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Authors
Steadman, David W
Franklin, Janet

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

David W. Steadman[a] and Janet Franklin[b,1]

[a]Florida Museum of Natural History, University of Florida, Gainesville, FL 32611; and [b]Department of Botany and Plant Sciences, University of California, Riverside, CA 92521

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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.

extinction | human impacts | island biogeography | landbirds | Pleistocene-to-Holocene transition

The related futures of biodiversity and humanity perhaps never have been at a crossroads more than now. The transfer of a zoonotic disease from wildlife to humans, which has resulted in a pandemic, is directly linked to biodiversity loss. As the human takeover of the biosphere becomes ever more pervasive, information on prehistoric plant and animal communities are increasingly useful to understand our planet's biotic potential in situations with little or no human influence. These historical legacies shaped the ecological communities we seek to conserve today.

In that spirit, our first objective is to compare the bird communities of the Bahamian Archipelago (Commonwealth of The Bahamas plus The Turks and Caicos Islands) for three successive time intervals: the relatively cool, dry Late Pleistocene (>10 ka [1,000 y ago]); the warmer, wetter Holocene prior to human arrival (10 to 1 ka); and the climatically similar to now Late Holocene subsequent to human arrival (1 to 0 ka). These analyses improve our understanding of the changing biogeography of West Indian birds overall, and Bahamian birds in particular, across evolutionarily short but ecologically long time intervals.

Our second goal is to assess what drives the loss of taxa by evaluating the Bahamian results in light of what we already know about the Late Quaternary loss versus persistence ("extinction filters") of individual species of birds on oceanic islands. The factors that influence the ability of a species to withstand the perturbations that come with human arrival are well-documented on Pacific islands (1–3). Those factors, which are not mutually exclusive, have been categorized as abiotic (e.g., island area, topography, soil type), biotic (e.g., floral and faunal diversity, species-specific ecological, behavioral, and morphological traits), and cultural (e.g., permanent vs. temporary human settlement, human population growth and density, introduction of nonnative plants and animals).

While 15 individual Bahamian islands have produced avian fossils (*SI Appendix*, Table S1), four islands from across the archipelago have the most comprehensive fossil records; we will use the data from those islands to model Bahamian birdlife under conditions free of human influence. Unlike in past analyses of bird fossils on oceanic islands (e.g., ref. 4), our objective here is not to estimate species–area relationships during a precise interval of time but rather to understand changes in faunal composition over time. In part this is because three of the four target islands have rigorous Pleistocene records of birds (Abaco, New Providence, Long), whereas the fourth (Middle Caicos) has a good Holocene fossil record but lacks Pleistocene fossils. For two of our target islands (Long, Middle Caicos), we present in this paper a complete set of identifications of bird fossils (*SI Appendix*, Tables S1 and S2), not previously published.

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Physical Settings of the Glacial and Interglacial Bahamas

The Bahamian Archipelago (Fig. 1) consists of limestone islands atop shallow carbonate banks. At present, and representing Holocene interglacial conditions, the islands are low-elevation (maximum 63 m), typically long and narrow with northwest-to-southeast

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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[1]To whom correspondence may be addressed. Email: janet.franklin@ucr.edu.

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trending ridges on the eastern or northern (Atlantic) sides, with a total land area of ∼12,000 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 ∼131,000 km^2 (estimated land areas and elevations are from ref. 6). The resulting large Bahamian islands during glacial intervals (maximum elevations from ∼120 to 180 m) were situated closer to the Greater Antilles (especially Cuba) than today; these larger Bahamian "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 interglacials, which include the present (the Holocene, MIS 1, ∼10 to 0 ka), MIS 5a (∼125 to 120 ka), and MIS 11 (∼410 to 400 ka), the archipelago consisted of many separate islands, as it does today, with a total land area of <15,000 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

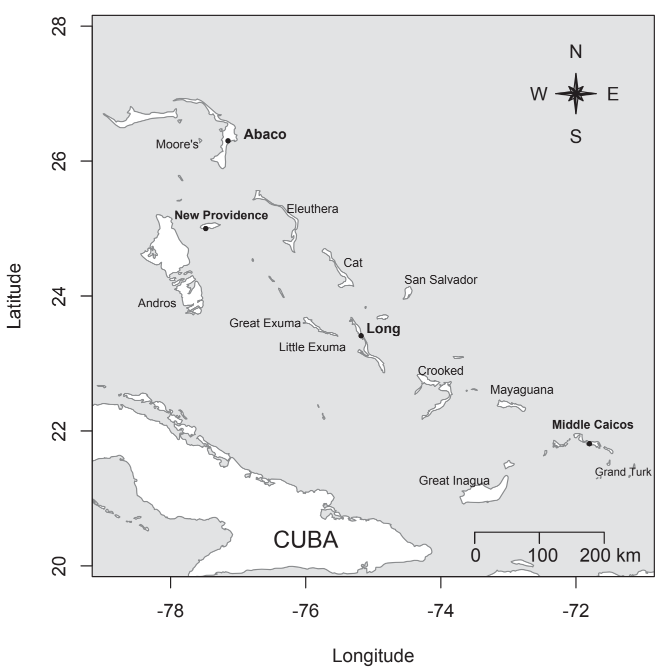

Fig. 1. Bahamian Archipelago. Islands mentioned in the text or tables are named. The four target islands that have single sites with >500 identified landbird fossils with chronological control are in bold.

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 (∼15 to 9 ka) are known as the Pleistocene-to-Holocene transition (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 (nonmarine, nonaquatic, breeding species that are part of the terrestrial food web; *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 (Abaco, New Providence, Long, Middle Caicos; Fig. 2). Among the 85 species of landbirds recorded from the four target sites, only 13 (15%) have been found in all sites (3 extinct, 4 extirpated, and 6 still widespread; Tables 1 and 2).

Comparing only the four target sites/islands (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 (Fig. 3). That we recorded 85 species of landbirds collectively in these fossil sites suggests strongly that none of these four large samples (together comprising nearly 6,000 fossils; 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 (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 (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 *Colaptes* cf. *fernandinae*, *Melanerpes superciliaris*, and *Xiphidiopicus percussus*, swallow *Petrochelidon pyrrhonota*, nuthatch *Sitta pusilla*, bluebird *Sialia sialis*, "highland tanager" *Xenoligea* cf. *montana*, sparrow *Passerculus sandwichensis*, meadowlark *Sturnella 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 *Titanohierax gloveralleni*, several of the flightless rails, the woodcock *Scolopax* undescribed sp., macaw *Ara* cf. *tricolor*, owls *Tyto pollens* and *Asio flammeus*, crow *Corvus palmarum*, and solitaire *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 (Tables 3 and 4 and *SI Appendix*, Table S1). Within the Bahamian Archipelago, for example, the parrot *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 *Melanerpes superciliaris*, which now lives only on Abaco and San Salvador, is widespread as a fossil. The same is true for the owl *Athene cunicularia* and crow *Corvus nasicus*. The pigeon *Patagioenas squamosa*, common as

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	—	—	6	2/7
	Accipiter striatus	—	4*	—	—	1/4
	Buteo quadratus†	1	10	3	38	4/52
	Buteo jamaicensis	—	—	—	2*	1/2
	Buteo swainsonii	1*	—	1*	—	2/2
	Titanohierax gloveralleni†	—	2	1	—	2/3
Falcons, caracaras	*Falco sparverius*	19	3	7	—	3/29
	Falco femoralis	—	—	—	12*	1/12
	Caracara creightoni†	—	6	1	—	2/7
	Caracara undescribed sp.†	—	—	1	8	2/9
Cranes	*Grus* undescribed sp.†	—	—	—	1	1/1
Rails	*Rallus cyanocavi*†	644	—	—	—	1/644
	Rallus gracilipes†	19	—	—	—	1/19
	Rallus undescribed sp. 1†	—	—	6	—	1/6
	Rallus undescribed sp. 2†	—	—	—	47	1/47
	Rallus/Porzana undescribed sp. 1†	—	—	4	—	1/4
	Rallus/Porzana undescribed sp. 2†	—	—	—	4	1/4
Thick-knees	*Burhinus nanus*†	5	25	24	1	4/55
Snipe, woodcocks	*Gallinago kakuki*†	4	6	15	4	4/29
	Scolopax undescribed sp.†	—	—	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 chrysia	6	34	45	10*	4/95
	Columbina passerina	7	4	12	7	4/30
Parrots, macaws	*Ara* cf. *tricolor*†	—	—	3	—	1/3
	Forpus undescribed sp.†	1	—	—	—	1/1
	Amazona leucocephala	2	40*	15*	46*	4/103
Cuckoos	*Coccyzus minor*	—	1	4	4	3/9
	Saurothera merlini	—	9*	13*	—	2/22
Barn owls	*Tyto alba*	2	5	—	2	3/9
	Tyto pollens†	—	27	5	—	2/32
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*,†	—	1*,†	—	—	1/1
Hummingbirds	*Mellisuga* sp.	—	—	—	5*	1/5
	Anthracothorax sp.	—	2?*	—	18*	2/20
	Chlorostilbon ricordii	—	3	—	8*	2/11
	Calliphlox evelynae	—	—	1	—	1/1
Woodpeckers	*Colaptes* cf. *fernandinae*	3*	10*	3*	—	3/16
	Melanerpes superciliaris	1	31*	26*	—	3/58
	Xiphidiopicus 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 (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 *Buteo swainsonii*, *Coccyzus 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. 5*A*). Among 27 species recorded in the

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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 sagrae	—	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 nasicus*	3*	126*	7*	59	4/195
	Corvus palmarum	—	10*	—	—	1/10
Vireos	*Vireo altiloquus*	—	1	—	2	2/3
	Vireo crassirostris	—	2	—	3	2/5
Swallows	*Tachycineta cyaneoviridis*	5	—	—	—	1/5
	Petrochelidon pyrrhonota	33*	—	1*	—	1/34
	Petrochelidon fulva	30*	1*	—	1*	3/32
Nuthatches	*Sitta pusilla*	20*	—	1*	—	2/21
Mockingbirds, etc.	*Mimus 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
	Sialia sialis	38*	5*	1*	—	3/44
	Turdus plumbeus	4	56	22*	4*	4/86
Warblers	*Setophaga pinus*	10	—	—	—	1/10
	Setophaga flavescens	3	—	—	—	1/3
	Geothlypis rostrata	12	—	1*	—	2/13
Bananquit	*Coereba flaveola*	1	7	—	2	3/10
Spindalis	*Spindalis zena*	1	11	—	3	3/15
Highland tanager	*Xenoligea* 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 megaplaga*	7*	—	1*	—	2/8
Totals	Total species	55	50	44	41	85
	Total species*,†	30	25	32	25	58
	Total species†	8	7	12	8	20
	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 sagrae*, *Tyrannus dominicensis*, *Vireo altiloquus*, and *Petrochelidon pyrrhonota*. 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.

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 once again dominate (Fig. 5*A*). This contrasts with modern times, when insectivorous birds tend to survive better than other feeding guilds on Caribbean islands following droughts or hurricanes (10, 11).

If we use the habitat preference classification in Steadman and Franklin (5), the species subjected to losses in the Pleistocene or Holocene represent all habitats in both time intervals, albeit with a larger proportion of species that prefer pine woodlands and broadleaf forest lost at the PHT than during the Holocene (Fig. 5*B*).

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 Bahamian Archipelago

Fig. 2. Four fossil sites targeted in this paper. (*A*) The Owl Roost deposit at 30-m depth in Sawmill Sink, Abaco (to give a sense of scale, the diagonal, upside-down tarsometatarsus of a burrowing owl indicated by the white arrow is 45 mm long). (*B*) Banana Hole, New Providence. (*C*) Hanging Garden Cave, Long Island. (*D*) Indian Cave, Middle Caicos. Photographs are by B. Kakuk (*A*), N. A. Albury (*B* and *D*), and J. A. Soto-Centeno (*C*).

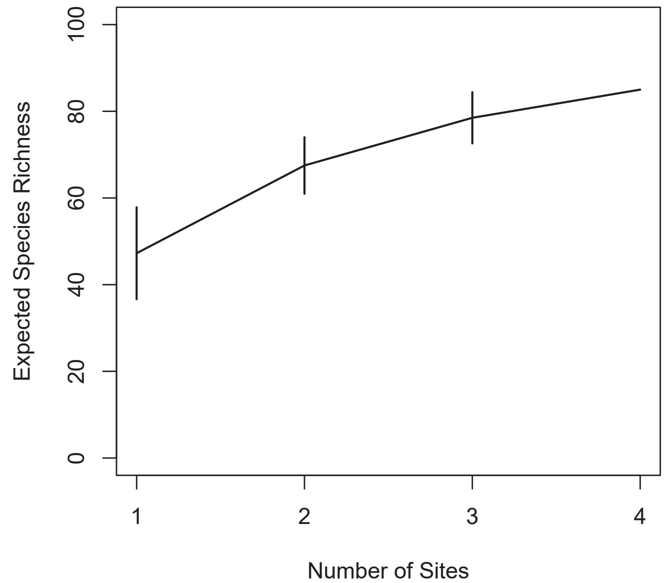

Fig. 3. Species accumulation curve for the four focal sites estimates the number of species for a given number of (number of species in one, two, three, or four) sites. The "exact" method used finds the expected (mean) species richness for a given number of sites based on rarefaction by site, with two SDs indicated by vertical lines.

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. *cubanensis*, 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

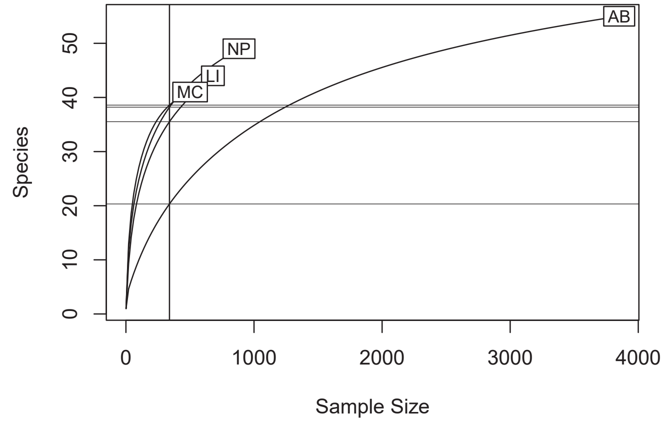

Fig. 4. Rarefaction curve for each of the four target fossil sites, estimating how many species are recorded cumulatively as bones are added to the sample. Sites are Abaco (AB), Middle Caicos (MC), New Providence (NP), and Long Island (LI). The vertical line indicates the size of the smallest sample (MC; $n = 501$) and the horizontal lines indicate the estimated species richness of the other sites for that sample size based on rarefaction.

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	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 gloveralleni	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
	Rallus cyanocavi	Extinct	BA	PI	2*	—
Rails	*Rallus gracilipes*	Extinct	BA	PI	2*	—
	Rallus undesc. sp. 1	Extinct	BA	PI	1*	—
	Rallus undesc. sp. 2	Extinct	BA	PI	—	1
	Rallus/Porzana undesc. sp. 1	Extinct	BA	PI	1*	—
	Rallus/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
	Scolopax undesc. sp.	Extinct	GA	PI	2*	—
Pigeons, doves	*Patagioenas squamosa*	Extir-BA	GA	FG	6	2
	Patagioenas cf. *inornata*	Extir-BA	GA	FG	—	1
	Geotrygon chrysia	Extir-iiB	BA,GA	FG	—	1
Parrots, macaws	*Ara* cf. *tricolor*	Extinct	CU	FG	2*	—
	Forpus undesc. sp.	Extinct	WN	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	*Mellisuga* sp.	Extir-BA	GA	NE	—	1
	Anthracothorax sp.	Extir-BA	GA	NE	1	1
Woodpeckers	*Colaptes* cf. *fernandinae*	Extir-BA	CU	PI	6*	—
	Melanerpes superciliaris	Extir-iiB	BA,CA,CU	PI	4	1
	Xiphidiopicus 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 pyrrhonota*	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	*Margarops fuscatus*	Extir-iiB	BA,LA	FG,PI	1	—
Thrushes	*Myadestes* sp.	Extir-BA	GA	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	*Xenoligea* 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 megaplaga*	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. pollens*, 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. pollens* 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. pollens* than the smaller *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	27/38
Status	Extinct	20
	Extir-BA	27
	Extir-iiB	15
Geographical affinities (extinct/Extir-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.

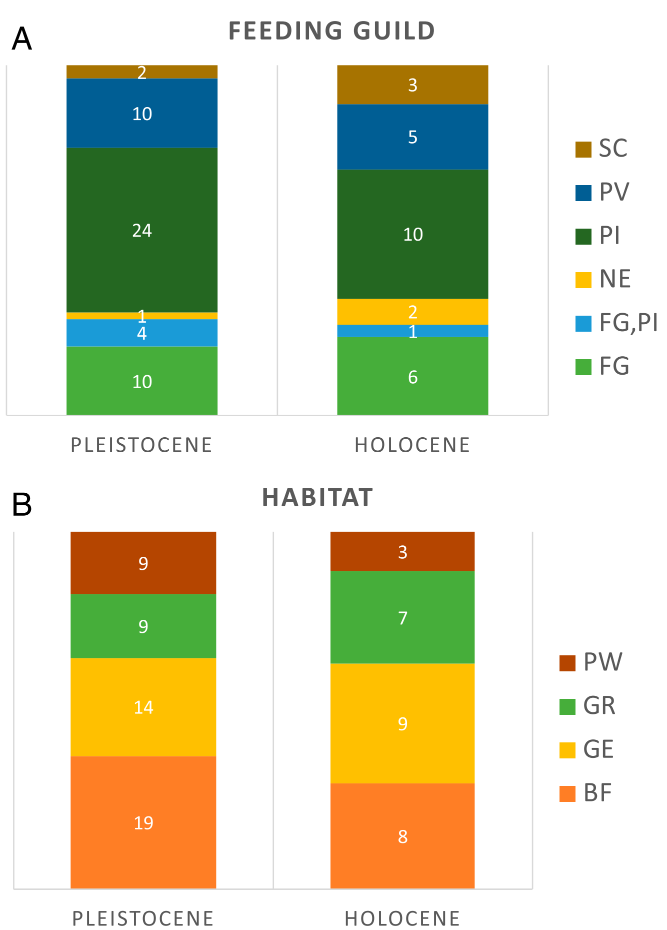

Fig. 5. Generalized feeding guilds (*A*) and primary habitat preferences (*B*) for the 62 landbird species showing fossil-based losses in the Bahamian Archipelago, ranging from single-island extirpations to global extinction (Tables 3 and 4). Number of species with one or more lost populations/species in the Late Pleistocene (*Left*; $n = 51$) and in the prehistoric Holocene (*Right*; $n = 27$). Feeding guilds are FG, frugivore/granivore; NE, nectarivore; PI, predator (invertebrates); PV, predator (vertebrates); and SC, scavenger (Table 3). Habitats are BF, broadleaf subtropical evergreen forest (called "coppice" in ref. 32); GE, generalist; GR, grassland; and PW, pine woodland (*SI Appendix*, Table S1).

ECOLOGY

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***	Steep, rugged
A3. Bedrock type	Sandy, or noncalcareous sedimentary	Limestone or knife-edge volcanics
A4. Soil type	Nutrient-rich	***Nutrient-poor***
A5. Isolation	Very isolated	Many nearby islands
A6. Climate	Seasonal aridity	Reliably wet
Indigenous biological factors		
B1. Floral diversity	***Depauperate***	Rich (short-term delay only)
B2. Faunal diversity	***Depauperate***	Rich (short-term delay only)
B3. Terrestrial mammals	***Absent****	Present
B4. Marine resources	Depauperate; difficult access	Rich (temporary delay only); easy access
B5. Species-specific ecological, behavioral, or morphological traits	Ground-dwelling; flightless; large; tame; fatty; good taste; colorful feathers; long and straight bones	Canopy-dwelling; volant; small; wary; little fat; bad taste; drab plumage; short and curved bones
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 (ref. 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 vegan (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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1. D. W. Steadman, Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* **267**, 1123–1131 (1995).
2. T. H. Worthy, R. N. Holdaway, *The Lost World of the Moa: Prehistoric Life of New Zealand*, (Indiana University Press, Bloomington, IN, 2002).
3. D. W. Steadman, *Extinction and Biogeography of Tropical Pacific Birds*, (University of Chicago Press, Chicago, IL, 2006).
4. J. Franklin, D. W. Steadman, Prehistoric species richness of birds on oceanic islands. *Oikos* **117**, 1885–1891 (2008).
5. D. W. Steadman, J. Franklin, Changes in an insular bird community since the Late Pleistocene. *J. Biogeogr.* **42**, 426–438 (2015).
6. D. W. Steadman, J. Franklin, Origin, paleoecology, and extirpation of bluebirds and crossbills in the Bahamas across the last glacial-interglacial transition. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 9924–9929 (2017).
7. J. Mylroie, M. Lace, N. Albury, J. Mylroie, Flank margin caves and the position of Mid-to Late Pleistocene sea level in the Bahamas. *J. Coast. Res.* **36**, 249–260 (2020).
8. R. Byrne, Man and the variable vulnerability of island life. A study of recent vegetation change in the Bahamas. *Atoll Res. Bull.* **240**, 1–200 (1980).
9. J. D. Mather, The influence of geology and karst development on the formation of freshwater lenses on small limestone islands. *Karst Hydrogeol. Karst Environ. Prot.* **1**, 423–428 (1988).
10. J. W. Wiley, J. M. Wunderle, The effects of hurricanes on birds, with special reference to Caribbean islands. *Bird Conserv. Int.* **3**, 319–349 (1993).
11. J. Faaborg, W. J. Arendt, Survival rates of Puerto Rican birds: Are islands really that different? *Auk* **112**, 503–507 (1995).
12. J. A. Oswald *et al*., Ancient DNA and high-resolution chronometry reveal a long-term human role in the historical diversity and biogeography of the Bahamian hutia. *Sci. Rep.* **10**, 1373 (2020).
13. W. F. Keegan, *Bahamian Archaeology*, (Media Publishing, Nassau, The Bahamas, 1997).
14. D. W. Steadman *et al*., Late Holocene faunal and landscape change in the Bahamas. *Holocene* **24**, 220–223 (2014).
15. G. K. Pregill, S. L. Olson, Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. *Annu. Rev. Ecol. Syst.* **12**, 75–98 (1981).
16. M. E. Kemp, E. A. Hadly, Early Holocene turnover, followed by stability, in a Caribbean lizard assemblage. *Quat. Res.* **85**, 255–261 (2016).
17. J. A. Soto-Centeno, D. W. Steadman, Fossils reject climate change as the cause of extinction of Caribbean bats. *Sci. Rep.* **5**, 7971 (2015).
18. E. Kjellmark, Late Holocene climate change and human disturbance on Andros Island, Bahamas. *J. Paleolimnol.* **15**, 133–145 (1996).
19. D. W. Steadman *et al*., Late Holocene historical ecology: The timing of vertebrate extirpation on Crooked Island, Commonwealth of The Bahamas. *J. Island Coast. Archaeol.* **12**, 572–584 (2017).
20. P. J. van Hengstum *et al*., The intertropical convergence zone modulates intense hurricane strikes on the western North Atlantic margin. *Sci. Rep.* **6**, 21728 (2016).
21. D. N. West, "Late Holocene charcoal stratigraphy and modern charcoal deposition in the pine rocklands of Great Abaco Island, The Bahamas," Master's thesis, University of Tennessee, Knoxville, TN (2007).
22. W. Suárez, S. L. Olson, Further characterization of *Caracara creightoni* Brodkorb based on fossils from the Quaternary of Cuba (Aves: Falconidae). *Proc. Biol. Soc. Wash.* **114**, 501–508 (2001).
23. W. Suárez, S. L. Olson, Systematics and distribution of the giant fossil barn owls of the West Indies (Aves: Strigiformes: Tytonidae). *Zootaxa* **4020**, 533–553 (2015).

24. D. W. Steadman, O. M. Takano, A new extinct species of snipe (Aves: Scolopacidae: Gallinago) from the West Indies. *Zootaxa* **4109**, 345–358 (2016).
25. D. L. Matthews, J. Y. Miller, T. A. Lott, R. W. Portell, J. K. Toomey, Biogeographic affinities of Guantanamo butterflies and a report on species recorded from the United States Naval Base, Cuba. *Bull. Allyn Mus.* **164**, 1–51 (2012).
26. M. E. Kemp, E. A. Hadly, Rocking Earth's biodiversity cradle: Challenges, advances, and prospects for conservation paleontology in the tropics. *J. Vertebr. Paleontol.* **36**, e1179640 (2016).
27. D. W. Steadman *et al*., Exceptionally well preserved Late Quaternary plant and vertebrate fossils from a blue hole on Abaco, The Bahamas. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19897–19902 (2007).
28. A. W. White, *A Birder's Guide to the Bahama Islands (Including Turks and Caicos)*, (American Birding Association, Colorado Springs, CO, 1998).
29. D. Currie, J. M. Wunderle, E. Freid, D. N. Ewert, D. J. Lodge, *The Natural History of the Bahamas: A Field Guide*, (Cornell University Press, Ithaca, NY, 2019).
30. J. Oksanen *et al*, vegan: Community Ecology Package. R package (R Version 2.5-6, 2019). https://CRAN.R-project.org/package=vegan. Accessed 24 March 2020.
31. R Core Team, R: A Language and Environment for Statistical Computing (Version 3.6.3, R Foundation for Statistical Computing, Vienna, Austria, 2018). http://www.R-project.org. Accessed 29 February 2020.
32. D. W. Steadman *et al*., Vertebrate community on an ice-age Caribbean island. *Proc. Natl. Acad. Sci. U.S.A.* **112**, E5963–E5971 (2015).
33. D. Steadman, J. Morris, N. Wright, A new species of Late Pleistocene rail (Aves: Rallidae) from Abaco, The Bahamas. *Paleontol. J.* **47**, 1355–1364 (2013).
34. P. Brodkorb, Pleistocene birds from New Providence Island, Bahamas. *Bull. Fla. State Mus. Biol. Sci.* **4**, 349–371 (1959).
35. S. L. Olson, W. B. Hilgartner, Fossil and subfossil birds from the Bahamas. *Smithson. Contrib. Paleobiol.* **48**, 22–56 (1982).
36. J. A. Oswald, D. W. Steadman, The Late Quaternary bird community of New Providence, Bahamas. *Auk* **135**, 359–377 (2018).