are the main focus of this paper.

In contrast, during high sea levels of the three warmest interglacial periods, which include the present (the Holocene, MIS 1, \( \sim 10 \) to \( \sim 0 \) ka), MIS 5a (\( \sim 125 \) to \( \sim 120 \) ka), and MIS 11 (\( \sim 410 \) to \( \sim 400 \) ka), the archipelago consisted of many separate islands, as it does today, with a total land area of \( <15,000 \text{ km}^2 \). If the sea levels during MIS 5a and MIS 11 reached as high as the latest sources estimate \((e.g., ref. 7)\), the Bahamian Archipelago would have been nearly completely submerged, with far fewer, smaller, and more isolated islands than even today. Therefore, much if not most of the Late Pleistocene and Holocene terrestrial flora and fauna has colonized the island group by overwater dispersal since MIS 5a. The physical geography of the archipelago has set the stage for patterns of accumulation, evolution, and extinction of the terrestrial biota during the last half-million years.

The most extensive terrestrial habitat in the archipelago today is broadleaf evergreen closed-canopy subtropical forest \((8)\). During glacial periods, the higher-elevation islands would have had less water available for plant growth (in the root zone) owing to greater depth to the water table \((9)\). Thus, terrestrial habitats would have been more xeric than today. The Pleistocene avifauna from Abaco representing the terminal glaciation (MIS 2, corresponding to the Last Glacial Maximum) is dominated by obligate open-habitat (grassland and pine woodland) species \((e.g., Loxia megaplaga\) is a pine woodland obligate in Hispaniola today), consistent with a terrestrial environment more xeric than in modern times \((5, 6)\). The changes in climate and sea level from MIS 2 to 1 \((\sim 15 \text{ to } 9 \text{ ka})\) are known as the Pleistocene-to-Holocene transition \((\text{PHT})\).

### Results

#### Diversity and Distribution

Our entire dataset consists of 7,600+ identified fossils from 32 sites on 15 islands, representing 137 species of resident and migratory birds, of which 90 \((66\%)\) are resident landbirds \((\text{nonmarine, nonaquatic, breeding species that are part of the terrestrial food web}; \text{SI Appendix, Table S1})\). On five Bahamian islands, the number of identified bird fossils in our dataset is \(>500\). Four of these islands have single sites with \(>500\) identified landbird fossils with chronological control \((\text{Abaco, New Providence, Long, Middle Caicos}; \text{Fig. 2})\). Among the 85 species of landbirds recorded from the four target sites, only 13 \((15\%)\) have been found in all sites \((3 \text{ extinct, } 4 \text{ extirpated, and } 6 \text{ still widespread}; \text{Tables 1 and 2})\).

Comparing only the four target sites/islands \((\text{Tables 1 and 2})\), a species accumulation curve based on rarefaction by site shows, as expected, that as additional sites are considered, more species accumulate, although there is some flattening of the curve when all sites are added \((\text{Fig. 3})\). That we recorded 85 species of landbirds collectively in these fossil sites suggests strongly that none of these four large samples \((\text{together comprising nearly } 6,000 \text{ fossils}; \text{Table 2})\) approaches sampling the entire Late Quaternary Bahamian avifauna. Comparing the number of species added cumulatively to each site as fossils are added shows that New Providence, Long, and Middle Caicos, even with hundreds of fossils, are still accumulating species at a high rate \((\text{Fig. 4})\). On Abaco, with thousands of fossils, the curve is less steep than for the other sites because the Abaco sample is dominated by three extremely abundant species \((\text{Tables 1 and 2})\). Therefore, even on Abaco, where the species accumulation curve appears to be flattening, if new fossils were identified from Sawmill Sink or a similar site, we would expect new species to continue to be added, at a slow rate.

Twelve species occur in two or three of the Pleistocene sites but not in the Holocene Indian Cave fauna on Middle Caicos, namely the woodpeckers \(\text{Colaptes cf. femsandinae, Melanerpes supercilarius, and Xiphidipicus percutius, swallow Petrochelidon pyrrhonota, nuthatch Sitta pusilla, bluebird Sialia sialis, “highland tanager Xenoligea cf. montana, sparrow Passerculus sandwichensis, meadowlark Stumella magna, cowbirds “genus uncertain” and Molothrus ater, and crossbill L. megaplaga}\). These 12 species, all either woodpeckers or passerines, seem likely to have been lost during the major PHT changes in climate, habitat, and island size/isolation. Other species that may have been lost from Bahamian islands during the PHT but with less thorough fossil records include the eagle \(\text{Tacheanax goliathus, several of the flightless rails, the woodcock Scolopax undescribed sp., macaw Ara cf. tricolor, owls Tyto polons and Asio flavipennis, crow Corvus palmarum, and solitary Myadestes sp. (Tables 1, 2, and 3 and SI Appendix, Table S1)}\).

Fossil-documented distributional changes are evident in 62 of the 90 total species of landbirds \((69\%)\), ranging from single-island extirpations to global extinction \((\text{Tables 3 and 4 and SI Appendix, Table S1})\). Within the Bahamian Archipelago, for example, the parrot \(\text{Amazona leucocephala}\) occurs today only on Abaco and Great Inagua, a geographically illogical distribution. We have discovered Holocene fossils of this parrot on five other Bahamian islands. Similarly, the woodpecker \(\text{Melanerpes supercilarius}\), which now lives only on Abaco and San Salvador, is widespread as a fossil. The same is true for the owl \(\text{Athene cuculina}\) and crow \(\text{Corvus nasicus}\). The pigeon \(\text{Patagioenas squamosa}\), common as

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**Fig. 1.** Bahamian Archipelago. Islands mentioned in the text or tables are named. The four target islands that have single sites with >500 identified landbird fossils with chronological control are in bold.
Hawks, eagles

*Accipiter undescribed sp.*¹

†Accipiter striatus

Buteo quadratus²

Buteo jamaicensis

Buteo swainsonii

Titanohierax gloveralleni³

Falco sparroweri

Falco femoralis

Caracara creightonii⁴

Caracara undescribed sp.⁴

Grus undescribed sp.⁴

Falco grallipes⁴

Rallus undescribed sp. 1⁴

Rallus undescribed sp. 2⁴

Rallus/Porzana undescribed sp. 1⁴

Rallus/Porzana undescribed sp. 2⁴

Burhinus nanus¹

Gallinago kakui⁵

Scolopax undescribed sp.¹

Patagioenas leucocephala¹

Patagioenas squamosa¹

Patagioenas cf. inornata

Zenaida aurita

Zenaida asiatica

Zenaida macroura

Geotrygon chrysa

Columbina passerina

Ara cf. tricolor²

Forpus undescribed sp.¹

Amazona leucocephala¹

Coccozys minor

Saurothera merlini

Tyto alba

Tyto pollens¹

Athene cunicularia, 1,962* 110* 326* 34* 4/2,427

Asio flammeus 1* — — — 1/1

Chordeiles gundlachii 3 1 — — 2/4

Antrostomus cf. cubanensis 1* — — — 1/1

Genus uncertain*⁺,⁵

Mellisuga sp. — — — 5* 1/5

Anthracothorax sp. 2 3/27

Chlorostilbon ricuki — — 8* 2/11

Calliphlox evelynae — — 1 1/1

Colaptes cf. fernandinae 3* 10* 3* — 3/16

Melanerpes superciliearius 1 31* 26* — 3/58

Xiphidiopus percussus 1* 2* 4* — 3/7

Picoides villosus 3 1 — — 2/4

Table 1. Number of bones of resident nonpasserine landbirds identified from the four richest prehistoric sites in the Bahamian Archipelago (vultures through woodpeckers)

| Family          | Species                      | Abaco | New Providence | Long Island | Middle Caicos | No. sites/bones |
|-----------------|------------------------------|-------|----------------|-------------|---------------|-----------------|
| Vultures        | Cathartes aura               | 1     | —              | 1*          | 22*           | 3/24            |
| Hawks, eagles   | Accipiter undescribed sp.¹   | 1     | —              | 6           | 2/7           |
|                 | Accipiter striatus           | 4*    | —              | —           | 1/4           |
|                 | Buteo quadratus²             | 1     | 10             | 3           | 38            | 4/52            |
|                 | Buteo jamaicensis            | —     | —              | —           | 2*            | 1/2             |
|                 | Buteo swainsonii             | 1*    | —              | 1*          | —             | 2/2             |
| Falcons, caracaras | Falco sparroweri             | 19    | 3              | 7           | —             | 3/29            |
|                 | Falco femoralis              | —     | —              | —           | 12*           | 1/12            |
|                 | Caracara creightonii⁴        | —     | 6              | 1           | —             | 2/7             |
|                 | Caracara undescribed sp.⁴    | —     | —              | 1           | 8             | 2/9             |
| Cranes          | Grus undescribed sp.⁴        | —     | —              | —           | 1             | 1/1             |
| Rails           | Rallus cyanocavi¹             | 644   | —              | —           | —             | 1/644           |
|                 | Rallus grallipes⁴            | 19    | —              | —           | —             | 1/19            |
|                 | Rallus undescribed sp. 1⁴    | —     | —              | 6           | —             | 1/6             |
|                 | Rallus undescribed sp. 2⁴    | —     | —              | —           | 47            | 1/47            |
|                 | Rallus/Porzana undescribed sp. 1⁴ | — | —              | 4           | —             | 1/4             |
|                 | Rallus/Porzana undescribed sp. 2⁴ | — | —              | 4           | —             | 1/4             |
| Thick-knees     | Burhinus nanus¹               | 5     | 25             | 24          | 1             | 4/55            |
| Snipe, woodcocks | Gallinago kakui²             | 4     | 6              | 15          | 4             | 4/29            |
|                 | Scolopax undescribed sp.¹    | —     | —              | 3           | —             | 1/3             |
| Pigeons, doves  | Patagioenas leucocephala     | 2     | 123            | 25          | 20            | 4/170           |
|                 | Patagioenas squamosa         | 9*    | 53*            | 26*         | 6*            | 4/94            |
|                 | Patagioenas cf. inornata     | —     | —              | —           | 4*            | 1/4             |
|                 | Zenaida aurita               | 4     | 30             | 38          | 6             | 4/78            |
|                 | Zenaida asiatica             | 1     | 8              | 5           | 26            | 4/40            |
|                 | Zenaida macroura             | —     | 1              | 4           | —             | 2/5             |
|                 | Geotrygon chrysa              | 6     | 34             | 45          | 10*           | 4/95            |
|                 | Columbina passerina          | 7     | 4              | 12          | 7             | 4/30            |
| Parrots, macaws | Ara cf. tricolor²            | —     | —              | 3           | —             | 1/3             |
|                 | Forpus undescribed sp.¹      | 1     | —              | —           | —             | 1/1             |
|                 | Amazona leucocephala         | 2     | 40*            | 15*         | 46*           | 4/103           |
| Cuckoos         | Coccozys minor               | —     | 1              | 4           | 4             | 3/9             |
|                 | Saurothera merlini           | —     | 9*             | 13*          | —             | 2/22            |
| Barn owls       | Tyto alba                    | 2     | 5              | —           | 2             | 3/9             |
|                 | Tyto polllens¹               | —     | 27             | 5           | —             | 2/22            |
| Owls            | Athene cunicularia, 1,962*   | 110*  | 326*           | 34*         | —             | 4/2,427         |
|                 | Asio flammeus                | 1*    | —              | —           | —             | 1/1             |
| Nightjars       | Chordeiles gundlachii        | 3     | 1              | —           | —             | 2/4             |
|                 | Antrostomus cf. cubanensis   | 1*    | —              | —           | —             | 1/1             |
|                 | Genus uncertain*⁺,⁵           | —     | 1* —           | —           | 1/1           |
| Hummingbirds    | Mellisuga sp.                | —     | —              | —           | 5*            | 1/5             |
|                 | Anthracothorax sp.           | —     | 27*            | —           | 18*           | 2/20            |
|                 | Chlorostilbon ricuki         | —     | 3              | —           | 8*            | 2/11            |
|                 | Calliphlox evelynae          | —     | —              | 1           | —             | 1/1             |
| Woodpeckers     | Colaptes cf. fernandinae     | 3*    | 10*            | 3*          | —             | 3/16            |
|                 | Melanerpes superciliearius   | 1     | 31*            | 26*         | —             | 3/58            |
|                 | Xiphidiopus percussus        | 1*    | 2*             | 4*          | —             | 3/7             |
|                 | Picoides villosus            | 3     | 1              | —           | —             | 2/4             |

Data sources (largely derived from SI Appendix, Table S1): Abaco, herein and refs. 5, 6, 27, 32, and 33; New Providence, refs. 34 and 36; Long Island, SI Appendix, Table S1; and Middle Caicos, SI Appendix, Tables S1 and S2. We assume that all of these species bred (nestled) on these islands, even though not all of them are “permanent residents.” For example, postbreeding movements, within or outside of the Bahamian islands, were likely in some populations of *Buteo swainsonii*, *Coccozys minor*, *Athene cunicularia*, and *Chordeiles gundlachii*. Seabirds, aquatic birds, and migratory species are not included. *Extirpated species (extant elsewhere, but no longer occurs on the island in question).†Extinct species. Islands (target sites): Abaco (Sawmill Sink Owl Roost), New Providence (Banana Hole), Long Island (Hanging Garden Cave), and Middle Caicos (Indian Cave). Rarefaction analyses are based on data from Tables 1 and 2.

both a Pleistocene and Holocene fossil on Bahamian islands, occurs only in the Great Antilles today.

The 62 extinct or extirpated species include frugivores/granivores, nectarivores, invertebrate predators, vertebrate predators, and scavengers; no feeding guilds were spared losses (Table 4). Among the 51 species recorded as Pleistocene fossils that lost some or all populations in the Bahamian Archipelago or went extinct globally, insectivores (predators of invertebrates) dominate, with frugivore/granivores and birds of prey also sustaining substantial losses (Fig. 5A). Among 27 species recorded in the
Holocene fossil record that lost some or all populations or went extinct globally, the species classified as birds of prey, frugivores/granivores, or especially predators of invertebrates are likely to be relatively small, flat, and low. These factors fuel the high vulnerability of Bahamian birds to human impact because few if any species are permanent residents. For example, postbreeding movements, within or outside of the Bahamian islands, were likely in some populations of Myiarchus sagrei, Tyrannus dominicensis, Vireo altitoquus, and Petrochelidon pyrrhonta. Seabirds, aquatic birds, and migratory species are not included.

Extinction Factors. With tropical Pacific islands in mind, Steadman (3) proposed three sets of factors (abiotic, indigenous biological, and cultural) that affect human-caused extinction of birds on oceanic islands. Here we evaluate how these factors (Table 5) apply to Bahamian birds, especially compared with birds on the nearby Greater Antilles. The two abiotic factors that dramatically distinguish Bahamian islands are A1 and A2, their tendency to be relatively small, flat, and low. These factors fuel the high vulnerability of Bahamian birds to human impact because few if any places on these islands are too remote or rugged to prohibit human access.

Among the indigenous biological factors, perhaps the most distinctive for the Bahamas is B3, the absence of terrestrial mammals [other than hutias on the GBB only (12)]. This situation is one component of the generally depauperate Bahamian flora and fauna (factors B1, B2) compared with the Greater Antillean biota. Cultural factors in the Bahaman Archipelago

Table 2. Number of bones of resident passerine landbirds identified from the four richest prehistoric sites in the Bahamian Archipelago and summaries (total numbers of species and identified bones) from Table 1 and herein

| Family       | Species                          | Abaco | New Providence | Long Island | Middle Caicos | No. sites/bones |
|--------------|----------------------------------|-------|----------------|-------------|---------------|----------------|
| Flycatchers  | Contopus caribaeus                | 5     | —              | —           | 2*            | 2/7            |
|              | Myiarchus sagrei                  | —     | 3              | 3*          | —             | 2/6            |
|              | Tyrannus dominicensis             | 3     | 1              | —           | —             | 2/4            |
|              | Tyrannus caudifasciatus           | 6     | 1              | 2           | —             | 3/9            |
|              | Tyrannus cubensis                 | 2*    | 1*             | —           | 2*            | 3/5            |
| Crows        | Corvus nasius                     | 3*    | 126*           | 7*          | 59            | 4/195          |
|              | Corvus palmarum                   | —     | 10*            | —           | —             | 1/10           |
| Vireos       | Vireo altitoquus                  | —     | 1              | —           | 2             | 2/3            |
|              | Vireo crassirostris               | —     | 2              | —           | 3             | 2/5            |
| Swallows     | Tachycinetey cyanoeviridis        | 5     | —              | —           | —             | 1/5            |
|              | Petrochelidon pyrrhonta           | 33*   | —              | 1*          | —             | 1/34           |
|              | Petrochelidon fulva               | 30*   | 1*             | —           | 1*            | 3/32           |
| Nuthatches   | Sitta pusilla                     | 20*   | —              | 1*          | —             | 2/21           |
| Mockingbirds | Minimus gundlachii                | 1     | 75             | 5           | 13            | 4/94           |
|              | Margarops fuscatus                | 1*    | —              | 2           | 41            | 3/44           |
| Gnatcatchers | Polioptila caerulea               | —     | 4              | —           | 3             | 2/7            |
| Thrushes     | Myadestes sp.                     | 7*    | —              | —           | —             | 1/7            |
|              | Siala sialis                      | 38*   | 5*             | 1*          | —             | 3/44           |
| Warblers     | Setophaga pinus                   | 10    | —              | —           | —             | 1/10           |
|              | Setophaga flavescens              | 3     | —              | —           | —             | 1/3            |
|              | Geothlypis rostrata               | 12    | —              | 1*          | —             | 2/13           |
| Bananquilt   | Coereba flavoeola                 | 1     | 7              | —           | 2             | 3/10           |
| Spindalis    | Spindalis zena                    | 1     | 11             | —           | 3             | 3/15           |
| Highland tanager | Xenoligaa cf. montana         | 5*    | 1*             | —           | —             | 2/6            |
| Finches, sparrows | Tiaris bicolor                  | 6     | 5              | —           | 1             | 3/12           |
|              | Loxigilla violacea                | 5     | 1              | —           | 27            | 3/33           |
|              | Ammodramus savannarum             | 1*    | —              | 1*          | 3*            | 3/5            |
|              | Passerculus sandwichensis         | 2*    | 5*             | —           | —             | 2/7            |
|              | Spizella passerina                | 12*   | —              | —           | 1*            | 2/13           |
| Blackbirds, etc. | Sturnella magna                | 1,101* | 12*           | 8*          | —             | 3/1,121        |
|              | Agelaius phoeniceus               | 4     | —              | —           | —             | 1/4            |
|              | Genus uncertain (large cowbird)   | 6*    | —              | 1           | —             | 2/7            |
|              | Molothrus ater                    | —     | 3*             | 1*          | —             | 2/4            |
|              | Icterus northropi                 | 4*    | —              | —           | —             | 1/4            |
| Crossbills   | Loxia megaplagia                  | 7*    | —              | 1*          | —             | 2/8            |
| Totals       | Total species                     | 55    | 50             | 44          | 41            | 85             |
|              | Total species*                    | 30    | 25             | 32          | 25            | 58             |
|              | Total species1                    | 8     | 7              | 12          | 8             | 20             |
| Totals       | Total identified bones            | 4,042 | 883           | 679         | 508           | 6,112          |

Data sources (largely derived from SI Appendix, Table S1): Abaco, herein and refs. 5, 6, 27, 32, and 33; New Providence, refs. (34–36); Long Island, SI Appendix, Table S1; and Middle Caicos, SI Appendix, Tables S1 and S2. We assume that these species bred (nested) on these islands, even though not all of them are permanent residents. For example, postbreeding movements, within or outside of the Bahamian islands, were likely in some populations of Myiarchus sagrei, Tyrannus dominicensis, Vireo altitoquus, and Petrochelidon pyrrhonta. Seabirds, aquatic birds, and migratory species are not included.

*Extinct species. Islands (target sites): Abaco (Sawmill Sink Owl Roost), New Providence (Banana Hole), Long Island (Hanging Garden Cave), and Middle Caicos (Indian Cave). Rarefaction analyses are based on data from Tables 1 and 2.
differ little from those in the Greater Antilles except in their scale of expression, leading to what seems to have been permanent, island-wide settlement (C1, C2). Prehistoric cultivation of crops in the Bahamas, especially manioc, probably was facilitated through the burning of broadleaf forest in the dry season (factor A6, seasonal aridity [13, 14]), although we do not know if it took place at a scale large enough to negate the potential limiting effect on agriculture of Bahamian nutrient-poor soils (factor A4).

Discussion

Changes in Bird Diversity (Including Endemism) since the Late Pleistocene. Across the Bahamian Archipelago, at least 30 species and 62 populations of landbirds were lost during the dramatic climatic and environmental changes of the Pleistocene-to-Holocene transition. The true numbers would be higher, especially for populations, if the fossil record were complete. This amounts to losses of 38% of the 79 species and 42% of the 149 populations found in our large and geographically broad Pleistocene sample. As previously documented for Abaco (5) and now more comprehensively here, these PHT losses were dominated taxonomically by passerines and trophically by insectivores. Similar PHT phenomena took place elsewhere in the West Indies, involving reptiles as well as birds (15).

Nevertheless, many species and populations of Bahamian birds survived the dramatic PHT changes in island area and proximity, depth to water table, habitat, and climate. Some of the populations/species that persisted through the PHT disappeared in the Late Holocene, when the prehistoric fossil record features 38 populations of 27 extinct or extirpated species (Table 4). The Late Holocene losses included species from all feeding guilds and habitat preferences (see also ref. 5). Holocene losses are also documented for other vertebrate groups (e.g., refs. 16 and 17). Human impact is the most likely culprit in most latest Holocene (the last millennium) losses of Bahamian birds (18), although the effect of sea-level rise on island area in the last seven millennia was dramatic (19), intense hurricane activity was heightened from 2,500 to 1,000 y ago (20), and habitats fluctuated (18, 21) during the Late Holocene prior to human arrival.

The Bahamian islands are very young geologically (7), so we might expect lower levels of endemism than on the much older islands of the Greater Antilles. While this generally may be the case, the Bahamian fossil record also has disclosed that some species previously considered to be endemic to Cuba (or elsewhere in the Greater Antilles) once had distributions that included Bahamian islands. This certainly occurred during the last Pleistocene glacial interval when the island group was much larger. These “pseudoendemic species” (following ref. 3) include the Cuban macaw Ara cf. tricolor, Cuban nightjar Antrostomus cf. cubensis, Cuban flicker Colaptes cf. fernandinae, Cuban green woodpecker Xiphidiopicus percussus, giant kingbird Tyrannus cubensis, highland tanager Xenoligea cf. montana, and likely others. Some prehistorically extinct species, such as the snipe...
Table 3. Resident species of landbirds for which fossils reveal a broader Bahamian distribution in the past, showing the number of islands with fossil-based extirpated Pleistocene and Holocene populations

| Family              | Species                      | Status          | Biogeogr. | Guild          | Extirpated Pleistocene | Extirpated Holocene |
|---------------------|------------------------------|-----------------|-----------|----------------|------------------------|---------------------|
| Vultures            | Cathartes aura               | Extir-iiB       | BA,GA,NA,WN | SC             | —                      | 1                   |
| Hawks, eagles       | Ictinia cf. plumbea          | Extir-BA        | WN        | PV             | 1*                     | —                   |
|                     | Accipiter undesc. sp.        | Extinct         | ??        | PV             | 1                      | —                   |
|                     | Accipiter striatus           | Extir-BA        | GA,NA     | PV             | 2*                     | —                   |
|                     | Buteo quadratus              | Extinct         | BA        | PV             | 4                      | 1                   |
|                     | Buteo jamaicensis            | Extir-iiB       | BA,GA,NA  | PV             | —                      | 1                   |
|                     | Buteo swainsonii             | Extir-BA        | NA        | PV             | 2*                     | —                   |
|                    | Titanohierax volverallenii   | Extinct         | ??        | PV             | 3*                     | —                   |
| Falcons, caracaras  | Falco femoralis              | Extir-BA        | WN        | PV             | —                      | 1                   |
|                     | Caracara creightoni          | Extinct         | CU        | SC             | 2                      | 1                   |
|                     | Caracara undesc. sp.         | Extinct         | ??        | SC             | 1                      | 1                   |
| Cranes              | Grus canadensis              | Extir-BA        | NA        | PI             | —                      | 1                   |
|                     | Grus undesc. sp.             | Extinct         | NA        | PI             | —                      | 1                   |
|                     | Railus cyanocavi             | Extinct         | BA        | PI             | 2*                     | —                   |
| Rails               | Railus gracilipes            | Extinct         | BA        | PI             | 2*                     | —                   |
|                     | Railus undesc. sp. 1         | Extinct         | BA        | PI             | 1*                     | —                   |
|                     | Railus undesc. sp. 2         | Extinct         | BA        | PI             | —                      | 1                   |
|                     | Railus/Porzana undesc. sp. 1 | Extinct         | BA        | PI             | 1*                     | —                   |
|                     | Railus/Porzana undesc. sp. 2 | Extinct         | BA        | PI             | —                      | 1                   |
| Thick-knees         | Burhinus nanus               | Extinct         | BA        | PI             | 4                      | 3                   |
| Snipe, woodcocks    | Gallinago kakuki             | Extinct         | CA,CU     | PI             | 4                      | 1                   |
|                     | Scoplopa sp.                 | Extinct         | GA        | PI             | 2*                     | —                   |
| Pigeons, doves      | Patagioenas squamosa         | Extir-BA        | GA        | FG             | 6                      | 2                   |
|                     | Patagioenas cf. inornata     | Extir-BA        | GA        | FG             | —                      | 1                   |
| Parrots, macaws     | Ara cf. tricolor             | Extinct         | CU        | FG             | 2*                     | —                   |
|                     | Forpus undesc. sp.           | Extinct         | BN        | FG             | 1*                     | —                   |
|                     | Amazona leucocephala         | Extir-iiB       | BA,CA,CU  | FG             | 4                      | 3                   |
| Cuckoos             | Saurothera merlini           | Extir-iiB       | BA,CU     | PI             | 3                      | —                   |
| Barn owls           | Tyto pollens                | Extinct         | CU        | PV             | 4*                     | —                   |
| Owls                | Athene cunicularia           | Extir-iiB       | BA,GA,NA,WN | PV          | 6                      | 5                   |
|                     | Glaucidium sp.               | Extir-BA        | CU        | PV             | 1*                     | —                   |
|                     | Asio flammeus               | Extir-BA        | CU,NA     | PV             | 1*                     | —                   |
| Nightjars           | Antrostomus cf. cubanensis   | Extir-BA        | CU        | PI             | 1*                     | —                   |
|                     | Genus uncertain              | Extinct         | ??        | PI             | 1*                     | —                   |
| Hummingbirds        | Melissuga sp.                | Extir-BA        | GA        | NE             | —                      | 1                   |
|                     | Anthracothorax sp.           | Extir-BA        | GA        | NE             | 1                      | 1                   |
| Woodpeckers         | Colaptes cf. fernandinae     | Extir-BA        | BA,CA,CU  | PI             | 6*                     | —                   |
|                     | Melanerpes superciliaris     | Extir-iiB       | BA,CA,CU  | PI             | 4                      | 1                   |
|                     | Xiphipicus percussus         | Extir-BA        | CU        | PI             | 2*                     | —                   |
| Flycatchers         | Contopus caribaeus           | Extir-iiB       | BA,CU     | PI             | —                      | 1                   |
|                     | Myiarchus sagrae             | Extir-iiB       | BA,CU     | PI             | 1                      | —                   |
|                     | Tyrannus cubensis           | Extir-BA        | CU        | PI             | 2                      | 1                   |
| Crows               | Corvus nasicus               | Extir-iiB       | BA,CU     | FG,PI           | 6                      | 3                   |
|                     | Corvus palmarum             | Extir-BA        | CU        | FG,PI           | 2*                     | —                   |
| Swallows            | Petrochelidon pyrrhona       | Extir-BA        | NA        | PI             | 2*                     | —                   |
|                     | Petrochelidon fulva          | Extir-BA        | GA,NA,WN  | PI             | 3                      | 1                   |
| Nuthatches          | Sitta pusilla                | Extir-iiB       | BA,NA     | PI             | 2                      | —                   |
| Thrashers           | Marginops fuscatus           | Extir-iiB       | BA,LA     | FG,PI           | 1                      | —                   |
| Thrushes            | Myadestes sp.                | Extir-BA        | BA        | FG             | 1*                     | —                   |
|                     | Sialia sialis                | Extir-BA        | NA        | FG,PI           | 3*                     | —                   |
|                     | Turdus plumbeus              | Extir-iiB       | BA,GA,LA  | FG             | 1                      | 1                   |
| Warblers            | Geothlypis rostrata          | Extir-iiB       | BA        | PI             | 1                      | —                   |
| Highland tanager    | Xenoliga cf. montana         | Extir-BA        | HI        | PI             | 2*                     | —                   |
| Finches, sparrows   | Ammodramus savannarum        | Extir-BA        | GA,NA     | FG             | 2                      | 1                   |
|                     | Passerculus sandwichensis    | Extir-BA        | NA        | FG             | 2*                     | —                   |
|                     | Spizella passerina           | Extir-BA        | NA        | FG             | 1*                     | —                   |
| Blackbirds, etc.    | Sturnella magna              | Extir-BA        | CU,NA     | PI             | 6*                     | —                   |
|                     | Genus uncertain (cowbird)    | Extinct         | ??        | PI             | 2*                     | —                   |
|                     | Molothrus ater               | Extir-BA        | NA        | PI             | 2*                     | —                   |
|                     | Icterus northropi            | Extir-iiB       | BA        | PI             | 1                      | —                   |
| Crossbills          | Loxia megapagala             | Extir-BA        | HI        | FG             | 3*                     | —                   |

Biogeogr., geographical affinities; guild, generalized feeding guilds. Status categories: extinct, globally extinct; Extir-BA, extirpated today throughout the Bahamas; Extir-iiB, extirpated on individual islands in the Bahamas. Geographical affinity categories: BA, Bahamian Archipelago; CA, Cayman Islands; CU, Cuba; GA, Greater Antilles; HI, Hispaniola; LA, Lesser Antilles; NA, North America; WN, widespread Neotropics. Very generalized feeding guilds: FG, frugivore/granivore; NE, nectarivore; PI, predator (invertebrates); PV, predator (vertebrates); SC, scavenger. Undesc. sp., undescribed species.

*Not recorded in the Holocene from any island. Derived from data in Table 1 and SI Appendix, Tables S1 and S2.
Gallinago kakuki, caracara Caracara creightoni, and owl T. pol·lens, were described from Bahamian fossils and then found to have lived on Cuba as well (22–24). The strong Cuban affinities of the Bahamian biota are not confined to vertebrates. For example, of the 42 species of butterflies recorded at Guantanamo (southeastern Cuba), 37 also occur in the Bahamas (25).

The Future. Finally, informed by studies of its past (26), it may be appropriate to speculate about the future of bird diversity in the Bahamian Archipelago. The future, of course, is impossible to predict but inappropriate to ignore. We find it difficult to be optimistic about the long-term future of Bahamian bird communities. The threats to these small islands include hurricanes and more direct human impacts of all sorts. Exacerbated by ocean warming and sea-level rise, the frequency and severity of hurricanes are increasing through time; major if not catastrophic damage to terrestrial habitats (and human infrastructure) has taken place during just the past decade on Crooked, Long, San Salvador, Abaco, and Grand Bahama. Conforming to global trends, the human population of the archipelago is growing, and with that comes more deforestation and continued introduction of nonnative plants and animals. These factors are all interrelated, synergistic, and ultimately detrimental to native species.

To end on a positive note, however, a solid system of national parks and nature reserves exists in the Bahamian Archipelago, thereby enhancing the overall resiliency to habitat loss. Some of these parks, such as on Abaco, were set aside primarily to provide extensive tracts of upland habitat for endangered birds, such as the parrot A. leucocephala. Furthermore, the populations of birds that still exist on Bahamian islands have a 1,000-y tradition of surviving alongside people. We wish them luck.

Materials and Methods
We use the term “fossil” to refer to any prehistoric bone, whether it derives from a paleontological or archaeological site. Our field methods (stratigraphic excavation, screen washing, etc.) and laboratory/curatorial methods and analyses are summarized in earlier papers (5, 19, 27). Our primary sources of data (large sets of identified bird fossils) are from four major noncultural sites, namely Sawmill Sink (Abaco, on the LBB), Banana Hole (New Providence, on the GBB), Hanging Garden Cave (Long Island, on the GBB), and Indian Cave (Middle Caicos, on the Caicos Bank). Each of these sites is a noncultural deposit in a limestone cave or sinkhole; Sawmill Sink is flooded (a blue hole), whereas the others are dry. The bird fossils accumulated primarily as prey items of barn owls, the extant Tyto alba for Abaco and Middle Caicos, and the larger, extinct T. pol·lens for New Providence and Long. The greater frequency of columbid fossils at New Providence and Long probably is because these relatively large birds were consumed more routinely by T. alba. The abundance of flightless rail fossils on Abaco suggests that “natural trap” activity also was involved at this very deep, precipitous sinkhole. Many other prehistoric sites, both cultural and noncultural, also have yielded smaller sets of bird fossils, helping to round out the archipelago-wide picture (SI Appendix, Table S1). The sites span the length of the Bahamian Archipelago, thus capturing the island group’s climatic extremes (becoming warmer and drier from northwest to southeast). We use the term “extinct” to mean a global loss (no surviving populations); “extirpated” means the loss of an individual island population of a species that still exists elsewhere. Data on the modern distribution of birds are from White (28) and Currie et al. (29).

Table 4. Summaries for resident species of landbirds in which fossils reveal a broader Bahamian distribution in the past (from Table 3), showing total numbers of species or populations lost by time period, status categories, geographical affinities, and generalized feeding guilds

| Attribute                      | Category       | No. species |
|--------------------------------|----------------|-------------|
| Time period (lost species/populations) | Pleistocene     | 51/121      |
|                                | Pleistocene*    | 29/62       |
|                                | Holocene        | 27/28       |
| Status                         | Extinct        | 20          |
|                                | Extirr-BA       | 27          |
|                                | Extirr-iB       | 15          |
| Geographical affinities (extinct/Extirr-BA) | GA             | 12/8        |
|                                | BA             | 8/0         |
|                                | CU             | 4/8         |
|                                | CA             | 1/0         |
|                                | NA             | 1/12        |
|                                | WN             | 1/3         |
|                                | HI             | 0/1         |
|                                | ??             | 5/0         |
| Feeding guilds (extinct/extirpated) | FG             | 14/12       |
|                                | NE             | 2/2         |
|                                | PI             | 32/20       |
|                                | PV             | 12/8        |
|                                | SC             | 3/1         |

*Recorded only in the Pleistocene.
Table 5. Factors affecting the extinction of birds (and other vertebrates) on oceanic islands

| Extinction factor | Potentially promotes extinction | Potentially delays extinction |
|-------------------|--------------------------------|-----------------------------|
| Abiotic factors   |                                |                             |
| A1. Island size   | Small                          | Large                       |
| A2. Topography    | Flat, low                      | Large                       |
| A3. Bedrock type  | Sandy, or noncalcareous sedimentary | Steep, rugged             |
| A4. Soil type     | Nutrient-rich                  | Limestone or knife-edge volcanics | Nutrient-poor |
| A5. Isolation     | Very isolated                  | Many nearby islands         |
| A6. Climate       | Seasonal aridity               | Reliably wet                |
| Indigenous biological factors |                    |                             |
| B1. Floral diversity | Depaerate                      | Rich (short-term delay only) |
| B2. Faunal diversity | Depaerate                      | Rich (short-term delay only) |
| B3. Terrestrial mammals | Absent*                        | Present                     |
| B4. Marine resources | Ground-dwelling; flightless; large; tame; fatty; good taste; colorful feathers; long and straight bones | Canopy-dwelling; volant; small; wavy; little fat; bad taste; drab plumage; short and curved bones |
| B5. Species-specific ecological, behavioral, or morphological traits |                                |                             |
| Cultural factors  |                                |                             |
| C1. Occupation    | Permanent                      | Temporary                   |
| C2. Settlement pattern | Island-wide                   | Restricted (coastal)       |
| C3. Population growth and density | Rapid growth; high density | Slow growth; low-density |
| C4. Subsistence   | Farmers as well as h-f-g        | H-f-g only, especially if marine-oriented |
| C5. Introduced plants | Many species; invasive         | Few species; noninvasive   |
| C6. Introduced animals | Many species; feral populations | Few or no species; no feral populations |

From Steadman (3, table 16-5), except that conditions in columns 2 and 3 in italicized bold indicate when the general condition in the Bahamian Archipelago differs from that in the Greater Antilles. See text for additional information. h-f-g, hunter-fisher-gatherer.

*Except the rodent Geocapromys ingrahami is indigenous on islands of the GBB.

Our comparison of the number of species and fossil specimens in target sites used the package vegran (30, 31) for rarefaction-based estimates of species accumulation in sites (function rarecurve) and across sites (function specaccum).

Data Availability. All data used in the figures are included in the tables and SI Appendix, Tables S1 and S2. Fossil specimens are deposited at the Florida Museum of Natural History, on long-term loan from the National Museum of The Bahamas.

All study data are included in the article and SI Appendix.

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